An attempt to explain the distribution of the tree species composing the riparian forests of Lake Duparquet, southern boreal region of Quebec, Canada

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Abstract: The objective of this study was to evaluate the most important environmental factors determining the distribution of tree species within the riparian zone of Lake Duparquet, located in the southern boreal region of Quebec, Canada. Occurrence and relative basal area of 10 species were recorded within an altitudinal range of 200 cm above mean water level along 95 transects. Stepwise logistic regression and canonical correspondence analyses were performed on the overall data set as well as separately for the five geomorphological shore types distinguished (depositional flats, floodplains, beaches, terraces, and rock outcrops). The elevation gradient, representing seasonal floodings, is the main factor determining the distribution of the species. The differences between the geomorphological shore types with respect to composition and arrangement of the arborescent vegetation along the elevation gradient are at least partially explained by surficial substratum, topography, aspect, and fire. Exposure to wave activity seems to be of minor importance only. However, since they are the driving force of erosion and sedimentation, the waves are to a great part responsible for the morphological differentiation of the shoreline. The distribution of the tree species along a characteristic physiographic cross-section is illustrated for each geomorphological shore type.

Key words: boreal forest, flooding, geomorphology, physiographic cross-section, Quebec, riparian forest.

Résumé : Nous avons évalué l'importance de différents facteurs environnementaux pouvant régir la distribution des espèces arborescentes retrouvées dans les forêts ripariennes du Lac Duparquet dans la région boréale méridionale du Québec, Canada. La présence et la surface terrière relative de 10 espèces arborescentes ont été mesurées le long de 95 transects établis à partir du bord du lac, jusqu'à 200 cm au-dessus du niveau moyen d'eau. Des régressions logistiques et des analyses canoniques des correspondances ont été effectuées sur l'ensemble des données et pour les cinq types géomorphologiques de berges pris séparément (plaines d'accumulation, plaines d'inondation, plages, terrasses et escarpements rocheux). Le gradient d'élévation, reflétant les inondations saisonnières, est le facteur principal expliquant la distribution des espèces. Le type de dépôt de surface, la topographie, l'orientation et les incendies de forêt expliquent, du moins partiellement, les changements de composition observés pour chacun des types géomorphologiques selon un gradient d'élévation. L'exposition aux vagues semble ne jouer qu'un rôle mineur. Cependant, étant donné que les vagues sont responsables de l'érosion et de la sédimentation, celles-ci déterminent largement la différenciation morphologique du périmètre lacustre. Des toposéquences présentant la distribution des espèces caractéristiques sont illustrées pour chacun des types géomorphologiques de berge.

Mots clés : forêt boréale, inondation, géomorphologie, toposéquence, Québec, forêt riparienne.

Introduction

The riparian vegetation surrounding lakes is generally arranged into several parallel shoreline belts, each of them under the influence of different environmental factors. Thus, species of nonwoody riparian vegetation belts proximal to the shoreline are arrayed mainly along gradients of increasing wave energy (exposure) and water depth (Keddy 1983; Wilson and Keddy 1985). However, zonation patterns within the riparian forests (distal from the shoreline) are mainly determined by the species' tolerances to frequency, duration, and period of flooding (Sigafoos 1961; Beschel and Webber 1962; Bell 1974; Bell and del Moral 1977; Robertson et al. 1978, 1984; Metzler and Damman 1985; Tardif and Bergeron 1992; Nakamura et al. 1997). Soil texture, shore slope, and topography also play an important role as they modify drainage capacity and, hence, duration of flooding (Robertson et al. 1978, 1984; Frye and Quinn 1979; Buchholz 1981; Metzler and Damman 1985; Vincent et al. 1986; Tardif and Bergeron 1992). Some studies focus on the importance of flood-induced disturbances such as water and sediment flow, wave activity, ice push, erosion, and sedimentation figure in the distribution of the shoreline species and the dynamics of the riparian forest (White 1979; Pickett 1980; Hupp 1982; Hupp and Osterkamp 1985; Harris 1987; Bégin and Lavoie 1988; Bégin and Payette 1989; Nakamura

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et al. 1997). Along the shore slope of rivers and lakes, these disturbances and the stress caused by seasonal immersion form a complex gradient that is represented by the elevation relative to the water level. However, hydrological (e.g., ice push) and geomorphological processes can modify this elevation gradient through the creation of landforms such as levees, beach ridges, and terraces (Frye and Quinn 1979; Buchholz 1981; Hupp and Osterkamp 1985; Harris 1987; Hupp 1988; Nakamura et al. 1997). Thus, vertical and lateral patterns of vegetation along the perimeter of the same body of water, be it river or lake, are a function of permanent shore characteristics and their multiple variations associated with shore dynamics (Hupp 1982, 1988; Nakamura et al. 1997).

In the domain of the southern boreal forest, the few studies that have focused on the composition of the woody vegetation adjoining lakes in relation to environmental factors were restricted to a subset of tree species only (Tardif and Bergeron 1992; Bergeron et al. 1997). The aim of the present study is to identify the most important environmental factors that determine the distribution of the shoreline tree species all around Lake Duparquet (Quebec). Unlike most of the bigger lakes in the southern boreal region of Quebec, the water level of this lake has never been regulated by man. This allows the examination of the influence of a natural regime of water level fluctuations on the riparian vegetation.

Our hypothesis was that the species composition of the riparian forests around Lake Duparquet reflects the complex structure of its shoreline with regard to topography, surficial substratum, and disturbance regime. Therefore the distribution of the tree species was analyzed not only in its entirety, but also separately for the several geomorphological shore types distinguished for this purpose. In addition, most of the tree species encountered in the riparian zone of Lake Duparquet are not restricted to the land–water interface, and their distributions also react to terrestrial environmental factors. Therefore, fire was included in the analyses as an independent variable, as it is the most important terrestrial disturbance type in the area (Bergeron 1991).

Methods

Study area

The study area is part of the Lake Duparquet Research and Teaching Forest, located approximately 550 km northwest of Montreal in western Quebec, Canada (Fig. 1). Landscape depressions are mainly covered by clay deposits that are remnants of the proglacial Lakes Barlow and Ojibway (Veillette 1994) whereas the higher elevations are mostly characterized by the presence of glacial till and rocky outcrops (Bergeron et al. 1983). Climate is continental with cold winters and warm summers. The mean annual temperature and precipitation between 1961 and 1990 (measured at La Sarre, 42 km to the north) are 0.8°C and 856.8 mm, respectively (Environment Canada 1993). The Lake Duparquet region is situated in the southern part of the boreal forest within the domain of the balsam fir – white birch mixedwood forest (Grandtner 1966; Rowe 1972). Balsam fir (*Abies balsamea*[2]), in association with white birch (*Betula papyrifera*), trembling aspen (*Populus tremuloides*), and white spruce (*Picea glauca*), characterize the mesic sites (Bergeron and Bouchard 1984). Tamarack (*Larix laricina*), black spruce (*Picea mariana*), eastern white cedar (*Thuja occidentalis*), and black ash (*Fraxinus nigra*) dominate the hydric sites around Lake Duparquet (Bergeron et al. 1983). The latter species, and sporadically balsam poplar (*Populus balsamifera*), occupy the floodplains of the lake (Tardif and Bergeron 1992).

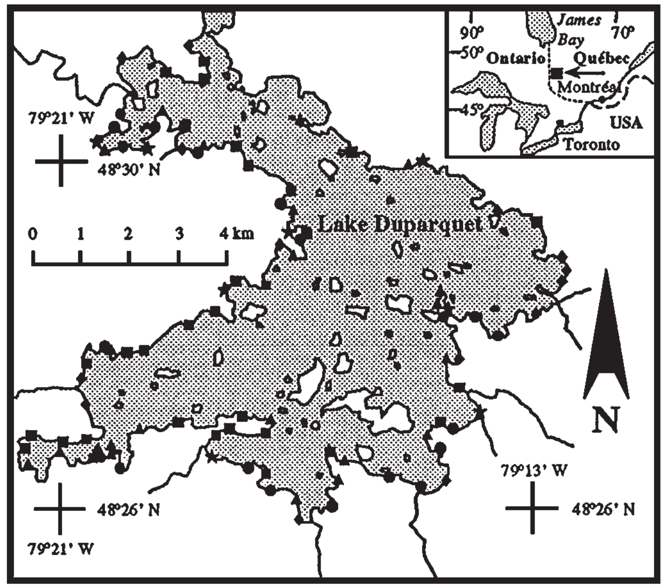


Fig. 1. Location of the Lake Duparquet study area and the 95 transects analyzed. Each of them belongs to one of five geomorphological shore types: depositional flats (◆), floodplains (★), beaches (●), terraces (■), and rock outcrops (▲).

