# Gradient analysis of *Larix laricina* dominated wetlands in Canada's southeastern boreal forest

**Martin-Philippe Girardin, Jacques Tardif, and Yves Bergeron**

**Abstract**: With the objective of understanding how vegetation was structured in four *Larix laricina* (Du Roi) K. Koch dominated wetlands in north-western Quebec, 186 point-centred quarters were sampled in four stands. For each point, both biotic and abiotic variables were collected and species cover was recorded. Divisive hierarchical classification analysis (Twinspan) identified nine vegetation clusters: *i*) *Larix laricina* & *Spiraea alba*, *ii*) *Larix laricina* & *Kalmia angustifolia*, *iii*) *Larix laricina*, *Picea mariana* & *Alnus rugosa*, *iv*) *Larix laricina* & *Betula pumila*, *v*) *Thuja occidentalis* & *Trientalis borealis*, *vi*) *Abies balsamea* & *Betula papyrifera*, *vii*) *Fraxinus nigra* & *Onoclea sensibilis*, *viii*) *Alnus rugosa,* and *ix*) *Eleocharis smallii*. Results of the canonical correspondence analyses indicated that the distribution of these clusters was mainly related to (*i*) distance from shore, (*ii*) shade (canopy cover), (*iii*) substrate nitrate concentration (in relation to the abundance of *Kalmia angustifolia* and *Alnus rugosa*), (*iv*) substrate pH (in relation to the abundance of *Sphagnum* spp.), and (*v*) substrate conductivity. Several characteristics of the water table also affected species distribution, including pH, depth, and carbon concentration. Further studies should address the effect of the presence of *Kalmia angustifolia* and *Alnus rugosa* on larch growth.

*Key words*: larch, wetland, vegetation analysis, flooding, boreal forest.

**Résumé** : Avec pour objectif de comprendre la distribution de la végétation dans quatre tourbières dominées par *Larix laricina* (Du Roi) K. Koch au Nord-Ouest de la forêt boréale québécoise, 186 quadrants centrés sur le point ont été échantillonnés à l'intérieur de quatre sites. Pour chacun des points, des variables abiotiques et biotiques ont été récoltées et le recouvrement en espèces a été noté. L'analyse par classification divisive hierarchique (Twinspan) a désigné neuf groupements végétaux: (*i*) *Larix laricina* & *Spiraea alba*, (*ii*) *Larix laricina* & *Kalmia angustifolia*, (*iii*) *Larix laricina*, *Picea mariana* & *Alnus rugosa*, (*iv*) *Larix laricina* & *Betula pumila*, (*v*) *Thuja occidentalis* & *Trientalis borealis*, (*vi*) *Abies balsamea* & *Betula papyrifera*, (*vii*) *Fraxinus nigra* & *Onoclea sensibilis*, (*viii*) *Alnus rugosa* et (*ix*) *Eleocharis smallii*. Les analyses canoniques des correspondances ont indiqué que la distribution de ces groupements était principalement reliée à (*i*) la distance de la rive, (*ii*) l'interférence lumineuse et certaines caractéristiques du substrat, entre autre (*iii*) la concentration en nitrate du substrat (notamment en relation avec l'abondance de *Kalmia angustifolia* et d'*Alnus rugosa*), (*iv*) le pH (en relation avec l'abondance de *Sphagnum* spp.) et (*v*) la conductivité. Un lien a été démontré entre les caractéristiques de la nappe phréatique et la distribution des espèces, notamment en relation avec le pH, la profondeur et la concentration en carbone. Des études plus approfondies devraient être conduites afin de déterminer l'impact de la présence des espèces *Kalmia angustifolia* et *Alnus rugosa* sur la croissance du mélèze.

*Mots clés* : mélèze, tourbière, analyse de végétation, inondation, forêt boréale.

## Introduction

The study of ecological gradients has been widely used as an approach for defining interactions between plant species and their spatial distribution in relation to physical, chemical, and biological factors. In floodplains and wetlands, most of the partitioning between species (including trees, shrubs, and herbaceous species) is related to soil moisture: the elevation above a water body or the depth of the water table (Keddy 1983; Tardif and Bergeron 1992; Jeglum and He 1995). Thus, emphasis was put on discussing the importance of the period, frequency, and duration of flooding on species establishment, which mainly depends on their tolerance of flooding (Robertson et al. 1978; Keddy 1983; Kenkel 1986; Glaser et al. 1990; Shipley et al. 1991; Tardif and Bergeron 1992; Jean and Bouchard 1993; Jeglum and He 1995).

In wetland environments, the main ecological gradient is not composed of a single factor, but elevation or distance from the shore does, however, account for large-scale variability (Robertson et al. 1978; Vitt and Bayley 1984; Kenkel 1986). Complex gradients combining peat thickness – moisture gradients and pH–calcium gradients were previously found by Jeglum and He (1995). Moreover, herbaceous plants and shrub species are sometimes distributed as a function of fine scale factors (or secondary gradients), which are responsible for more heterogeneous patterns. Microtopographic relief, resulting from the erosion and de-

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position of materials during spring flooding for example, creates a multitude of micro-environmental conditions which lead to a patchy distribution of plant species (Wistendahl 1958; Robertson et al. 1978; Hardin and Wistendahl 1983).

In the definition of wetland community types, a study conducted by Kenkel (1986) in the western Ontario boreal forest stressed the importance of the nutrient gradient and suggested that the distinction between oligotrophic and eutrophic peatland types should be based on nutrient status. However, Jeglum and He (1995) discussed the controversy surrounding the explanation of species distribution in relation to nutrient gradients. Many studies have produced contradictory results relative to the importance of this complex gradient, mostly concerning the relationships between nitrates and cations and species abundance. As an example, in wetlands of the northern Ontario clay belt, Jeglum and He (1995) reported that the pH–calcium gradient and the nitrogen gradient were responsible for the majority of the explained variation in plant distribution. In contrast, Jean and Bouchard (1993) observed little correlation between plant distribution and nutrient variables. Similarly, Glaser et al. (1990) found little correlation between vegetation and the cation gradient.

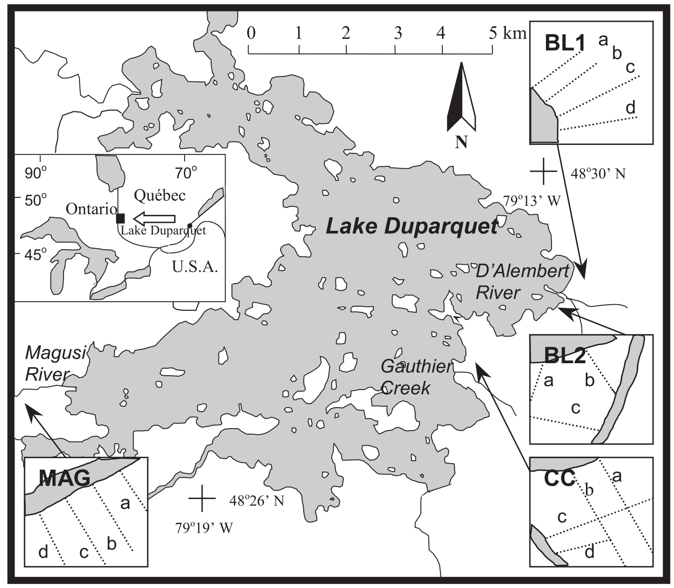
Some authors attribute this lack of consistency to the effect of multiple factors, such as changes in natural disturbance regimes (i.e., fire frequency and climate change; Vitt and Bayley 1984; Kenkel 1986; Glaser et al. 1990; Jean and Bouchard 1993) or anthropogenic disturbances (i.e., water level changes; Jean and Bouchard 1993; Jeglum and He 1995). It seems that the significance of the nutrient gradient may be dependent on the presence or absence of disturbances, which maintain community structure in successional stages and produce changes in abiotic conditions (Vitt and Bayley 1984; Jean and Bouchard 1993). Heinselman (1970) also insisted on the difficulty of predicting the development of wetlands because of their different history, the local topography, the circulation of water, erosion, and global climatic changes.

This study follows an earlier study undertaken by Denneler et al. (1999) at Lake Duparquet in the southwestern boreal forest of Quebec. In their study, Denneler et al. (1999) concluded that physical phenomena related to flooding, notably wave effects, were the main factors contributing to the presence or absence of larch (*Larix laricina* (Du Roi) C. Koch) in the wetlands of Lake Duparquet. However, their study did not include other species or account for biological interactions such as shading or nutrient interference and the influence of distance from the shore on the chemical properties of the substrate and of the water table. The first objective for this study was to define the main plant communities in stands dominated by larch on the shores of Lake Duparquet. The second objective was to determine which ecological factors were associated with species distribution in the wetlands of Lake Duparquet.

### Study area

The study area is located on the shores of Lake Duparquet, 700 km north of Montreal in the Abitibi region, southwestern Quebec (48°28′N, 79°17′W) (Fig. 1). This large lake (50 km$^2$) drains northward through the Duparquet River toward James Bay. The region is part of the Northern

**Fig. 1.** Map of Lake Duparquet showing the location of the four *Larix laricina* stands studied: BL1, BL2, CC, and MAG. Lengths of the longest transects for each stands are respectively 500, 720, 720, and 240 metres.




Clay Belt of Quebec and Ontario, a geomorphological feature resulting from the maximum extension of the postglacial lakes Barlow and Ojibway (Vincent and Hardy 1977). Mean annual temperature is 0.8°C and total annual precipitation varies from 800 to 900 mm (Environment Canada 1993). The mean frost-free period is 64 days, but frost can occur at any time of the year (Environment Canada 1982).

Four larch stands were selected along the shores of Lake Duparquet using aerial photographs (years 1926, 1945, and 1994). These stands were chosen because the water level of the lake has not been purposefully modified in the past and no lethal fires have been reported since the mid-nineteenth century (Bergeron 1991; Bergeron 2000). Also, logging has not occurred inside the study stands or within the wetland watersheds. All stands showed a mixed dominance of larch, black spruce (*Picea mariana* Mill.), and white cedar (*Thuja occidentalis* L.).

## Methods

### Sampling design

In August 1999, for each selected stand (BL1, BL2, CC, MAG; Fig. 1), three to four transects (a, b, c, d) were placed perpendicularly to the water bodies (stream, river, or lake) with a distance of 50–100 m between each. A total of seven transects were put in place perpendicular to the lake (BL1a,b,c,d, BL2a, and CCa,b), and six perpendicular to streams or rivers (BL2c, CCc,d, and MAGa,b,c). One transect (BL2b) was located between Lake Duparquet and the D'Alembert River. From the shoreline to the upper limit of the distribution of larch, sampling points were located at 30–40 m intervals. A total of 186 points were sampled (number of points per stand: BL1=52; BL2=50; CC=60; MAG=24).

For each point, distance from the shore was recorded. The point-centred quarter (PCQ) method was used to determine tree (diameter at breast height (DBH) > 5 cm) species importance values at the sample points (Cottam and Curtis 1956; Lindsey et al. 1958; Warde and Petranka 1981; Barbour et al. 1987). In each of four quadrants DBH, height, and distance of the nearest tree to the point centre were measured. A cut-off point of 15 m from the point centre was established and a missing value was recorded when a tree was not found within this distance.

Regeneration (DBH < 5 cm), shrub, and herbaceous species cover was determined in 1 $m^2$ quadrats located over each of the 186 PCQs. After measurement of the shrub height, percent cover was assigned for each species using coverage classes (0 < 1 < 1%; 1% ≤ 2 < 5%; 5% ≤ 3 < 25%; 25% ≤ 4 < 50%; 50% ≤ 5 < 75%; 75% ≤ 6 < 100%; 7 = 100%; Tardif and Bergeron 1992). For species located outside the 1-$m^2$ quadrats (cut-off point at 2 m from the point centre), a percent cover value of 0.5% was given. Vascular plant nomenclature followed Marie-Victorin (1995). Nonvascular plants were included in the study in two categories: *Sphagnum* spp. and bryophytes (which includes the cover of all mosses other than *Sphagnum* spp.).

At each PCQ the number of dead trees was estimated in a 5 m radius. The cut-off point of 5 m was chosen because in most cases this was a representative sample of the quantity of logs and snags observed in the PCQ vicinity. Afterward, a tree cover class within a 5 m radius was assigned following the Montague and Givnish (1996) criteria: (*i*) dominant: complete penetration of light from the top and partially from the sides; (*ii*) codominant: complete penetration of light from the top and low penetration from the sides; (*iii*) intermediary: partial penetration of light from the top and no penetration from the sides; and, (*iv*) suppressed: no penetration of light.

In each 1-$m^2$ quadrat, substrate was identified as peat, hummock, or clay and logs were noted as present or absent. Wherever peat occurred, its minimal depth (up to 130 cm) was measured using a graduated stick. Also, depth of the water table was measured and corrections were made following daily measurements of the Lake Duparquet water level.

Samples of substrate and soil water from the water table (when present) were taken in each 1-$m^2$ quadrat to determine pH, nitrate and ammonium concentration, and conductivity (Heinselman 1970). Water samples were taken at a depth of 30 cm to avoid the influence of recent rainfalls. Mineral nitrogen ($NH_4^+$ and $NO_3^-$) was extracted from substrate samples (2 g) in 40 mL of KCl solution (Maynard and Kalra 1993). Afterwards, water table and substrate samples were frozen until injection analysis using a Tecator FIAStar 5020 (Foss Danmark, Hillerod, Denmark). For the substrate, the measurement of pH and conductivity was conducted by adding distilled water to the substrate samples in a 4:1 ratio (by volume). A carbon concentration index was also determined for water table samples by measuring the absorbency at 465 nm (Stevenson 1982).

## Data analysis

In this study, both understory and overstory plant species were analysed simultaneously. The following formula was used to calculate tree species importance values in each PCQ. The parameters $d_A$ and $D_A$ respectively stand for diameter and distance to the PCQ (in metres) of trees of species A (for details, see Mueller-Dombois and Ellenberg (1974), and Barbour et al. (1987)):

[1] Importance value of species $A$

$$= (RD_A + RB_A + PI_A) / 3$$

where,

[2] $RD_A$ = Relative density of species A

$$= (\text{No. of trees of species A} / 4) \times 100$$

[3] $RB_A$ = Relative basal area of species A

$$= (\text{basal area of A} / \sum \text{ of all basal areas}) \times 100$$

[4] $$\text{Basal area of species A} = \sum \pi d_A{}^2/4$$

[5] $$PI_A = \text{Proximity index of species A} = [\sum ((15 - D_A)/15) \times 100] / \text{No. of trees of species A}$$

For the understory, each coverage class of shrub and herbaceous species was scaled to 100 using the median of each class.

The environmental matrix contained a total of 21 variables for each of the 186 PCQs: relative distance from the shore (distance scaled to 100), longitude and latitude (degree), minimal peat thickness (m), average shrub and tree height (m), canopy classes (1–4; dominant, codominant, intermediary, and suppressed), average distance between trees and point centre (m), presence/absence of logs on the ground (binary variable), number of dead trees (counts), percent of surface in pools (percent of the substrate surface covered by the water table (Heinselman 1970)), pH (substrate and water table samples), conductivity (μMhos, substrate and water table samples), nitrate and ammonium concentrations ($\mu g \cdot ml^{-1}$, soil and water table samples), carbon concentration index (water table samples only), and water table depth (cm).

The water table level was adjusted so that it was a positive value by adding ten to each measurement (ter Braak and Smilauer 1998). For the analysis of cations, Heinselman (1970) suggested correcting the values for conductivity (which accounts for all ions) to eliminate for the effects of $H^+$ ions. However, because the conductivity values obtained in this study were superior to the critical value of 4.1 suggested by Heinselman (1970), no correction factor was applied. Finally, for the PCQs located on clay and hummocks ($n = 16$), no water table was found within a 30 cm depth, which resulted in missing values for pH, nitrate, ammonium, and conductivity in the environmental matrix. This has important effects in the ordination analyses because the CANOCO program recognises all missing values as zeros (ter Braak and Smilauer 1998). To overcome this problem, missing values were replaced by the mean value of each corresponding variable.

Vegetation groups were determined using the Twinspan method (Hill 1979), where the advantage lies in the use of indicator species. Default parameters were conserved. Gradient lengths were calculated using detrended correspondence analysis (DCA; Legendre and Legendre 1998) and environment–species relationship analysis was done with canonical correspondence analysis (CCA). Both methods have the advantage of preserving the $\chi^2$ distance, which has the property of excluding every pair of zeros in the quantification of the object–descriptors relationship (Legendre and Legendre 1998). Note that the detrended canonical correspondence analysis (DCCA) method was avoided, as suggested by Legendre and Legendre (1998), notably because detrending methods are largely arbitrary when interpreting complex gradients (Wartenberg et al. 1987). A forward selection of environmental variables was done and variables significant at $p < 0.05$ were preserved in the CCA models (999 permutations were generated). The CANOCO software (Version 4.0; ter Braak and Smilauer 1998) was used in all ordination analyses.