The main disturbance type in the area is forest fire (Bergeron 1991, 1998). The reconstruction of fire history for the lakeshore area and the islands in Lake Duparquet, however, shows a considerable decrease of both frequency and extent of fires since about 1850, which is explained by an increase of precipitation (Bergeron and Archambault 1993). Fire influences the composition of the forests by favoring monospecific stands either of jack pine (*Pinus banksiana*), white birch, or trembling aspen. These fire-adapted pioneer species are later replaced by others such as balsam fir, black spruce, white spruce, and eastern white cedar, which are more shade tolerant and able to reproduce under a closed canopy (Bergeron 1998). This species replacement strongly influences the gap disturbance regime. Early successional forests are characterized by individual or small-group tree mortality, whereas forests of later successional stages are particularly affected by spruce budworm (*Choristoneura fumiferana*) outbreaks, killing whole stands of balsam fir and creating thus larger gaps (Bergeron et al. 1995; Kneeshaw and Bergeron 1998). Three outbreaks have been reconstructed for the 20th century, occurring at intervals of 25–30 years (Morin et al. 1993).

Lake Duparquet is a medium-sized lake (about 50 km^2) with a perimeter characterized by deep embayments separated by long ledges. This highly structured shoreline and the extensive number of islands (over 150) emphasize the low depth of the basin. Seasonal water level fluctuations can exceed 3 m. Long-term variations show an upward trend since the mid-19th century, the maximal spring high water levels having approximately increased by 1 m (Tardif and Bergeron 1997). The riparian forests have not been affected by the extensive forestry activities in the catchment area of Lake Duparquet, which began in the late 1970s (Harvey and Bergeron 1989). However, in earlier times there might have been some cutting along lakeshores, the timber being floated on the Duparquet River and Lake Abitibi down to Iroquois Falls in

[2] Nomenclature of the species names follows that of Burns and Honkala (1990).

Ontario where a large paper mill was built in 1913 (Perron 1989; Asselin and Gourd 1995). Potential indirect effects of logging on runoff, sedimentation, and erosion are supposed to be negligible because of the relatively few clearcuts in the vicinity of the lake, and because most of the rivers flowing into Lake Duparquet pass through small lakes acting as sediment traps. Mining and building activities destroyed the natural vegetation of a part of the lake perimeter, particularly on the north shore. Nevertheless, the bulk of the shoreline of Lake Duparquet remains almost untouched.

Data collection

The first step consisted in the establishment of a classification system of the shores based on several criteria that included form of the shoreline (bay, ledge), substratum, topography, and predominant geomorphological processes (erosion, sedimentation). This resulted in the distinction of five geomorphological shore types: depositional flats, floodplains, beaches, terraces, and rock outcrops. Depositional flats are large, flat areas created by the hydrodynamic redistribution of fine mineral sediments over the preexisting surface. High groundwater levels favor the accumulation of thick peat layers. In some cases, wave activity heaped up beach ridges parallel to the shoreline. Floodplains are large, flat areas inundated during periods of high water but without considerable sedimentation in comparison with the depositional flats. Beaches are narrow edges of fine sediment in embayments with moderate slopes. Strong erosion can cause a retrogression of the shoreline creating pocket beaches flanked by rocky ledges. Terraces are raised flats delimited on the landside by a talus of erosion and on the lakeside by a boulder-bordered slope originating from wave breaking. Rock outcrops are mostly steep shores with less than 25 cm sediment over bedrock.

The entire perimeter of Lake Duparquet (without islands) was mapped with the object of associating one of these shore types to each homogeneous section of the shoreline with a minimal length of 50 m. Next, 106 shoreline points were chosen as locations for the establishment of transects in the unaltered parts of the lake perimeter (Fig. 1). One hundred points were selected randomly, the number of points per shore type corresponding approximately with the relative length of its total shoreline section.[3] To cover all of the rare tamarack stands, six additional transects were drawn through them.

The starting point of all transects was positioned relative to a reference water level of 266 m above sea level, which roughly represents the mean level of Lake Duparquet. From each shoreline point, a transect perpendicular to the topographic contours was drawn to analyze the composition of the tree layer of the riparian forest within a 3-m-wide strip. An exception was made for the sparse tamarack forests where a 10-m width was used in order to reach a sufficient number of trees. Transects ended at 2 m above mean lake level. The geomorphological situation indicated that it was about the position of high water levels. However, some transects could not be completed up to this height, because the topographic divide between the lake and adjacent water bodies did not exceed 2 m in elevation. In this case, data collection ended approximately at the culminating point. The length of the transects varied between 2 m and almost 400 m. The elevation gradient of each transect was divided into four equal parts, all of these so-called plots covering thus a vertical interval of 50 cm. Very long plots were further subdivided until their length did not exceed 20 m in order to get a better resolution of the horizontal distance to the lakeshore. Within each plot, the stem diameter at breast height (dbh) of all living trees bigger than 5 cm was measured.

Environmental variables

The environmental data comprise the following factors, recorded for all shoreline points: geomorphological shore type, inclination and aspect of the slope, fetch to the opposite shore of the lake, exposure to wave activity, and year of the last forest fire. Type of substratum, elevation, and horizontal distance to the lakeshore, however, were determined for each plot.

Inclination and aspect of the slope

The inclination of the slope is defined as the angle, measured with a clinometer, between the horizontal at mean water level and the highest point of the transect. The aspect of the slope is represented by the closest of the eight main cardinal points (N, NE, ..., W, NW).

Fetch and exposure

The energy of the waves arriving at the shore is related to wave height, which is in turn a function of speed and duration of winds, fetch, and water depth (Pond and Pickard 1978). In this study, a modification of the approach of Keddy (1982, 1984) was applied using fetch measurements, wind data, and shore slope to calculate exposure measurements.

Direct fetch: A map of Lake Duparquet at a scale of 1 : 20 000 was fixed on a drawing board to measure, for each of the 106 shoreline points, the distance to the opposite shore of the lake (mainland or island) in 36 different directions (i.e., at 10° intervals). Directions from which waves cannot arrive have a zero value. The mean of this so-called direct fetch for each shoreline point was used as a separate environmental variable (Table 1).

Effective fetch: Narrow embayments and long ledges, but also the many small islands of Lake Duparquet, can result in extreme and less meaningful values for direct fetch (Keddy 1982). Therefore, a correction was performed by taking into account the adjacent fetch measurements: each effective fetch value is composed of the weighted direct fetch values of all adjacent directions that are less than 45° away (for calculations see Keddy 1982).

Wind exceedance: Presuming the shoreline trees are mainly disturbed by severe events, particular importance must be attached to strong winds. Thus, the exceedance value, cal-culated separately for each of the 36 compass bearings, represents the proportion of strong wind measurements (≥20 km/h) in relation to all wind measurements of the same direction based on hourly readings for the time period ranging from 1971 to 1997. The wind data that was used came from the weather station of Rouyn-Noranda, about 50 km southeast of Lake Duparquet. Exceedance was calculated for three different time periods: May, the growing season, and the ice-free period. During May, the ice of Lake Duparquet breaks up and ice scouring increases the effect of wave activity; during the growing season, from June to September, the trees might be particularly vulnerable to wave damage; and during the ice-free period, from May to November, the waves can affect shoreline vegetation.

Slope: Waves approaching the shore lose a part of their energy depending on the inclination of the lakebed. To consider this topographical effect, the exposure value was multiplied by the sine of the slope, assuming that the slope above the waterline is the same as that in the near offshore zone. Thus, the exposure value for a flat shore where the waves are broken by the gently rising lake bot-

[3] All sections of a particular shore type were numbered consecutively, and random numbers were used to select the shoreline sections within which the transects should be placed. To get a somewhat regular distribution of the transects all around the lake, three times as many random numbers were determined, and after arrangement in ascending order, only each third number was retained.

Table 1. Some descriptive statistics of the study sites for all plots and the five shore types.

		Geomorphological shore type				
Parameter	Overall	Depositional flats	Floodplains	Beaches	Terraces	Rock outcrops
Lake perimeter* (km)	85.7 (100%)	8.5 (9.9%)	1.9 (2.2%)	11.6 (13.5%)	29.8 (34.8%)	27.2 (31.7%)
No. of transects	95	14	8	20	31	22
No. of plots	241	69	33	45	66	28
Substratum (% of all plots)						
Bedrock	4.1	—	—	—	—	35.7
Glacial till	25.7	8.7	—	2.2	66.7	39.3
Glaciolacustrine clay	45.2	10.1	97.0	97.8	28.8	25.0
Fine mineral sediment	8.3	23.2	3.0	—	4.5	—
Peat	16.6	58.0	—	—	—	—
Slope† (°)	11.8±11.814	0.9±0.539	2.5±1.324	10.6±5.725	9.7±3.336	26.1±15.621
Horizontal distance‡ of the plots (m) and number of plots (in parentheses)						
0–50 cm§	2.7 (21)	57.2 (6)	6.0 (4)	1.3 (5)	2.2 (5)	1.2 (1)
50–100 cm	15.1 (74)	88.0 (35)	14.1 (10)	5.3 (11)	5.0 (16)	3.3 (2)
100–150 cm	14.5 (78)	53.6 (23)	37.5 (13)	8.3 (15)	7.8 (21)	4.6 (6)
150–200 cm	10.5 (68)	76.9 (5)	39.5 (6)	11.6 (14)	10.8 (24)	3.9 (19)
Direct fetch† (km)	0.429±0.247	0.424±0.201	0.320±0.185	0.244±0.159	0.525±0.226	0.478±0.287
Exposure† (E_S_DG)‖	0.363±0.461	0.025±0.017	0.059±0.058	0.185±0.133	0.360±0.219	0.853±0.687

*The shoreline sections modified by man (6.4 km = 7.5%) and an esker (0.3 km = 0.4%) were not considered for the selection of the transects.
†Mean ± SD.
‡Median.
§The four height intervals of the variable elevation.
‖Calculated with direct fetch (D) and wind exceedance during growing season (G).

tom decreases considerably (e.g., sin(1°) = 0.017 as the multiplier) whereas it doesn't change much for a steep slope (e.g., sin(60°) = 0.866).

By using fetch (direct, effective) and wind exceedance (May, growing season, ice-free period) in combination with or without the correction by the inclination of the lakeshore, 12 (2 × 3 × 2) different exposure values were received for each shoreline point. Six values were calculated by multiplying fetch with wind exceedance and the consecutive summation over all 36 directions:

$$[1] \qquad E = \sum_{i=1}^{36} (\text{fetch}_{10^\circ i} \times \text{exceedance}_{10^\circ i})$$

The resulting exposure values (E) were in turn multiplied by the sine of the angle of the slope (α) to get a second set of six exposure values (E_S):

$$[2] \qquad E_S = E \times \sin(\alpha)$$

Forest fire

At some shoreline points, trunks and stumps bearing fire scars were found indicating that forest fires have reached the lakeshore. Thus, the year of the last forest fire was determined for each transect using the stand initiation map of Bergeron et al. (1995), which is based on the fire history reconstruction of Bergeron (1991), and Dansereau and Bergeron (1993). Since the northeastern part of the lake perimeter was not mapped by these authors, nine transects with 35 plots have missing values. Showing only 11 different dates, fire was registered on ordinal scale with 1 for the oldest fire (A.D. 1717) and 11 for the youngest (A.D. 1944).

Substratum

At the center of each plot, a sample of the surficial substratum was taken with a tube sampler down to maximally 50 cm. The following five types were distinguished: bedrock, no sediment over the acid basaltic rock outcrop; glacial till, morainic deposition composed of all granulometric fractions from clay up to boulders; glaciolacustrine clay, almost pure clay deposited in the proglacial lakes Barlow and Ojibway; fine mineral sediment, a mixture of clay, silt, and (normally dominating) sand, eroded and redeposited by the wave activity; peat, accumulation of at least 40 cm of organic matter.

Elevation and horizontal distance to the lake

As already mentioned, the elevation of the plots corresponds with one of the four classes of 50 cm between zero and 2 m above mean lake level. The distance between the lakeshore and the center of each plot was measured at a precision of 0.5 m, and, for steep slopes (≥10°), corrected by the cosine of the angle to get a better value for the horizontal distance.

Data analyses

Only those species present in more than three transects were included in the analyses. Thus, *Pinus banksiana*, *Pinus strobus*, and *Pinus resinosa* were not considered. The major habitat of these three pine species seems to be on the islands of Lake Duparquet rather than on the mainland (Bergeron and Brisson 1990; Bergeron et al. 1997). Since the four encountered species of *Salix* (*S. discolor, S. lucida*, *S. petiolaris*, and *S. rigida*) were not present in more than three transects and because all of them can be associated with humid habitats (Marie-Victorin 1995), their analysis was limited to the genus level.

Of the 106 transects, 11 had to be omitted mainly because no living individual of the selected tree species was recorded within the 2-m vertical interval or, if some were present, they were too small to be considered (dbh < 5 cm). Plots without any living trees, quite often encountered at the lowest vertical interval (0–50 cm) where bare sediment or rock, herbs and shrubs predominate, were not included in the analyses. Hence, the overall data comprise 241 plots from 95 transects (Table 1). Twenty environmental variables were used as predictors to try to explain the distribution of the 10 common tree species occurring in the riparian zone of Lake Duparquet. In statistical calculations, the three nominal environ-

Table 2. Number of plots, diameters at breast height differentiated for the four elevation classes, and relative basal area of the 10 tree species.

		Diameter at breast height (mean±SD) of the four elevation classes				
Species name (abbr.)	Occurrences (plots)	0–50 cm (cm)	50–100 cm (cm)	100–150 cm (cm)	150–200 cm (cm)	Relative basal area* (%)
Abies balsamea (ABA)	61	—	7.8±2.360	11.3±4.650	9.9±3.949	37.0 (0.7–100.0)
Betula papyrifera (BPA)	24	—	8.5†	15.3±6.165	19.8±9.334	38.4 (2.1–100.0)
Fraxinus nigra (FNI)	79	11.9±7.758	12.6±7.352	14.3±9.174	9.5±4.928	63.5 (0.5–100.0)
Larix laricina (LLA)	26	10.3±3.830	14.4±6.038	17.7±6.944	—	72.6 (7.5–100.0)
Picea glauca (PGL)	13	—	—	24.9±11.919	19.5±8.246	56.6 (11.7–100.0)
Picea mariana (PMA)	12	—	10.2±4.264	13.0±3.599	12.0†	25.0 (2.1–65.4)
Populus balsamifera (POB)	25	15.5±8.846	20.1±9.628	15.5±9.423	21.9±11.588	48.2 (0.3–100.0)
Populus tremuloides (POT)	21	—	20.5±9.000	24.4±9.897	27.7±8.598	55.1 (1.2–100.0)
Salix spp. (SAL)	21	12.0†	11.0±5.492	11.3±5.128	8.0±0.866	25.5 (0.5–100.0)
Thuja occidentalis (TOC)	126	23.7±13.662	42.0±13.928	23.2±13.974	18.8±14.128	80.0 (2.5–100.0)

*Mean and range (in parentheses) of the relative basal area, using only plots where the corresponding species was present.
†Only one individual.

mental variables, namely shore type, substratum, and aspect, were transformed into dummy variables.

Stepwise logistic regression (SPSS Inc. 1997) was applied to help identify the combinations of factors that explain the occurrence of each species on the lakeshore. For this purpose, each plot was described in terms of presence or absence of every tree species. Environmental variables were entered in the model if their scores were significant at a level of 0.05, corrected by the method of Bonferroni (Sokal and Rohlf 1995). To deal with the problem of missing values for the fire variable, a first run was performed. If fire was not retained by the forward selection procedure, the calculations were redone without this variable, which allowed all observations to be included.