In this study, because the environmental variables, understory, and overstory were sampled at different scales, the assessment of associations between trees and environmental variables should be made with caution. The same caution applies when interpreting interspecific associations between the tree species and the understory species. Also, caution should be taken when interpreting relationships between environmental variables and species when only a small number of PCQs are clustered in a common vegetation type.

## Results

### Vegetation analysis

Nine vegetation clusters (or vegetation types) were defined with Twinspan (Fig. 2). Our classification was mainly based on the dominance of pseudospecies in the Twinspan division and on the dominant tree species. Species coverage, importance values, and frequencies are given in Table 1; environmental variables are given in Table 2; average tree species height, density, and importance values are given in Table 3. Tree importance values and densities were calculated following the formula of Barbour et al. (1987) and a correction factor was applied to account for quadrants in which tree species were absent (Warde and Petranka 1981).

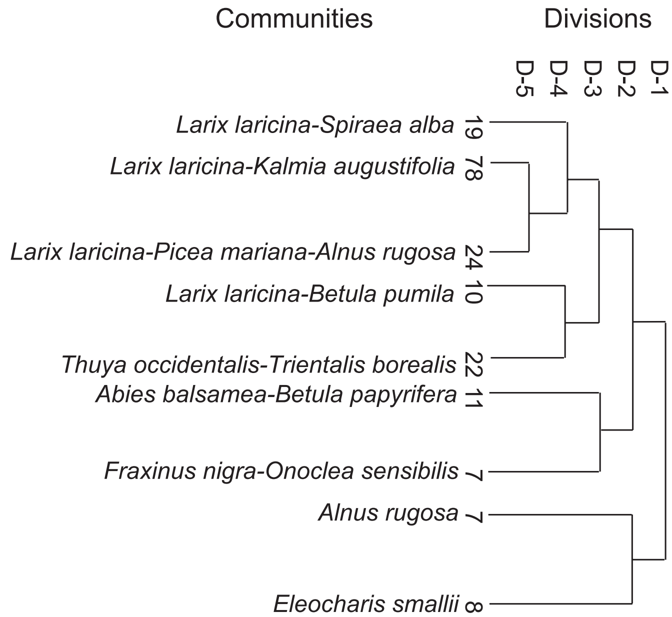
Larch trees dominate four of the nine clusters. The understory of the first cluster (*Larix laricina* & *Spiraea alba*) is mainly composed of *Alnus rugosa*, *Betula pumila*, *Cornus stolonifera*, *Spiraea alba*, and *Cassandra calyculata* (Table 1). Regeneration is mainly composed of balsam fir (*Abies balsamea* Mill.), black spruce, and larch, whereas black spruce and larch dominate the overstory (Tables 1 and 3). A total of 38 understory species are present, compared to 37, 32, and 34, respectively, for the other larch clusters. Peat is the main substrate in this environment. The tree cover class indicates a very open tree crown, with trees smaller on average than those of other vegetation types (Table 2).

In the second larch cluster (*Larix laricina* & *Kalmia angustifolia*), dominant understory species are *Kalmia angustifolia*, *Andromeda glaucophylla*, *Myrica gale*, *Ledum groenlandicum*, *Cassandra calyculata*, and *Smilacina trifolia* (Table 1). In this cluster, *Sphagnum* covers the surface almost entirely. Regeneration is similar to the preceding cluster, although black spruce and larch seedlings are present at higher frequencies. This part of the gradient is mostly dominated by larch; black spruce is found in only five of the 78 PCQs (Tables 1 and 3). Water analysis shows a high carbon concentration, whereas the pH values for the substrate and the water table are at their lowest (Table 2). The tree crown is slightly more suppressed than in the preceding cluster and the PCQs are generally distributed further away from the shore.

The third cluster (*Larix laricina*, *Picea mariana* & *Alnus rugosa*) is mainly characterized by an increase in the abundance of *Picea mariana* (both in the understory and the overstory; Table 1). Although larch density is less than half of the value found in the preceding cluster (Table 3), the average importance value is almost similar due to an increase in tree basal area. Also, the tallest larch trees are present in this cluster, averaging 10.4 m tall (Table 3). In the understory, dominant species are *Alnus rugosa*, *Ledum groenlandicum*, *Myrica gale*, and *Betula pumila*, and *Sphagnum* abundance is relatively low. A deep water table, high pH, and high carbon and ammonium concentrations in water table samples are associated with this cluster (Table 2). The shrub cover is relatively high in this vegetation type.

The understory of the fourth larch cluster (*Larix laricina* & *Betula pumila*) is mostly dominated by *Prunus virginiana*, *Alnus rugosa*, *Calamagrostis canadensis*, *Cassandra calyculata*, *Cornus stolonifera*, *Equisetum* spp., *Trientalis borealis*, and *Smilacina trifolia* (Table 1). *Sphagnum* covers the ground surface entirely and larch dominates the overstory (low cover but very tall trees; Table 3). White cedar is abundant, consisting of relatively short trees (1.9 m average), not in a dominant position (Table 3). No clear environmental variables strongly characterize this cluster (Table 2).

**Fig. 2.** Vegetation clusters retained after the Twinspan divisive hierarchical classification analysis.




White cedar completely dominates the fifth cluster, *Thuja occidentalis* & *Trientalis borealis*, although black spruce and larch are present in moderate numbers (Tables 1 and 3). Regeneration is equally divided between white cedar, black spruce, and larch and the understory is largely composed of *Alnus rugosa*, *Ledum groenlandicum*, *Carex trisperma*, and *Carex* spp. In this cluster, a total of 34 understory species are present. The tree cover class is near the intermediary class, indicating a higher level of suppression of light from the tree crown (Table 2). Analysis of the water table shows high pH and area occupied by pools, and low nitrate and ammonium concentrations (Table 2). As for the substrate, it has high nitrate and ammonium concentrations. This vegetation type occurs in the part of the distance gradient most elevated and away from shore (Table 2)

*Abies balsamea* is dominant in the sixth cluster (*Abies balsamea* & *Betula papyrifera*) with *Betula papyrifera* and is at a distance from the shore equivalent to the fourth cluster type (Table 2). Although white cedar and black spruce are found occasionally, larch is almost never present, and its seedlings are never present (Table 1). A few very tall white cedars are present (Table 3). The understory is dominated by *Sphagnum*, *Maianthemum canadense*, and *Alnus rugosa* and 34 other understory species are present (Table 1). In this environment, a decrease in peat thickness and a high water table (indicating high moisture conditions) are observed (Table 2). As indicated by the high tree cover class, a small amount of light penetrates the tree crown to reach the understory. Analyses also show that the water table has high cation and dissolved carbon concentrations. As for the substrate, high conductivity and high nitrate ammonium concentrations are observed.

*Fraxinus nigra*, *Thalictrum pubescens*, *Cornus stolonifera*, and *Rubus pubescens* mainly dominate the seventh cluster