To identify relationships between the various environmental factors and the relative abundance of the species, a direct gradient analysis was performed using stepwise canonical correspondence analysis (CCA; Ter Braak 1987) with the CANOCO software package. To do this, the relative basal area of each species was calculated as percentage of the basal area of all species present in the same plot. The forward selection is based on a Monte Carlo permutation test with 999 permutations; environmental variables were retained at a significance level of 0.001. To test if the selected variables play a significant role in determining the relative abundance of the species, an unconstrained analysis of the species data by correspondence analysis (CA) was performed. The resulting sample scores were compared with those obtained by CCA through the calculation of a correlation coefficient for each of the four ordination axes.

Logistic regression and the gradient analyses were performed for the complete data set and for each geomorphological shore type separately. In the latter case, only those species present in at least 10 plots of the corresponding shore type were considered.

Results

The highly structured shoreline of Lake Duparquet was reflected in the considerable length of its total perimeter of 85.7 km (Table 1). Terraces and rock outcrops each contributed to about one third of the total shore length, whereas the proportions of the three other shore types were much smaller. Beaches and floodplains were almost completely composed of glaciolacustrine clay (Table 1). Less than one fourth of all plots in the depositional flats revealed fine mineral sediments as substratum, because those are often covered by a thick layer of peat. In the terrace plots, two out of three borings contained glacial till. Finally, the rock outcrops were often overlain by thin layers of either clay or till.

Depositional flats and floodplains had very gentle slopes, whereas the rock outcrops fell precipitously to the lake (Table 1). However, the standard deviations of mean slope for all five shore types were high. The medians of the horizontal distance roughly reflected the slopes: the steeper the shore, the closer the plots were to the lake. But the values for the different elevations are not consistent, mainly because plots without living trees were excluded. Thus, relatively few plots lay in the lowest, and therefore most exposed, elevation class. Some of the more elevated plots had to be omitted either because they were in gaps created by a recent spruce budworm outbreak, or because elevation of the terrain did not reach 2 m. The flat terrain of the flood- and depositional plains resulted in a relatively high number of plots in the two middle elevation intervals because of the multiple subdivision of the very long parts of some transects. This led also to a high value of the median horizontal distance for the alluvial plains. The resulting unbalanced sampling design is no problem, because this study aimed principally at the description of the species' distribution along an ecological gradient and not at the precise prediction of their abundance as a function of the ecological variables. Therefore, it was important to cover the whole gradient but not to represent proportionally each part of it.

Terraces and beaches, respectively, showed the longest and shortest mean direct fetch (Table 1). The three other shore types presented the extreme values for exposure to wave activity. Slope was undoubtedly responsible for the infinitely small values for the very flat shoreline sections and the greatest index for the steep rock outcrops.

For all tree species, mean diameter at breast height did not vary significantly between the four elevation classes (Table 2). However, several species showed a slight trend towards higher values with increasing elevation from the lake up to about 1.5 m. Eastern white cedar had a considerably high value for the second elevation interval, indicating a concentration of large and probably old individuals. Relative basal area revealed that white cedar, tamarack, and black ash

Table 3. Variables retained by the forward selection procedure of the logistic regression and their explicative power (partial *r*) for each species* ($P \leq 0.004$).

Species	Variable	Partial *r*
Abies balsamea	1. Elevation	0.390
	2. Exposure (E_S_DG)†	–0.186
	3. Beaches	0.171
Betula papyrifera	1. Elevation	0.259
Fraxinus nigra	1. Fine sediment	0.221
	2. Floodplains	0.333
	3. Depositional flats	0.275
	4. Aspect SE	0.258
	5. Exposure (*E*_DG)†	–0.212
	6. Elevation	–0.210
	7. Aspect S	0.204
	8. Aspect NE	0.201
Larix laricina	1. Exposure (*E*_DG)†	0.420
Picea glauca	1. Elevation	0.265
Picea mariana	1. Horizontal distance	0.505
Populus balsamifera	1. Forest fire	0.232
Populus tremuloides	1. Aspect SE	0.318
	2. Beaches	0.308
	3. Floodplains	0.301
	4. Aspect W	0.223
Thuja occidentalis	1. Slope	0.242
	2. Glacial till	0.160

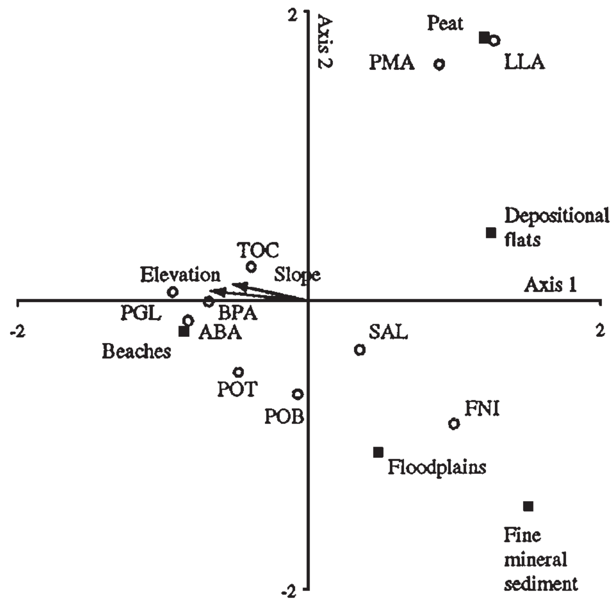
Note: The variables are in the order they were selected by the forward procedure.
*No variable was retained for *Salix* spp.
†Calculated with direct fetch (D) and wind exceedance during growing season (G).

were dominant in the plots where they occur, whereas black spruce, willow, balsam fir, and white birch were generally of minor importance (Table 2).

Logistic regression over all 241 plots selected elevation as the most significant factor explaining the presence of balsam fir, white birch, and white spruce (Table 3). The same variable also was retained for black ash, but with a negative partial correlation coefficient. Balsam fir was also associated to low exposure and the beach shore type. Black ash occurred mainly in floodplains and depositional flats, but the variation in the occurrence of this broadleaf species appeared to be affected by many of the environmental factors. Exposure was the prime predictor of the occurrence of tamarack. The only factor retained for black spruce was horizontal distance to the lakeshore, which indicates the presence of this species in large alluvial plains. Balsam poplar was the only species for which the variable forest fire was retained. In addition to southeastern and western aspect, beaches and floodplains were positively related to the occurrence of trembling aspen. For eastern white cedar, logistic regression selected slope followed by till, which was the principal substratum of the shore terraces (see Table 1). None of the analyzed environmental variables were significant predictors for the presence of the willows. This could indicate that the ecological range of the included species of *Salix* is too large to be analyzed at the level of the genus.

The forward selection of the stepwise canonical correspondence analysis (CCA) retained seven environmental variables as significant (Fig. 2). The first two canonical axes were strongly related to the selected environmental variables (species–environment correlation: $R_1 = 0.79$, $R_2 = 0.74$), and together accounted for 78.8% of the variance of the species–environment relationship as well as 16.8% of the variance of the species data. From the biplot, it can be seen that the first axis represents an elevation/slope gradient that separates the three shore types retained in the analysis. Species on the left, such as white spruce, balsam fir, and white birch, had high relative basal area values on elevated sites, whereas tamarack, black spruce, black ash, and willow dominated on the low sites. A third group, composed of balsam poplar, trembling aspen, and white cedar, took an intermediate position on the elevation gradient. Five species dominated the beaches, whereas black ash, willow, and balsam poplar were important in the floodplains. No species was close to the depositional flat shore type, because its two major substrata were strongly separated by the second axis. This means that the dominant species of fine mineral sediments (black ash) were different from those observed on peat (tamarack and black spruce).

Fig. 2. Results of the stepwise canonical correspondence analysis of the Lake Duparquet data. Ordination diagram representing species scores (○), biplot scores of the environmental variables (arrows), and centroids of the nominal variables (■) for the first two canonical axes. See Table 2 for the abbreviations of the species names.