**Table 1.** Understory and overstory species relative frequency (F) and cover (C) in each of the vegetation clusters.

| | Vegetation clusters (No. of samples) | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 ($n$ = 19) | | 2 ($n$ = 78) | | 3 ($n$ = 24) | | 4 ($n$ = 10) | | 5 ($n$ = 22) | | 6 ($n$ = 11) | | 7 ($n$ = 7) | | 8 ($n$ = 7) | | 9 ($N$ = 8) | |
| | F% | C% | F% | C% | F% | C% | F% | C% | F% | C% | F% | C% | F% | C% | F% | C% | F% | C% |
| **Herbs and Shrubs** | | | | | | | | | | | | | | | | | | |
| *Thalictrum pubescens* | — | — | — | — | — | — | — | — | 5 | 2 | 18 | 2 | 86 | 26 | 14 | 15 | — | — |
| *Lycopus uniflorus* | — | — | — | — | — | — | — | — | — | — | 27 | 2 | 86 | 8 | 14 | 15 | 25 | 15 |
| *Glyceria canadensis* | — | — | 6 | 4 | — | — | 20 | 1 | — | — | 9 | 16 | — | — | 29 | 8 | — | — |
| *Carex oligosperma* | — | — | 4 | 6 | — | — | — | — | — | — | — | — | 14 | 15 | — | — | 13 | 1 |
| *Lysimachia terrestris* | — | — | — | — | — | — | 10 | 1 | — | — | 9 | 2 | 14 | 15 | — | — | 63 | 12 |
| *Calamagrostis canadensis* | 42 | 10 | 10 | 10 | — | — | 40 | 6 | 50 | 3 | 55 | 17 | 57 | 14 | 86 | 34 | 63 | 29 |
| *Salix discolor* | 5 | 15 | 1 | 1 | — | — | — | — | 5 | 6 | — | — | — | — | — | — | 63 | 40 |
| *Spiraea alba* | 63 | 11 | — | — | 4 | 15 | 10 | 3 | — | — | 9 | 4 | 57 | 11 | 86 | 19 | 63 | 10 |
| *Sium suave* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 75 | 2 |
| *Juncus pelocarpus* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 63 | 11 |
| *Eleocharis smallii* | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | — | 100 | 17 |
| *Prunus virginiana* | 32 | 15 | 9 | 6 | 8 | 2 | 30 | 23 | 9 | 9 | 36 | 11 | 14 | 1 | 29 | 32 | — | — |
| *Glyceria borealis* | 16 | 18 | 1 | 1 | 4 | 15 | — | — | — | — | 18 | 10 | — | — | 14 | 3 | — | — |
| *Cornus stolonifera* | 68 | 21 | 1 | 1 | 8 | 1 | 80 | 31 | 41 | 3 | 82 | 13 | 86 | 26 | 57 | 14 | — | — |
| *Carex lacustris* | 37 | 21 | 3 | 8 | 8 | 20 | 20 | 19 | — | — | 27 | 47 | — | — | 14 | 3 | 25 | 15 |
| *Viburnum lentago* | 21 | 4 | — | — | — | — | 10 | 15 | — | — | — | — | — | — | 29 | 8 | — | — |
| *Potentilla palustris* | 37 | 7 | 1 | 15 | 13 | 6 | 80 | 6 | 9 | 2 | — | — | — | — | 14 | 15 | 50 | 5 |
| *Rubus pubescens* | 47 | 11 | — | — | 25 | 8 | 100 | 13 | 64 | 11 | 82 | 42 | 71 | 24 | 29 | 9 | — | — |
| *Iris versicolor* | 11 | 1 | 5 | 1 | — | — | 50 | 1 | 18 | 9 | 9 | 2 | 29 | 1 | — | — | 25 | 9 |
| *Smilacina trifolia* | 68 | 8 | 83 | 18 | 58 | 6 | 100 | 9 | 82 | 9 | 55 | 14 | 29 | 9 | 57 | 21 | — | — |
| *Myrica gale* | 47 | 30 | 99 | 26 | 79 | 21 | 30 | 5 | 73 | 9 | 55 | 4 | — | — | 100 | 49 | 88 | 47 |
| *Carex* sp. | 68 | 14 | 95 | 14 | 92 | 21 | 90 | 12 | 95 | 29 | 73 | 14 | 71 | 12 | 43 | 10 | 13 | 15 |
| *Alnus rugosa* | 100 | 19 | 83 | 12 | 100 | 30 | 100 | 21 | 100 | 22 | 91 | 38 | 71 | 18 | 71 | 20 | — | — |
| *Cassandra calyculata* | 89 | 46 | 90 | 25 | 96 | 27 | 100 | 27 | 82 | 24 | 45 | 2 | — | — | 29 | 26 | — | — |
| *Carex trisperma* | 11 | 15 | 59 | 15 | 33 | 14 | 10 | 15 | 55 | 18 | 27 | 12 | — | — | 14 | 15 | — | — |
| *Betula pumila* | 100 | 15 | 96 | 16 | 88 | 21 | 90 | 23 | 18 | 5 | 27 | 14 | — | — | 29 | 19 | — | — |
| *Lonicera villosa* | 42 | 8 | 13 | 16 | 13 | 3 | 60 | 10 | 32 | 7 | 27 | 22 | — | — | — | — | — | — |
| *Ledum groenlandicum* | 47 | 18 | 83 | 22 | 92 | 48 | 100 | 27 | 100 | 20 | 64 | 8 | 14 | 15 | — | — | — | — |
| *Vaccinium oxycoccos* | 5 | 15 | 56 | 11 | 63 | 33 | 60 | 12 | 14 | 3 | — | — | — | — | — | — | — | — |
| *Kalmia augustifolia* | 5 | 3 | 78 | 17 | 13 | 10 | 30 | 1 | 23 | 11 | 27 | 28 | — | — | — | — | — | — |
| *Carex canescens* | 32 | 13 | 9 | 9 | 4 | 15 | 20 | 9 | — | — | 9 | 16 | — | — | — | — | — | — |
| *Andromeda glaucophylla* | 63 | 14 | 92 | 19 | 79 | 17 | 70 | 14 | 32 | 8 | — | — | — | — | — | — | — | — |
| *Amelanchier* sp. | 26 | 8 | 5 | 8 | 4 | 3 | 20 | 8 | — | — | — | — | — | — | — | — | — | — |
| *Vaccinium myrtilloides* | — | — | 18 | 8 | — | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *Salix pedicellaris* | 58 | 13 | 31 | 6 | 42 | 9 | 20 | 15 | — | — | — | — | — | — | — | — | — | — |
| *Salix bebbiana* | 5 | 38 | 23 | 12 | 4 | 1 | — | — | 5 | 2 | — | — | — | — | — | — | — | — |
| *Kalmia polifolia* | 11 | 9 | 18 | 10 | 8 | 2 | — | — | — | — | — | — | — | — | — | — | — | — |
| *Carex tenuiflora* | — | — | 5 | 15 | 4 | 3 | — | — | — | — | — | — | — | — | — | — | — | — |
| *Sphagnum* sp. | 84 | 12 | 97 | 40 | 75 | 12 | 100 | 44 | 86 | 28 | 73 | 44 | 29 | 26 | — | — | — | — |

| | | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Carex paupercula* | 21 | 5 | 13 | 4 | — | — | 20 | 15 | 5 | 2 | 18 | 10 | — | — | — | — | — | — |
| *Carex disperma* | — | — | 6 | 7 | 29 | 32 | — | — | 23 | 16 | 18 | 16 | — | — | — | — | — | — |
| *Viola pallens* | 11 | 9 | — | — | — | — | — | — | 5 | 4 | 55 | 11 | 57 | 18 | — | — | — | — |
| *Trientalis borealis* | 11 | 9 | — | — | — | — | 40 | 2 | 59 | 5 | 45 | 5 | 29 | 2 | — | — | — | — |
| *Onoclea sensibilis* | — | — | — | — | — | — | — | — | — | — | — | — | 86 | 19 | — | — | — | — |
| *Nemopanthus mucronatus* | 16 | 30 | 1 | 1 | — | — | 50 | 14 | 5 | 2 | 9 | 2 | 29 | 8 | — | — | — | — |
| *Maianthemum canadense* | 5 | 3 | — | — | 29 | 10 | 40 | 15 | 50 | 6 | 82 | 21 | 43 | 10 | — | — | — | — |
| *Galium labradoricum* | 11 | 2 | — | — | — | — | 40 | 2 | 5 | 2 | 18 | 2 | 14 | 1 | — | — | — | — |
| *Equisetum* sp. | 32 | 11 | 18 | 2 | 21 | 16 | 90 | 12 | 68 | 8 | 73 | 6 | 71 | 7 | — | — | — | — |
| *Cystopteris fragilis* | 11 | 20 | 1 | 3 | — | — | — | — | 5 | 2 | 45 | 8 | 14 | 1 | — | — | — | — |
| *Cornus canadensis* | — | — | — | — | 4 | 3 | — | — | 45 | 3 | 36 | 24 | 14 | 1 | — | — | — | — |
| *Carex intumescens* | — | — | — | — | — | — | — | — | — | — | 55 | 7 | 29 | 8 | — | — | — | — |
| Grass sp. | — | — | 1 | 15 | 13 | 23 | — | — | 5 | 38 | 18 | 8 | — | — | — | — | — | — |
| Bryophytes | 89 | 5 | 73 | 7 | 75 | 1 | 90 | 10 | 82 | 8 | 100 | 14 | 71 | 12 | — | — | — | — |
| **Trees and regeneration** | | | | | | | | | | | | | | | | | | |
| *Abies balsamea** | 5 | 25 | 5 | 44 | 8 | 38 | — | — | 59 | 32 | 82 | 45 | 43 | 42 | — | — | — | — |
| *Betula papyrifera** | — | — | 1 | 1 | 4 | 1 | 10 | 1 | 14 | 2 | 82 | 2 | 29 | 1 | — | — | — | — |
| *Fraxinus nigra** | — | — | — | — | — | — | 10 | 1 | 9 | 2 | 9 | 2 | 86 | 16 | — | — | — | — |
| *Larix laricina** | 37 | 46 | 63 | 38 | 67 | 30 | 50 | 50 | 77 | 41 | — | — | 29 | 38 | 14 | 50 | | |
| *Picea mariana** | 11 | 33 | 29 | 36 | 79 | 37 | 70 | 33 | 82 | 45 | 18 | 34 | 14 | 33 | — | — | — | — |
| *Thuja occidentalis** | — | — | — | — | — | — | 70 | 20 | 73 | 45 | — | — | 14 | 20 | — | — | — | — |
| *Larix laricina*** | 63 | 29 | 99 | 79 | 96 | 66 | 90 | 49 | 64 | 25 | 9 | 6 | — | — | — | — | — | — |
| *Thuja occidentalis*** | — | — | — | — | — | — | 70 | 20 | 86 | 49 | 9 | 7 | 29 | 13 | — | — | — | — |
| *Picea mariana*** | 11 | 3 | 6 | 2 | 46 | 17 | 50 | 19 | 27 | 10 | 9 | 10 | — | — | — | — | — | — |
| *Abies balsamea*** | — | — | — | — | — | — | — | — | 5 | 1 | 73 | 45 | 29 | 17 | — | — | — | — |
| *Betula papyrifera*** | — | — | 3 | 16 | — | — | — | — | 9 | 2 | 55 | 21 | — | — | — | — | — | — |
| *Fraxinus nigra*** | — | — | — | — | — | — | — | — | 5 | 1 | 9 | 4 | 86 | 57 | — | — | — | — |

**Note:** F%, species frequencies; C%, covers (shrub and herb species) and importances values (tree species). 1, *Larix laricina* & *Spiraea alba*; 2, *Larix laricina* & *Kalmia augustifolia*; 3, *Larix laricina*, *Picea mariana* & *Alnus rugosa*; 4, *Larix laricina* & *Betula pumila*; 5, *Thuja occidentalis* & *Trientalis borealis*; 6, *Abies balsamea* & *Betula papyrifera*; 7, *Fraxinus nigra* & *Onoclea sensibilis*; 8, *Alnus rugosa*; 9, *Eleocharis Smalii*. *, regeneration. **, trees.

**Table 2.** Average and standard deviation of variables recorded in each vegetation cluster.

| | Vegetation clusters (No. of samples) | | | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 1 (*n* = 19) | | 2 (*n* = 78) | | 3 (*n* = 24) | | 4 (*n* = 10) | | 5 (*n* = 22) | | 6 (*n* = 11) | | 7 (*n* = 7) | | 8 (*n* = 7) | | 9 (*n* = 8) | |
| | AV | SD | AV | SD | AV | SD | AV | SD | AV | SD | AV | SD | AV | SD | AV | SD | AV | SD |
| Average distance among trees | 1.7 | 1.5 | 1.4 | 0.9 | 1.4 | 0.9 | 1.2 | 0.9 | 1.0 | 0.9 | 0.5 | 0.7 | 0.8 | 0.4 | — | — | — | — |
| Average tree height (TreeH) | 6.4 | 4.9 | 9.5 | 2.8 | 9.7 | 3.7 | 8.6 | 2.4 | 8 | 3.2 | 8.6 | 4.4 | 9.3 | 1.8 | — | — | — | — |
| Carbon index (Carbon) | 0.06 | 0.02 | 0.11 | 0.03 | 0.07 | 0.02 | 0.04 | 0.01 | 0.06 | 0.03 | 0.10 | 0.06 | 0.08 | 0.02 | 0.07 | 0.02 | — | — |
| Tree cover class (Cover) | 1.1 | 0.3 | 1.6 | 0.6 | 1.8 | 0.5 | 1.6 | 0.5 | 2.8 | 1.0 | 3.5 | 1.1 | 2.9 | 1.1 | 1 | 0.0 | 1 | 0.0 |
| No. dead trees (DT) | 3.4 | 3.3 | 3.7 | 2.8 | 4.6 | 3.0 | 5.5 | 3.5 | 5 | 2.6 | 8.6 | 9.4 | 4.6 | 2.8 | 0.6 | 1.5 | 0 | 0.0 |
| Peat depth (PeatD) | 1.0 | 0.3 | 1.0 | 0.3 | 0.9 | 0.2 | 1.0 | 0.4 | 1.0 | 0.2 | 0.7 | 0.4 | 0.2 | 0.3 | 0.6 | 0.2 | 0.0 | 0.1 |
| Relative distance (Dist) | 32.9 | 20.6 | 50.9 | 24.0 | 51.8 | 20.6 | 61.1 | 31.4 | 81.7 | 18.1 | 65.6 | 44.6 | 2.4 | 5.8 | 8.8 | 2.6 | 0.0 | 0.0 |
| Shrub height (Shrub) | 1.5 | 0.3 | 1.3 | 0.4 | 1.6 | 0.3 | 1.7 | 0.3 | 1.3 | 0.5 | 1.7 | 0.7 | 1.8 | 1.0 | 1.4 | 0.3 | 1.2 | 0.1 |
| Soil conductivity (Soilcon) | 124.9 | 42.2 | 111.0 | 36.6 | 121.5 | 37.6 | 120.9 | 25.8 | 148.5 | 44.9 | 162.7 | 57.0 | 129.0 | 44.2 | 125.7 | 34.2 | 137.7 | 49.5 |
| Soil $NH_4$ (SoilNH4) | 15.40 | 9.14 | 14.03 | 6.60 | 26.38 | 10.18 | 14.76 | 12.86 | 20.34 | 5.03 | 21.65 | 15.21 | 16.03 | 14.67 | 24.86 | 7.90 | 10.71 | 8.79 |
| Soil pH (SoilpH) | 5.65 | 0.52 | 4.90 | 0.37 | 5.55 | 0.41 | 5.82 | 0.43 | 5.94 | 0.55 | 5.67 | 0.59 | 5.75 | 0.47 | 5.33 | 0.37 | 6.11 | 0.56 |
| Soli $NO_3$ (SoilNO3) | 0.03 | 0.05 | 0.02 | 0.02 | 0.03 | 0.02 | 0.02 | 0.01 | 0.05 | 0.06 | 0.05 | 0.05 | 0.03 | 0.02 | 0.09 | 0.08 | 0.18 | 0.42 |
| Percent in pools (Pools) | 2.0 | 2.5 | 1.6 | 2.8 | 5.5 | 6.0 | 8.0 | 5.1 | 16.6 | 9.8 | 13.8 | 18.9 | 4.6 | 8.7 | 0.4 | 1.0 | 0.0 | 0.0 |
| Water table depth (Watlev) | 20.1 | 8.9 | 23.8 | 9.8 | 25.0 | 10.6 | 16.5 | 4.3 | 24.4 | 10.4 | 14.6 | 9.0 | 9.8 | 8.6 | 26.1 | 12.8 | — | — |
| Water conductivity | 64.4 | 11.9 | 65.3 | 8.8 | 68.4 | 10.9 | 66.7 | 23.8 | 74.2 | 15.8 | 74.9 | 25.7 | 67.3 | 1.1 | 71.7 | 14.1 | — | — |
| Water $NH_4$ | 0.08 | 0.02 | 0.09 | 0.03 | 0.08 | 0.02 | 0.07 | 0.02 | 0.06 | 0.02 | 0.07 | 0.01 | 0.08 | 0.01 | 0.08 | 0.01 | — | — |
| Water $NO_3$ | 0.48 | 0.35 | 0.46 | 0.35 | 0.73 | 0.37 | 0.30 | 0.26 | 0.37 | 0.23 | 0.58 | 0.43 | 0.45 | 0.13 | 0.75 | 0.57 | — | — |
| Water pH (WatpH) | 6.88 | 0.36 | 6.09 | 0.51 | 6.61 | 0.29 | 7.12 | 0.36 | 6.82 | 0.57 | 6.67 | 0.29 | 6.63 | 0.37 | 6.66 | 0.25 | — | — |

**Note:** AV, average value; SD, standard deviation. For cluster number definitions see Table 1. Abbreviations apply to Figs. 4–6. For the units associated with the variables see text section Data analysis in Methods.