The correlations of the sample scores from direct and indirect gradient analyses were significant for all four axes (Table 4A). Whereas the coefficients for the first and fourth axes took positive values, those for the two other axes were negative. The eigenvalues of the axes were quite different between the two ordination models. The eigenvalues of the third and fourth canonical axes of the CCA were low, and not very important. The strongly correlated sample scores showed that the environmental variables entered in the analysis partially predicted the distribution of the species data. However, the considerable differences in the respective ei-

Table 4. Comparison of indirect (CA) and direct (CCA) gradient analyses.

	1st axis	2nd axis	3rd axis	4th axis
A. Correlation coefficients and eigenvalues for all transects				
Pearson's *r*	0.2164	–0.2278	–0.7742	0.8174
(Prob.)	(0.001)	(0.000)	(0.000)	(0.000)
Eigenvalues				
CA	0.923	0.872	0.792	0.765
CCA	0.539	0.500	0.192	0.063
B. Eigenvalues for the geomorphological shore types				
Depositional flats				
CA	0.969	0.826	0.409	0.330
CCA	0.722	0.141	0.116	0.033
Floodplains				
CA	0.725	0.000	0.000	0.000
CCA	0.468	0.257	0.000	0.000
Beaches				
CA	0.877	0.828	0.000	0.000
CCA	0.432	0.079	0.749	0.445
Terraces				
CA	0.859	0.812	0.684	0.000
CCA	0.400	0.116	0.062	0.748

Note: Pearson's product–moment correlation coefficient (*r*) for the sample scores obtained by CA and CCA of the whole data set (A), and the eigenvalues of both gradient analysis techniques for the first four ordination axes, for all plots (A) and for each shore type (B), respectively. Rock outcrops were not considered because no CCA could be calculated for this shore type (only one species).

genvalues of the CA and CCA indicate the presence of other revealing environmental factors that were not measured.

Analyses of species distribution according to geomorphological shore types

The results of the logistic regression for each shore type, which included only those species occurring in at least 10 plots, are presented in Table 5. Given that within the considered height interval of 2 m tamarack and black spruce were almost completely restricted to the depositional flats, the stepwise procedure for this shore type alone retained the same variables for them as in the overall analysis (see Table 3). Exposure was selected for black ash and southeastern aspect for the willows. The presence of white cedar was predicted by peaty soil and high elevations. In the floodplains too, this species tended to occupy the higher sites. The only species with significant predictors for the beach shore type was balsam fir for which logistic regression retained elevation as the prime factor and (negative) exposure as the second factor (Table 5). On the lacustrine terraces, the occurrence of balsam fir and white birch increased with rising elevation and distance to the lake, respectively. Black ash, however, colonized the lower parts of the terraces. White cedar remained without any retained variable. The case is the same for the rock outcrops where this species was the only one present in more than 10 plots.

The comparison of the eigenvalues of the CA and CCA for each shore type (Table 4B) shows that the first canonical axis explained most of the variation in the species data, and thus the ordination diagrams of Fig. 3 must be particularly interpreted with regard to this axis. In the depositional flats, eastern white cedar, tamarack, and black spruce had high relative basal areas in plots with peaty soil (Fig. 3A). The latter two species were mostly associated with west- and northwest-facing alluvial plains. Black ash and willow, however, dominated those with a southeastern aspect. Stepwise CCA for the floodplain data retained elevation and distance as significant predictors, and both lie on the first axis (Fig. 3B). The two species included in the analyses, black ash and white cedar, occupy opposite positions on this elevation/distance gradient. In the beach shore type, balsam fir dominated the elevated plots, whereas balsam poplar and white cedar had high relative basal area values in the lower plots (Fig. 3C). On the terraces, balsam fir, white birch, cedar, and black ash are arrayed along a high-to-low elevation gradient (Fig. 3D). The second axis represents an age-of-fire gradient. Paper birch had high relative basal areas on those sites where the last fire passed recently. For the rock outcrops, CCA could not be performed, because only white cedar was present in more than 10 plots.

Discussion

All five geomorphological shore types distinguished in this study are the product of several factors that include surficial substratum (partly inherited from postglacial deposits), topography, and the long-term activity of the waves (shore breaking and littoral drift). Consequently, each of them has its own characteristic physiographic cross-section of tree species in the shore immersion zone (Fig. 4).

Depositional flats

The dominant tree species in the fens of the depositional flats is tamarack (Fig. 4, illustrations Aa and Ab). This species occurs exclusively on peaty soil where it often forms pure and sparse stands. Most of the tamarack forests are situated in the large bays on the east side of the lake. These bays face west or northwest and have long fetches to the opposite shore, which results in high exposure. The exposure measure retained by logistic regression (E_DG; Table 5) seems to indicate that the gently sloping lakebed does not play a major role. This suggests that exposure during periods of high water maintains the large, treeless belt of shrubby vegetation fronting the tamarack forests (Fig. 4, illustration Aa). But this also signifies that high exposure merely explains the absence rather than the presence of tamarack. This is emphasized by the situation observed in the only larch population in an east-facing bay (Fig. 4, illustration Ab). Instead of a shrub belt, there is a beach ridge that is colonized by black ash and, on the top, eastern white cedar. As in the other bays, tamarack occupies the low, peaty sites and is not found on the ridge. Thus, it is assumed that the principal reasons for the presence of tamarack are (*i*) its tolerance of prolonged flooding, (*ii*) a habitat relatively protected from wave activity either by a beach ridge or a large shrub belt associated with a gently sloped lakebed, and (*iii*) the capacity to reproduce on a thick layer of organic matter.

The absence of tamarack on the beach ridges and in the other shore types might be explained by both, its intolerance to shade (Burns and Honkala 1990) resulting in a low competition capability, and the necessity to recolonize after fire out of preserved zones like the humid riparian fens. Black spruce and especially eastern white cedar accompany tam-

Table 5. Number of plots, relative basal area, and the results of the stepwise logistic regression with forward selection procedure for each geomorphological shore type including only those species that were present in at least 10 plots.

Shore type			Step 1		Step 2	
Species	Plots	rBA* [%]	Variable	Partial $r^{\dagger}$	Variable	Partial $r^{\dagger}$
Depositional flats	69					
Fraxinus nigra	37	71.7	Exposure (E_DG)‡	–0.429	—	
Larix laricina	26	72.6	Exposure (E_DG)‡	0.457	—	
Picea mariana	11	22.8	Horizontal distance	0.448	—	
Salix spp.	10	22.7	Aspect SE	0.357	—	
Thuja occidentalis	20	69.7	Peat	0.334	Elevation	0.285
Floodplains	33					
Fraxinus nigra	25	63.3	—		—	
Thuja occidentalis	10	49.8	Elevation	0.348	—	
Beaches	45					
Abies balsamea	21	47.8	Elevation	0.338	Exposure (E_FI)‡	–0.279
Populus balsamifera	10	61.7	—		—	
Thuja occidentalis	22	81.7	—		—	
Terraces	66					
Abies balsamea	18	39.5	Elevation	0.372	—	
Betula papyrifera	11	49.1	Horizontal distance	0.357	—	
Fraxinus nigra	11	58.1	Elevation	–0.387	—	
Thuja occidentalis	50	83.1	—		—	
Rock outcrops	28					
Thuja occidentalis	24	93.1	—		—	

*Mean of the relative basal area, using only plots where the corresponding species was present.
†$P \leq 0.009$.
‡Calculated with direct (D) or effective (F) fetch and wind exceedance during the growing season (G) or the ice-free period (I), respectively.

arack in some alluvial plains. Black ash and, to a lesser degree, arborescent willows can also be found in the depositional flats where their occurrence is explained by the presence of mineral soil. Thus, they occupy either the marginal zones around the alluvial fens or the beach ridges. Similar habitats along the rivers that discharge into Lake Duparquet are mainly colonized by black ash (Bergeron et al. 1983).

Floodplains

The floodplains of Lake Duparquet are composed of glaciolacustrine clay, which is in some rare cases overtopped by a thin layer of sandy material deposited there by the waves (Table 1). They are the domain of black ash, a species well adapted to prolonged seasonal inundation (Fig. 4, illustration B). Balsam fir, white cedar, willow, trembling aspen, and especially balsam poplar may accompany it. Pure stands of the latter species, however, are rare and relatively small. Eastern white cedar sometimes forms a narrow, monospecific fringe between the black ash stands and the mesic forests above the riparian zone.

Beaches

Almost pure glaciolacustrine clay and a considerable slope (see Table 1) facilitate the erosive activity of the waves in the embayments, which leads to a retrogression of the shoreline. This morphological instability of the shore hinders almost completely the development of riparian vegetation (Fig. 4, illustration C). Balsam poplar and eastern white cedar can dominate the low sites in some bays less affected by the waves.

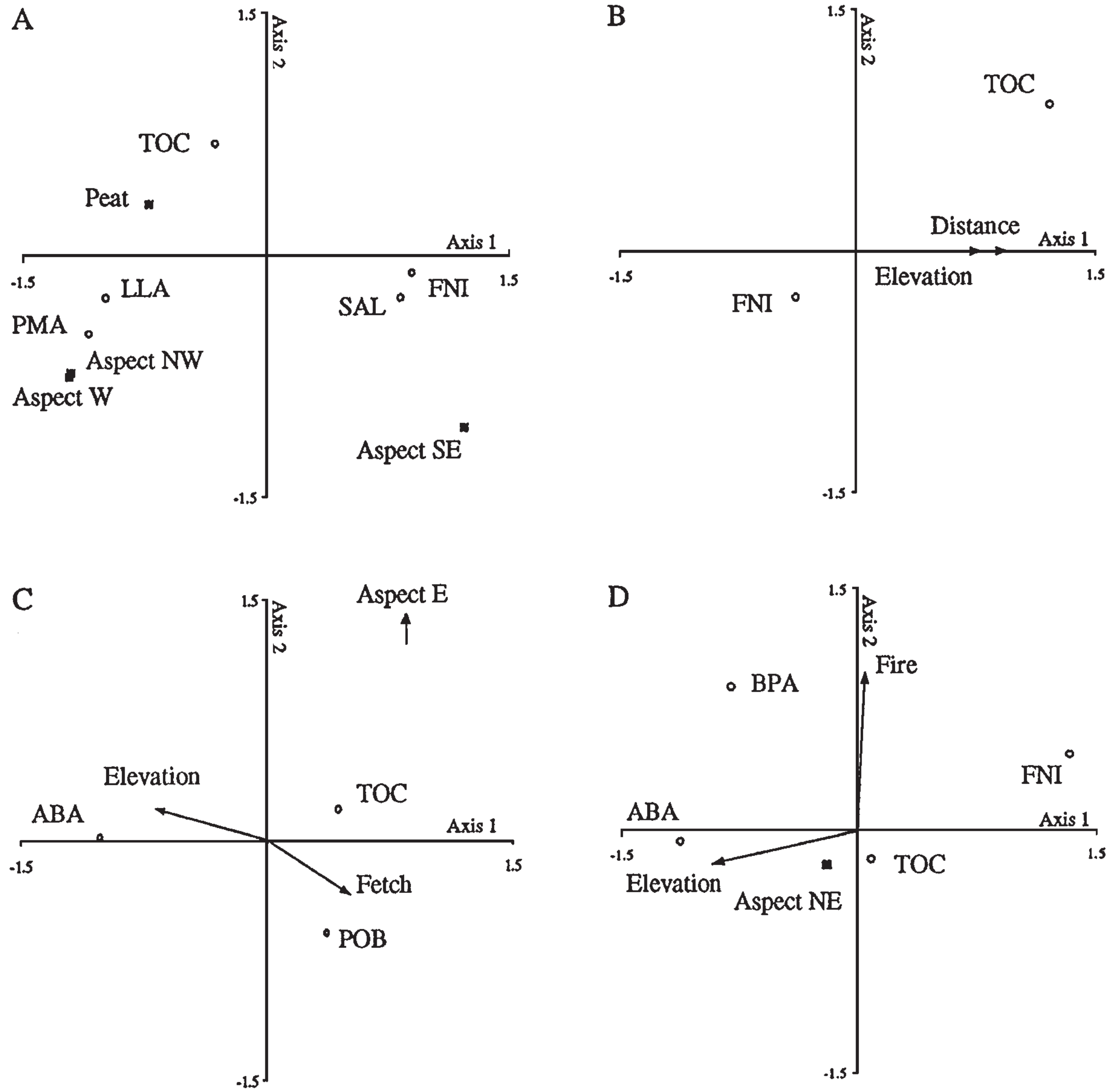
Terraces

The heterogeneous composition of glacial till, the principal substratum of the terraces (see Table 1), could be the reason for the existence, or at least the persistence, of this shore type. Selective erosion of the small particles leaves rocks and boulders on the lakeside slope of the terraces that protect them from being eroded despite generally long fetches and high exposure to waves. Where it was not disturbed by fire, the vegetation shows a distinct physiographic cross-section (Fig. 4, illustration D). Black ash occupies the lowest elevations. In contrast with what is observed on the floodplains, the trees on the terraces are often relatively small, and stump sprouting is common. This is the consequence of high exposure to wave activity and ice push. Black ash is followed by eastern white cedar, which dominates the main part of the terraces, often accompanied by some individuals of balsam fir, white birch, white spruce, or trembling aspen. However, these species are more common in the upper part of the riparian zone.

Rock outcrops

Although rocky outcrops constitute nearly a third of the whole lake perimeter (see Table 1), only few trees were recorded within the riparian zone, because these sites are unfavorable to tree establishment and growth. This might be the reason why logistic regression did not select this shore type as a significant predictor of the occurrence of black spruce (see Table 3) although this species is very common on xeric bedrock. Protection from fire due to the proximity of the water in combination with a relative longevity on xeric sites (Archambault 1989) might be the reasons why eastern white

Fig. 3. Results of the stepwise canonical correspondence analyses for four of the shore types: depositional flats (A), floodplains (B), beaches (C), and terraces (D). No CCA was performed for the rock outcrops because there was only one species in more than 10 plots. See Fig. 2 for the symbols and Table 2 for the abbreviations of the species names.



cedar was more frequently recorded than other species (Fig. 4, illustration E).