**Table 3.** Height, density, and cover of the tree species (DBH > 5 cm).

| | Vegetation clusters | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 |
| **Average height (m)** | | | | | | | | |
| *Abies balsamea* | — | — | — | — | 6.3 | 10.1 | 10.2 | — |
| *Betula papyrifera* | — | 4.8 | — | — | 6.5 | 9.6 | — | — |
| *Fraxinus nigra* | — | — | — | — | 6.9 | 5.4 | 7.3 | — |
| *Larix laricina* | 6.3 | 9.6 | 10.4 | 10.4 | 7.1 | 2.7 | — | 8.4 |
| *Picea mariana* | 0.7 | 0.7 | 1.8 | 0.9 | 4.1 | 15.4 | 4 | — |
| *Thuja occidentalis* | — | — | — | 1.9 | 4 | 10.1 | 1.4 | — |
| **Density (ha)** | | | | | | | | |
| *Abies balsamea* | — | — | — | — | 7.9 | 223.3 | 89.1 | — |
| *Betula papyrifera* | — | 2 | — | — | 15.7 | 105.8 | — | — |
| *Fraxinus nigra* | — | — | — | — | 7.9 | 11.8 | 445.3 | — |
| *Larix laricina* | 27.2 | 258.7 | 207.5 | 98.3 | 196.6 | 11.8 | — | 1 |
| *Picea mariana* | 4.7 | 6.8 | 43.2 | 43 | 55 | 35.3 | — | — |
| *Thuja occidentalis* | — | — | — | 79.9 | 353.8 | 11.8 | 89.1 | — |
| **Cover ($m^2$/ha)** | | | | | | | | |
| *Abies balsamea* | — | — | — | — | 0.04 | 3.32 | 3.15 | — |
| *Betula papyrifera* | — | 0.01 | — | — | 0.04 | 1.35 | — | — |
| *Fraxinus nigra* | — | — | — | — | 0.05 | 0.03 | 11.93 | — |
| *Larix laricina* | 0.63 | 4.54 | 4.32 | 2.78 | 3.96 | 0.41 | — | 0.06 |
| *Picea mariana* | 0.02 | 0.09 | 0.25 | 0.75 | 0.77 | 2.24 | — | — |
| *Thuja occidentalis* | — | — | — | 5.28 | 9.61 | 3.17 | 6.32 | — |

**Note:** Variables not assessed for species in cluster 9.

(*Fraxinus nigra* & *Onoclea sensibilis*) (Table 1). The tree canopy closure is similar to that observed in the fifth cluster, but most of the PCQs for this vegetation type are located close to open water. Species such as *Viola pallens* and *Onoclea sensibilis* are also common in this cluster, composed of a total of 26 understory species. *Thuja occidentalis* and *Abies balsamea* also occur. Peat is generally absent in this vegetation type (Table 2), although some PCQs occur on the borders of wetlands where the peat does not exceed 40 cm in thickness. In such places, the substrate surface is almost entirely covered by the water table (large percent area consisting of pools).

Two clusters have no tree species and both are located beside water bodies. *Cornus stolonifera*, *Alnus rugosa*, *Calamagrostis pubescens*, *Myrica gale*, and *Smilacina trifolia* dominate the eighth cluster (*Alnus rugosa*) (Table 1). A few larch seedlings are present. In this environment, the water table is deep and rich in cations, nitrate, and carbon (Table 2). Peat thickness ranges from 10 to 90 cm. As for the ninth cluster, *Eleocharis smallii*, it is dominated by *Salix discolor*, *Lysimachia terrestris*, *Calamagrostis canadense*, *Spiraea alba*, *Myrica gale*, *Sium suave*, *Eleocharis smallii*, and *Juncus pelocarpus* (Table 1). Fine mineral sediment is the common substrate of this cluster, with the exception of a few PCQs located on peat (less than 2-cm thick). The substrate of this vegetative type is rich in nitrate and pH values are very high (Table 2).

## Spatial distribution

The spatial location of the vegetation clusters determined using the 186 point GPS data and the aerial photographs are represented in Fig. 3. It illustrates the confinement of *Eleocharis smallii* and *Fraxinus nigra* & *Onoclea sensibilis* clusters near the shore (relative distance close to 0%) and the *Thuja occidentalis* & *Trientalis borealis* and *Abies balsamea* & *Betula papyrifera* clusters at the upper limit (relative distance near 100%). Larch clusters are mainly distributed in specific stands. The *Larix laricina* & *Kalmia angustifolia* and *Larix laricina*, *Picea mariana* & *Alnus rugosa* clusters are not found in the Magusi River stand, whereas the *Larix laricina* & *Betula pumila* cluster is not found in the Lake Duparquet stands. As for the *Alnus rugosa* cluster, it is only found adjacent to the lakeshore.

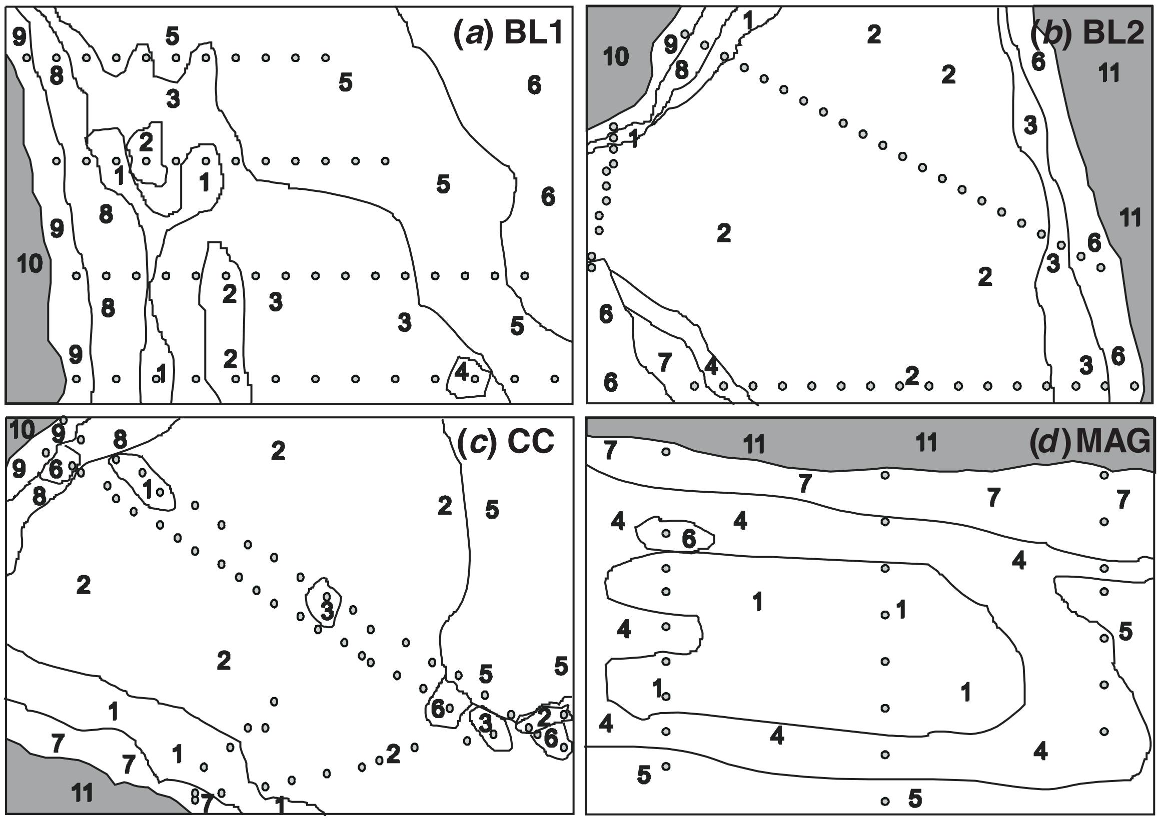
## Detrended correspondence analysis

The detrended correspondence analysis results indicate that the lengths of the first and second gradients are 4.451 and 3.989, respectively. Thus, the vegetation data set responded to the requirements formulated by Borcard et al. (1992) and Legendre and Legendre (1998); for instance, the necessity to have gradients longer than four (SD > 4) and a unimodal distribution of species for a proper application of canonical correspondence analysis.

## Canonical correspondence analyses

Canonical correspondence analysis for the entire vegetation data set indicates that the first axis of the species ordination is significantly correlated with the first environmental axis ($p < 0.01$). Eigenvalues and species–environment correlation coefficients for the first and second axes are respectively $E_1 = 0.369$, $E_2 = 0.284$, $r_1 = 0.815$, and $r_2 = 0.815$ (significance of all canonical axes at $p < 0.001$). The significant variables retained at $p < 0.05$ are illustrated in Fig. 4. Only the highest correlations are discussed in the text. The first axis is mainly related to the *Fraxinus nigra* & *Onoclea sensibilis* cluster in relation to soil pH and nitrate concentra-

**Fig. 3.** Spatial location of the nine vegetation clusters and the 186 PCQs in the studied stands: (*a*) BL1; (*b*) BL2; (*c*) CC; and, (*d*) MAG. The contours were hand drawn from GPS data, field notes, and aerial photographs. 1, *Larix laricina* & *Spiraea alba*; 2, *Larix laricina* & *Kalmia angustifolia*; 3, *Larix laricina*, *Picea mariana* & *Alnus rugosa*; 4, *Larix laricina* & *Betula pumila*; 5, *Thuja occidentalis* & *Trientalis borealis*; 6, *Abies balsamea* & *Betula papyrifera*; 7, *Fraxinus nigra* & *Onoclea sensibilis*; 8, *Alnus rugosa*; 9, *Eleocharis smallii*; 10, Lake Duparquet; and, 11, rivers.




tion (positive relationships between these variables and this cluster), and with peat thickness (negative relationship). We also found that the *Abies balsamea* & *Betula papyrifera* cluster is largely influenced by the second axis in relation to the opening of the tree crown (cover class), percent area of pools, and tree mortality (positive relationship). However, a negative relationship is found between this cluster and the carbon index. The second axis is also related to the *Eleocharis smallii* cluster because of the following variables: soil nitrate concentration (positive relationship), average tree height, relative distance from shore, and peat thickness (all negative relationships).