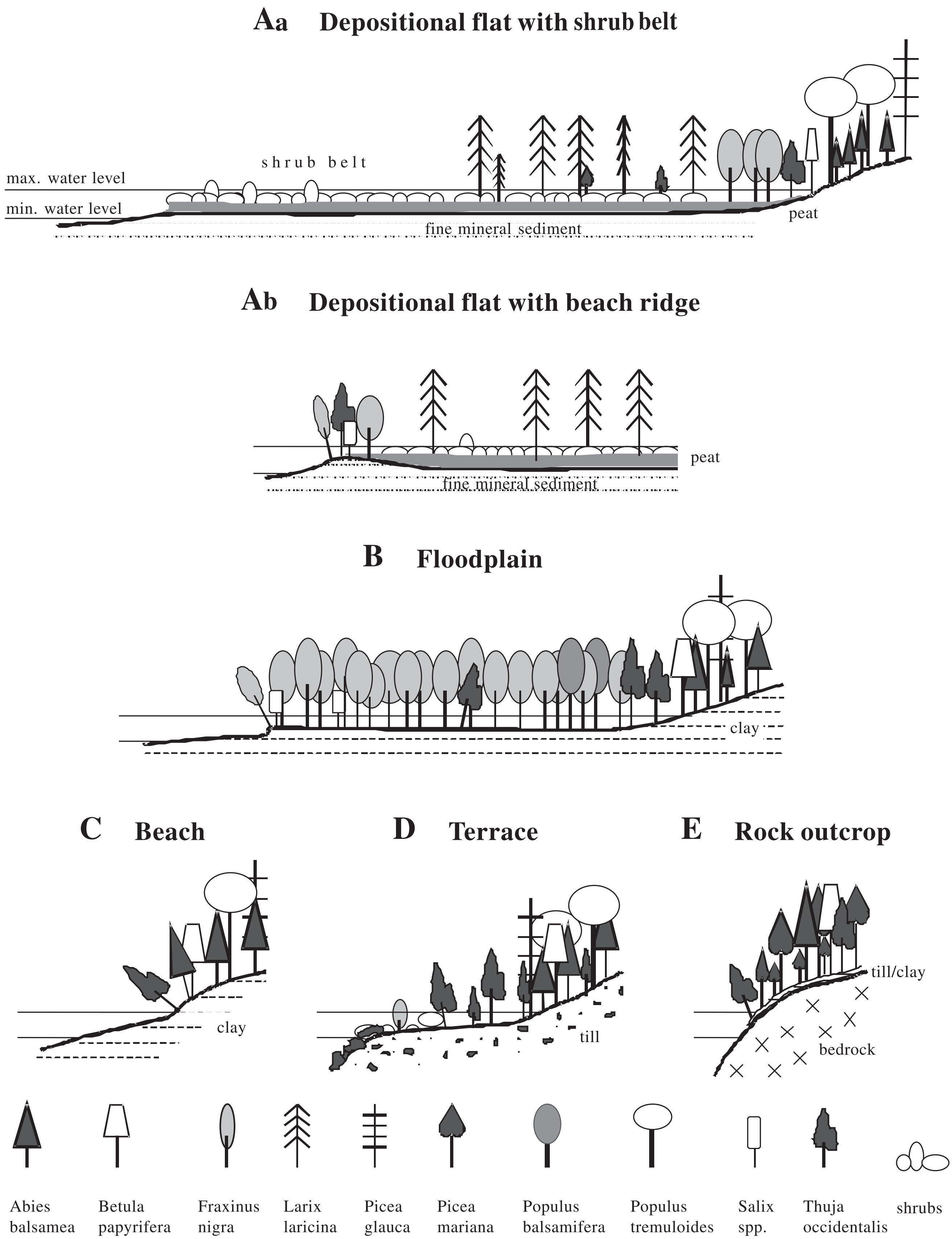
Overall data

If all study sites are taken together, one can distinguish three different groups of species with respect to the occupied habitat. The first group includes tamarack, black spruce, black ash, balsam poplar, and willow. These species occupy the low sites that are heavily affected by high water levels, and thus are most common in depositional flats and floodplains. Their occurrence and relative basal area differ according to shore type, surficial substratum, topography, elevation, and aspect. The second group of species is composed of balsam fir, white birch, white spruce, and trembling aspen. Although occasionally found on low sites, they mainly occupy the higher elevations where they are rarely reached by the floods. Thus, they have been recorded in all shore types. However, in floodplains and depositional flats they are restricted to the foot of the slope as it corresponds with the transition to a mesic forest not affected by the seasonal floods of Lake Duparquet. Eastern white cedar, finally, forms its own group because it is omnipresent on hydric, mesic, and xeric sites. Its presence in almost 85% of all transects, in all geomorphological shore types, and on all substrata emphasizes its wide ecological range. In general, white cedar has the highest relative basal area on moderately elevated sites.

Environmental factors

Frequency and duration of seasonal flooding, as reflected in the importance of the variable elevation, emerge as the principal environmental factors determining the distribution of the tree species around Lake Duparquet. In other words, specific differences with respect to tolerance of temporary inundation are of prime importance for the occurrence and relative dominance of the species. However, flooding is not

Fig. 4. Schematic illustration of the distribution of the tree species along characteristic physiographic cross-sections for the five geomorphological shore types. Explanations are in the text.



the only environmental factor influencing the distribution of tree species. Substratum, slope, and geomorphological landform also play a role in structuring the riparian vegetation. These conclusions correspond with those from the pertinent literature (e.g., Robertson et al. 1978, 1984; Metzler and Damman 1985; Tardif and Bergeron 1992). But focusing exclusively on aquatic disturbances such as flooding, wave activity, ice push, erosion, and sedimentation as done by most studies dealing with riparian forest dynamics (e.g., Hupp 1982; Hupp and Osterkamp 1985; Bégin and Lavoie 1988; Nakamura et al. 1997) is not sufficient for regions with a dominant fire regime. The results of this study show clearly that fire, as a terrestrial disturbance type, may also influence the composition of the riparian forests and the relative importance of the tree species present. The occurrence of balsam poplar at Lake Duparquet, for example, was predicted by the time elapsed since the last fire (Table 3), indicating that it is a pioneer species after fire on hydric sites and confirming the observations made by Bergeron and Bouchard (1984). Also, the canonical correspondence analysis for the terrace transects alone (Fig. 3D) shows the influence of the forest fire dynamic on the relative abundance of some species. White birch, another pioneer tree after fire (Burns and Honkala 1990), dominates in plots where the last fire passed recently, whereas balsam fir and eastern white cedar, species that are typical of later successional stages, are more common where fire occurred a long time ago.

Unlike the nonwoody vegetation (e.g., Keddy 1983) and with the exception of tamarack on depositional flats without protecting beach ridge, the direct disturbing effect of the waves seems to be of minor importance for the distribution of the riparian tree species. The influence of the waves is rather indirect. Since they are the driving force of erosion and sedimentation, their activity is responsible, together with substratum and topography, for differentiation and modification of the shoreline, creating the geomorphological shore types.

The comparison between direct and indirect gradient analysis (Table 4) showed that the chosen environmental variables explain only a part of the observed variance in the vegetation data. Other factors, such as competitive interactions and reproductive behavior, may play a major role, as it has been shown for nonwoody riparian vegetation (Grace and Wetzel 1981; Keddy and Ellis 1985; Wilson and Keddy 1985, 1986). Herbivory might be of prime importance for the distribution of certain species at Lake Duparquet. As already mentioned, balsam fir is periodically attacked by spruce budworm outbreaks. In addition, it has been observed that the beaver (*Castor canadensis*) has cut many trees of trembling aspen close to the shoreline, particularly on the terraces, whereas stands more distant from the shore were unaffected. Thus, this diligent rodent, for which trembling aspen is the preferred resource (Bordage and Filion 1988), considerably influences the relative abundance of trembling aspen.

Since the analyses suggest flooding as the main environmental factor structuring the shore vegetation, it can be asked whether the supposed long-term rise of the water level of Lake Duparquet since the mid-19th century (Tardif et al. 1994; Tardif and Bergeron 1997) manifests itself in the distribution of the tree species. The lowest white cedar stands are, in contrast with the upper part of the riparian zone, dominated by thick and therefore probably old individuals. This observation is supported by the extremely high mean dbh of 42 cm in the second elevation class (see Table 2). This supposed skewed age structure let us assume that cedar exhibit a lack of reproduction on the low sites that could signify a landward shift of its realized ecological niche. On the terraces, black ash occupies exclusively the lowest sites (remember its negative partial *r* for elevation in Table 5) and is normally of small size. This could suggest a recent colonization, because the terraces became increasingly favorable for this hydric species on the course of the water level rise. The analysis of the age structure along the elevation gradient could be a promising approach to elucidate the effects of a long-term rise of the water level on the distribution of the tree species.

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References

Archambault, S. 1989. Les cèdres blancs (*Thuja occidentalis* L.) à grande longévité du Lac Duparquet, Abitibi: une étude dendroclimatique et écologique. M.Sc. thesis, Department of Biology, Université du Québec à Montréal, Montreal, Que.

Asselin, M., and Gourd, B.-B. 1995. La naissance de l'Abitibi rural: 1910–1930. *In* Histoire de l'Abitibi-Témiscamingue. *Edited by* O. Vincent. Les régions du Québec no. 7. Institut québécois de recherche sur la culture, Québec. pp. 197–234.

Bégin, Y., and Lavoie, J. 1988. Dynamique d'une bordure forestière et variations récentes du niveau du fleuve Saint-Laurent. Can. J. Bot. **66**: 1905–1913.

Bégin, Y., and Payette, S. 1989. La végétation riveraine du lac à l'Eau-Claire, Québec subarctique. Géog. Phys. Quat. **43**: 39–50.

Bell, D.T. 1974. Tree stratum composition and distribution in the streamside forest. Am. Midl. Nat. **92**: 35–46.

Bell, D.T., and del Moral, R. 1977. Vegetation gradients in the streamside forest of Hickory Creek, Will County, Illinois. Bull. Torrey Bot. Club, **104**: 127–135.

Bergeron, Y. 1991. The influence of island and mainland lakeshore landscapes on boreal forest fire regimes. Ecology, **72**: 1980–1992.

Bergeron, Y. 1998. Les conséquences des changements climatiques sur la fréquence des feux et la composition forestière au sud-ouest de la forêt boréale québécoise. Géog. Phys. Quat. **52**: 167–173.