To concentrate the CCA analysis on clusters dominated by larch, the three outlier clusters (*Fraxinus nigra*, *Eleocharis smallii*, and *Abies balsamea* & *Betula papyrifera)* were eliminated from the data matrix (a total of 26 PCQs), as suggested by Peet (1980). This ordination produced a projection of the *Larix laricina* & *Betula pumila* cluster on the first axis in relation to soil pH, soil conductivity, soil nitrate concentration, percent area of pools (positive relationships), and the water carbon index (negative relationship) (Fig. 5). The cluster *Thuja occidentalis* & *Trientalis borealis* is also highly associated with the first axis by the percent area of pools and the tree cover class (positive relationships). The distribution of *Larix laricina* & *Spiraea alba* and *Alnus rugosa* clusters along the second axis is related to shrub height (positive relationship), tree height, and the distance from the shore (negative relationships). Eigenvalues and species–environment correlation coefficients for the first and second axes are respectively $E_1$ = 0.252, $E_2$ = 0.177, $r_1$ = 0.900, and $r_2$ = 0.806 (significance of all canonical axes at $p < 0.001$).

A third CCA was conducted using only the tree, sapling, and seedling data (Fig. 6). Only the PCQs containing at least one tree species were used in this analysis (total of 162 PCQs). Eigenvalues and species–environment correlation coefficients for the first and second axes are respectively $E_1$ = 0.458, $E_2$ = 0.282, $r_1$ = 0.819, and $r_2$ = 0.806 (significance of all canonical axes at $p < 0.001$). Significant relationships are present between *Picea mariana* and *Larix laricina* and the water table depth and the peat thickness (all positive relationships). *Abies balsamea*, *Betula papyrifera*, and *Fraxinus nigra* are all negatively associated to these variables, but they are positively associated to a high number of dead trees and the tree cover class. Relationships also exist between *Thuja occidentalis* and the distance from the shore, percent area of pools, substrate and water pH (all positive relationships), and average tree height (negative relationship). Finally, larch and black spruce regeneration occurs mainly where a deep water table is found.

## Discussion

The wetlands studied around Lake Duparquet are similar to the minerotrophic swamp forest and poor minerotrophic

**Fig. 4.** Results of the canonical correspondence analysis (CCA) conducted on all PCQs sampled around Lake Duparquet. (*a*) The bi-plots yield approximates the correlation coefficient between descriptors and environmental factors and also among descriptors and environmental factors themselves. Variables with arrows at sharp angles are positively correlated, and the length of an arrow represents the size of the coefficient. By contrast, obtuse angles between variables indicates negative correlation. See Table 2 for definitions of abbreviations. (*b*) The position along the first two axes of the CCA of all 186 PCQs and the nine vegetation clusters.

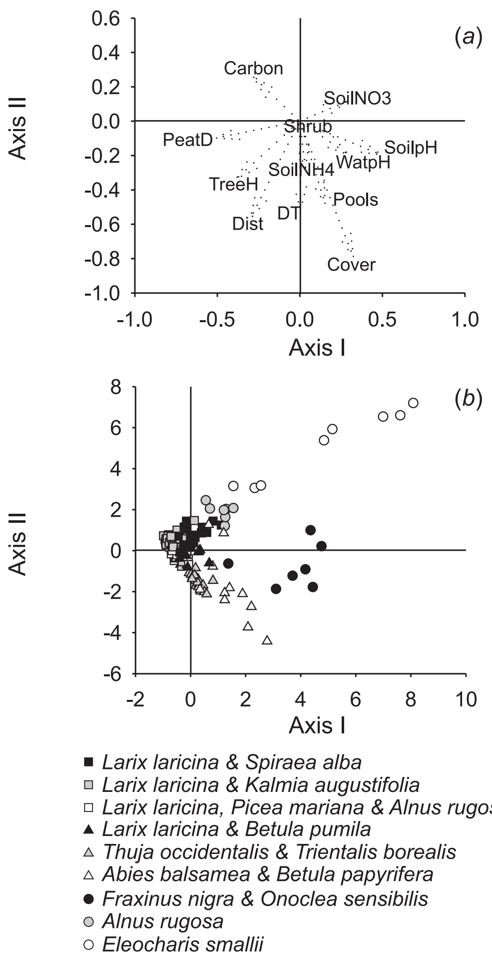
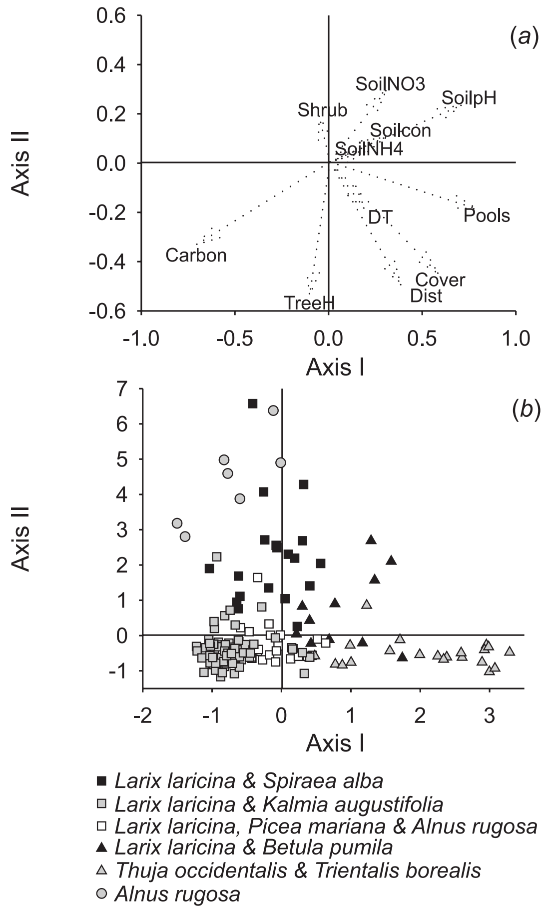



**Fig. 5.** Results of the canonical correspondence analysis (CCA) after the elimination of the outlier vegetation clusters. See Table 2 for definitions of abbreviations.



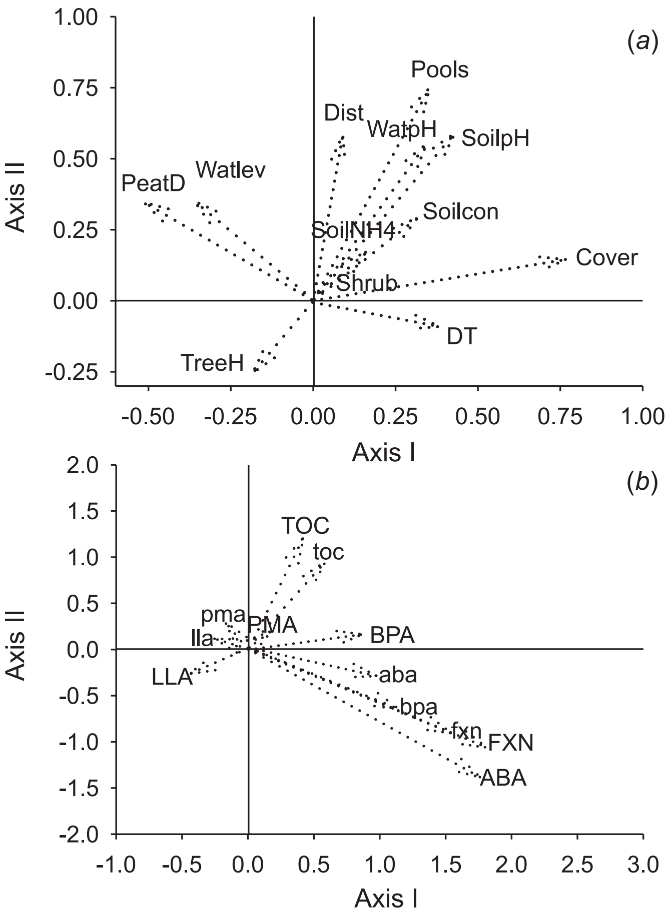

swamp forest described by Heinselman (1970) and by Vitt and Bayley (1984), notably because of the concave topography and the observed species. In explaining vegetation distribution, our results tend to support the existence of a complex gradient formed by nitrate, pH, conductivity (measure of the content in cations), and peat thickness. This gradient is formed mostly by the substrate variables, whereas the water table variables account for only a fraction of the explained variability. The opening of the tree crown (tree cover class) and the distance from the shore are also important parameters in explaining species distribution.

**Understory species**

Nutrient conditions, as indicated by nitrate concentration and pH, are strongly associated with understory species distribution. Among the clusters significantly related with the nitrate concentration is the *Alnus rugosa* cluster, found only a few metres from the lakeshore. This cluster is positively correlated with high concentrations of $NH_4$ and $NO_3$. *Alnus rugosa*, which is able to fix atmospheric nitrogen via its root nodules, may have contributed to the enrichment of the substrate following decomposition of its leaves (Daly 1966; Bares and Wali 1979; Ringius and Sims 1997; Schwintzer and Tjepkema 1997). The same observation can be extended to the cluster *Larix laricina*, *Picea mariana* & *Alnus rugosa*, where *A. rugosa* is also abundant. Vitt and Bayley (1984) also observed a relationship between the wetland nutrient status and the presence of this shrub.

In contrast with the *Alnus rugosa* – nitrate concentration relationship, a negative relationship occurs between the nitrate concentration and the increasing abundance of *Kalmia angustifolia*. However, it is not clear if *Kalmia* abundance is related to the lack of soil nitrate and if it has an effect on the growth of other species. Inderjit and Mallik (1999) have suggested that *Kalmia* could dominate microsites that were nutrient poor prior to its colonization. However, *Kalmia* leaf litter decreases the substrate nitrate concentration by its mobilization into *Kalmia* litter, either by a chelate process or by leachate (Facelli and Pickett 1991; Inderjit and Mallik 1996). As for the effects of *Kalmia* on the growth of other species, interference with larch growth may be possible, as was previously found for black spruce seedlings (Inderjit and Mallik 1996; Inderjit and Mallik 1999; Zhu and Mallik

**Fig. 6.** Results of the canonical correspondence analysis (CCA) conducted on the six tree species. LLA, *larix laricina*; PMA, *Picea mariana*; TOC, *Thuja occidentalis*; BPA, *Betula papyrifera*; FXN, *Fraxinus nigra*; and, ABA, *Abies balsamea*. Capital letters refer to trees, lower case letters to seedlings and saplings. See Table 2 for definitions of abbrevations.




1994). Zhu and Mallik (1994) have shown that *Kalmia* has an allelopathic effect on the primary roots of black spruce, which results in deficient regeneration.

The substrate pH is among the strongest gradients in this study, and we suspect *Sphagnum* spp. of partially influencing its values. The relationships between pH and *Sphagnum* spp. has been briefly discussed by Vitt and Bayley (1984). They mentioned that areas of low pH suggest stagnant waters in which a lowering of pH could be caused by a cation exchange with *Sphagnum* spp. (calcium and magnesium ions replaced with hydrogen ions). In some peatlands, the acidification of the water table would increase along a distance gradient as the *Sphagnum* spp. density increases away from the source waters (Vitt and Bayley 1984). Our results are not as clear as those found by Vitt and Bayley (1984), because the most important *Sphagnum* spp. cover observed in this study (found in the *Larix laricina* & *Betula pumila* cluster) correlates with high pH values. On the other hand, we did observe very low pH values in the *Larix laricina*, *Picea mariana* & *Alnus rugosa* cluster, which also has high *Sphagnum* spp. cover.

The most likely explanation for this contradiction is the input of mineral rich water in the *Larix laricina* & *Betula pumila* vegetation type, which could alter the alkalinity of the stagnant water (Glaser et al. 1990). Many of the *Larix laricina* & *Betula pumila* PCQs are located beside clusters of *Thuja occidentalis* & *Trientalis borealis* and *Fraxinus nigra* & *Onoclea sensibilis*. In accordance to Heinselman (1970) and Johnston (1990), the vegetation type *Thuja occidentalis* & *Trientalis borealis* may be benefiting from an input of mineral rich soil water, whereas the *Fraxinus nigra* & *Onoclea sensibilis* vegetation type is located on beach ridges subject to mineral deposition following spring floods (Bergeron and Bouchard 1983; Bergeron et al. 1983). Both of these vegetation types have high pH values and high conductivity, and it may be possible that the adjacent *Larix laricina* & *Betula pumila* vegetation type also benefited from the cation input. The cation exchange from *Sphagnum* spp. in the *Larix laricina* & *Betula pumila* vegetation type could thus be counteracted by an additional input of calcium and magnesium from the watershed or the rivers.

## Overstory species

The water table depth and the distance from the shore are among the most important variables related with tree species distribution. The periodic fluctuations of the water table with Lake Duparquet spring floods could limit the establishment of many trees, shrubs, and herbaceous species (Kenkel 1986; Denneler et al. 1999). Various effects resulting from prolonged flooding are reported; these would mainly be related to oxygen deficiency in the rooting zone (Kozlowski 1984). Some possible effects are decay in the root system, a high anaerobic metabolism from bacteria (responsible for the production of compounds toxic to seedlings), and a decrease in nutrient uptake (leading to lower plant productivity) (Zinkal et al. 1974; Crawford 1983; Kozlowski 1984; Lieffers and Rothwell 1986; Yamamoto et al. 1987). Thus, the absence of tree species in the *Alnus rugosa* and *Eleocharis* clusters is probably related to the frequency and duration of flooding, such that tree seedling survival is difficult (Brown et al. 1988). Nevertheless, as mentioned by Denneler et al. (2000), these parts of the stands are also highly exposed to wave effects and the physical damages created by the wave activity may explain, to a large degree, the absence of tree establishment.

As observed in the ordination results, the tree cover class explains a large part of the variability in tree distribution. Larch is known to be shade intolerant and less competitive than other tree species such as black spruce and white cedar (Montague and Givnish 1990; Johnston 1990). When all tree species co-occurred (in clusters *Larix laricina* & *Betula pumila* and *Thuja occidentalis* & *Trientalis borealis*), larch was often not in a dominant position and the density of its regeneration was in many cases lower than that of spruce and of cedar. Therefore, we may speculate that in these clusters either black spruce or white cedar will gradually replace larch. The flooding and the low water table depth could help maintain larch in the vegetation types *Larix laricina* & *Spiraea alba* and *Larix laricina* & *Kalmia angustifolia* (lower on the distance gradient and (or) lower water table depth) because seedling establishment of white cedar and black spruce, less tolerant than larch to flooding, is limited (Johnston 1990). Johnston (1990) mentioned that black spruce might also show a lack of reproduction under a dense white cedar cover.

The last variable that has a large influence on tree establishment is peat thickness. Although *Abies balsamea* and *Betula papyrifera* occupy a variety of habitats (in the present study they were found on beach ridges, clay deposits, and thin water saturated organic deposits), their establishment does not seem to be successful on thick organic deposits. The same observation can be extended to *Fraxinus nigra* found on the river beach ridges and immediately besides on the thin water saturated organic deposits. It is reported that, in water saturated sites, *Fraxinus nigra* will grow best where the water is constantly moving, so that the substrate remains aerated (Johnston 1990). As for *Betula papyrifera* and *Abies balsamea*, soil moisture may have been the most restrictive parameter (Johnston 1990). Larch and black spruce are therefore the most successful species on the stagnant water saturated peat layer.

### Conclusion

The distribution of plant species in the Lake Duparquet wetlands is mainly associated with nutrient conditions, as indicated by nitrate concentration, pH, and conductivity, and under the influence of peat thickness, water table depth, tree cover class, and distance from the shore. In accordance with the results of Vitt and Bayley (1984), we found a relationship between *Sphagnum* spp. cover and low substrate pH. However, this relationship was reversed in some parts of the stands where it is possible that periodic flooding, by adding calcium and magnesium to the substrate, may compensate for the pH lowering caused by *Sphagnum* spp. A comparison of samples taken at intervals throughout an entire season could elucidate this question. Moreover, because significant relationships were found between nitrate availability and *Alnus rugosa* abundance, and low nitrate levels and *Kalmia angustifolia* abundance, further studies should be conducted to determine if the substrate chemical conditions are actually caused by the presence of these two shrub species. These studies could also be focused on the effects of the abundance of these shrubs on the growth of larch trees, saplings, and seedlings.

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