Bergeron, Y., and Archambault, S. 1993. Decreasing frequency of forest fires in the southern boreal zone of Québec and its relation to global warming since the end of the "Little Ice Age." Holocene, **3**: 255–259.

Bergeron, Y., and Bouchard, A. 1984. Use of ecological groups in analysis and classification of plant communities in a section of western Quebec. Vegetatio, **56**: 45–63.

Bergeron, Y., and Brisson, J. 1990. Fire regime in red pine stands at the limit of the species range. Ecology, **71**: 1352–1364.

Bergeron, Y., Bouchard, A., Gangloff, P., and Camiré, C. 1983. La classification écologique des milieux forestiers de la partie ouest des cantons d'Hébécourt et de Roquemaure, Abitibi, Québec. Études écologiques no. 9, Université Laval, Ste-Foy, Qué.

Bergeron, Y., Leduc, A., Morin, H., and Joyal, C. 1995. Balsam fir mortality following the last spruce budworm outbreak in northwestern Quebec. Can. J. For. Res. **25**: 1375–1384.

Bergeron, Y., Leduc, A., and Li, T. 1997. Explaining the distribution of *Pinus* spp. in a Canadian boreal insular landscape. J. Veg. Sci. **8**: 37–44.

Beschel, R.E., and Webber, P.J. 1962. Gradient analysis in swamp forests. Nature (London), **194**: 207–209.

Bordage, G., and Filion, L. 1988. Analyse dendroécologique d'un milieu riverain fréquenté par le castor (*Castor canadensis*) au Mont du Lac-des-Cygnes (Charlevoix, Québec). Nat. Can. **115**: 117–124.

Buchholz, K. 1981. Effects of minor drainages on woody species distributions in a successional floodplain forest. Can. J. For. Res. **11**: 671–676.

Burns, R.M., and Honkala, B.H. 1990. Silvics of North America. Vol. 2. U.S. Dep. Agric. Agric. Handb. 654.

Dansereau, P., and Bergeron, Y. 1993. Fire history in the southern boreal forest of northwestern Quebec. Can. J. For. Res. **23**: 25–32.

Environment Canada. 1993. Canadian climate normals 1961–90. Canadian climate program. Environment Canada. Atmospheric Environment Service, Downsview, Ontario.

Frye, R.J., and Quinn, J.A. 1979. Forest development in relation to topography and soils on a floodplain of the Raritan River, New Jersey. Bull. Torrey Bot. Club, **106**: 334–345.

Grace, J.B., and Wetzel, R.G. 1981. Habitat partitioning and competitive displacement in cattails (*Typha*): experimental field studies. Am. Nat. **118**: 463–474.

Grandtner, M.M. 1966. La végétation du Québec méridional. Les Presses de l'Université Laval, Ste-Foy, Qué.

Harris, R.R. 1987. Occurrence of vegetation on geomorphic surfaces in the active floodplain of a California alluvial stream. Am. Midl. Nat. **118**: 393–405.

Harvey, B., and Bergeron, Y. 1989. Site patterns of natural regeneration following clearcutting in northwestern Quebec. Can. J. For. Res. **19**: 1458–1469.

Hupp, C.R. 1982. Stream-grade variation and riparian-forest ecology along Passage Creek, Virginia. Bull. Torrey Bot. Club, **109**: 488–499.

Hupp, C.R. 1988. Plant ecological aspects of flood geomorphology and paleoflood history. *In* Flood geomorphology. *Edited by* V.R. Baker, R.C. Kochel, and P.C. Patton. John Wiley & Sons, New York. pp. 335–356.

Hupp, C.R., and Osterkamp, W.R. 1985. Bottomland vegetation distribution along Passage Creek, Virginia, in relation to fluvial landforms. Ecology, **66**: 670–681.

Keddy, P.A. 1982. Quantifying within-lake gradients of wave energy: interrelationships of wave energy, substrate particle size and shoreline plants in Axe Lake, Ontario. Aquat. Bot. **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 Gillfillan Lake, Nova Scotia. Can. J. Bot. **62**: 301–309.

Keddy, P.A., and Ellis, T.H. 1985. Seedling recruitment of 11 wetland plant species along a water level gradient: shared or distinct responses? Can. J. Bot. **63**: 1876–1879.

Kneeshaw, D.D., and Bergeron, Y. 1998. Canopy gap characteristics and tree replacement in the southeastern boreal forest. Ecology, **79**: 783–794.

Marie-Victorin, Frère 1995. Flore laurentienne. 3rd ed. Les Presses de l'Université de Montréal, Montréal, Qué.

Metzler, K.J., and Damman, A.W.H. 1985. Vegetation patterns in the Connecticut River flood plain in relation to frequency and duration of flooding. Nat. Can. **112**: 535–547.

Morin, H., Laprise, D., and Bergeron, Y. 1993. Chronology of spruce budworm outbreaks in the lake Duparquet region, Abitibi, Québec. Can. J. For. Res. **23**: 1497–1506.

Nakamura, F., Yajima, T., and Kikuchi, S. 1997. Structure and composition of riparian forests with special reference to geomorphic site conditions along the Tokachi River, northern Japan. Plant Ecol. **133**: 209–219.

Perron, M. 1989. L'histoire de l'exploitation forestière dans la région de La Sarre de 1910 à 1980. La Sarre, Qué.

Pickett, S.T.A. 1980. Non-equilibrium coexistence of plants. Bull. Torrey Bot. Club, **107**: 238–248.

Pond, S., and Pickard, G.L. 1978. Introductory dynamic oceanography. Pergamon, Oxford.

Robertson, P.A., Weaver, G.T., and Cavanaugh, J.A. 1978. Vegetation and tree species patterns near the northern terminus of the southern floodplain forest. Ecol. Monogr. **48**: 249–267.

Robertson, P.A., MacKenzie, M.D., and Elliott, L.F. 1984. Gradient analysis and classification of the woody vegetation for four sites in southern Illinois and adjacent Missouri. Vegetatio, **58**: 87–104.

Rowe, J.S. 1972. Les régions forestières du Canada. Service canadien des forêts, Ministère de l'Environnement. Information Canada, publication no. 1300F.

Sigafoos, R.S. 1961. Vegetation in relation to flood frequency near Washington, D.C. U.S. Geol. Surv. Prof. Pap. **424-C**: 248–249.

Sokal,, R.R., and Rohlf, F.J. 1995. Biometry: the principles and practice of statistics in biological research. 3rd ed. W.H. Freeman and Company, New York.

SPSS Inc. 1997. SPSS for Windows, release 8.0.0. SPSS Inc., Chicago, Ill.

Tardif, J., and Bergeron, Y. 1992. Analyse écologique des peuplements de frêne noir (*Fraxinus nigra*) des rives du lac Duparquet, nord-ouest du Québec. Can. J. Bot. **70**: 2294–2302.

Tardif, J., and Bergeron, Y. 1997. Ice-flood history reconstructed with tree-rings from the southern boreal forest limit, western Québec. Holocene, **7**: 291–300.

Tardif, J., Dery, S., and Bergeron, Y. 1994. Sexual regeneration of black ash (*Fraxinus nigra* Marsh.) in a boreal floodplain. Am. Midl. Nat. **132**: 124–135.

Ter Braak, C.J.F. 1987. The analysis of vegetation–environment relationships by canonical correspondence analysis. Vegetatio, **69**: 69–77.

Veillette, J. 1994. Evolution and paleohydrology of glacial lakes Barlow and Ojibway. Q. Sci. Rev. **13**: 945–971.

Vincent, G., Bergeron, Y., and Meilleur, A. 1986. Plant community pattern analysis: a cartographic approach applied in the Lac des Deux-Montagnes area (Québec). Can. J. Bot. **64**: 326–335.

White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. Bot. Rev. **45**: 229–299.

Wilson, S.D., and Keddy, P.A. 1985. Plant zonation on a shoreline gradient: physiological response curves of component species. J. Ecol. **73**: 851–860.

Wilson, S.D., and Keddy, P.A. 1986. Species competitive ability and position along a natural stress/disturbance gradient. Ecology, **67**: 1236–1242.