Trends and interrelationships in boreal wetland vegetation

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Multivariate statistical methods were used to examine trends and interrelationships in 132 wetland stands at the southern edge of the boreal forest near Elk Lake, Ont., Canada. A total of nine vegetation types and seven species groups were recognized using cluster analysis. Nonmetric multidimensional scaling ordination of the stands indicated the underlying importance of nutrient status to the development of trends in vegetational variation. However, other factors such as the nature of the substratum, degree and periodicity of flooding, drainage, and water table level also appeared to be important. Analysis of the correspondence between vegetation types and species ecological groups indicated a trend toward the development of one-to-one relationships, suggesting that boreal wetlands may best be described as a series of relatively discrete communities. It is also suggested that species indicator values may be useful in characterizing boreal wetland stands.

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Des méthodes statistiques multidimensionnelles ont été utilisées pour étudier les tendances et interrelations chez 132 groupes d'espèces de marécages à la limite sud de la forêt boréale près de Elk Lake, en Ontario, au Canada. Un total de neuf types de végétations et sept groupes d'espèces ont été identifiés à l'aide d'analyses de groupes. Une ordination de normalisation multidimensionnelle non métrique des groupes a révélé l'importance fondamentale du statut trophique au développement des tendances dans la variation de la végétation. Cependant, d'autres facteurs tels que la nature du substrat, le degré et la périodicité d'inondation, le drainage et le niveau hydrostatique semblent importants aussi. L'analyse de la correspondance entre les types de végétations et les groupements écologiques d'espèces a indiqué une tendance vers le développement de relations un-à-un, suggérant que les marécages boréaux sont peut-être mieux décrits comme une série de communautés relativement bien séparées. L'auteur suggère que les valeurs d'espèces indicatrices peuvent être utiles pour caractériser les groupes dans les marécages boréaux.

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Introduction

Wetlands are an important component of the Canadian landscape, occupying 18% of the land surface of the country (Zoltai and Pollett 1983) and almost half the province of Ontario (Ketcheson and Jeglum 1972); yet despite their extent and importance both economically and as wildlife habitat, Canadian wetlands remain poorly understood. This likely reflects the extent, inaccessibility, and inhospitality of most boreal wetland regions.

Most studies of boreal wetlands in North America have been descriptive in nature, often with an underlying classificatory objective. Influences of European phytosociological schools underlie most studies. For example, the Cajander site-type approach (Ruuhijarvi 1983) has been applied in Canada by Hustich (1955, 1957), Kalela (1962), and others. The Swedish approach (Sjörs 1983), which utilizes species composition in determining stand nutrient status, has also been applied to Canadian wetlands (e.g., Sjörs 1959, 1961*a*, 1961*b*, 1963). The concept of indicator species implicit in this approach has gained wide acceptance in wetland community studies (e.g., Glaser *et al.* 1981; Wells 1981; Sims *et al.* 1982; Glaser 1983).

In recent years the methods of the Zürich–Montpellier school (Westhoff and van der Maarel 1978) have been widely used in the description of North American wetlands (e.g., Janssen 1967; Gaudreau 1979; Wells 1981; Glaser *et al.* 1981; Glaser 1983). Various other descriptive methods employing physiognomic and floristic criteria have also been used. Dansereau (1959) (also, Dansereau and Segadas-Vianna 1952; Segadas-Vianna 1955) emphasized wetland physiognomy, while Heinselman (1970) described wetland vegetation types in Minnesota based on both physiognomy and floristics. The widely used classification scheme of Jeglum *et al.* (1974) emphasizes physiognomy and dominance (see also Jeglum 1973*a*; Schwintzer 1978; Sims *et al.* 1982), while the hierarchical classification suggested by Zoltai and Pollett (1983) incorporates considerations of physiognomy, landform, and vegetation characteristics. Although most of these studies have been concerned primarily with the classification and description of wetland vegetation, they also offer useful inferential information regarding stand dynamics, environmental relationships, and trends and interrelationships of the vegetation types described. Zoltai and Pollet (1983) offer a comprehensive review of the literature on Canadian wetlands.

Numerical methods of classification and ordination have until recently been rarely utilized in ecological studies of Canadian wetlands and, when applied, have often been used to determine interrelationships among stands already classified using one of the preferential strategies discussed above. Studies by Vitt and Slack (1975), Vitt *et al.* (1975), Slack *et al.* (1980), Vitt and Bayley (1984), and Vitt and Slack (1984) used polar ordination (Bray and Curtis 1957) and sum of squares agglomerative cluster analysis (Ward 1963) to examine interrelationships among subjectively delineated stands of bog and fen vegetation. The limitations of polar ordination are numerous (Dale 1975; Anderson 1971); in particular, the subjectivity of end-point selection and the limited amount of information used in defining interrelationships render this ordination strategy suboptimal given the availability of objective methods (Austin 1985; Kenkel and Orlóci 1986). Jeglum (1973*b*) successfully applied principal components analysis to the examination of vegetation–environmental relationships in emergent fen, sedge fen, shrub fen, and treed *Sphagnum*-rich vegetation stands in central Saskatchewan. Jasieniuk and Johnson (1982) utilized a modified version of principal components analysis (Johnson 1981) to examine

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vegetation and environmental trends in the lowlands of the Northwest Territories. Sims *et al.* (1982) used detrended correspondence analysis (Hill and Gauch 1980) to examine interrelationships among stands of fen vegetation previously defined using physiognomic criteria. While a numerical approach to the classification of Canadian wetlands has yet to be undertaken, the recent success of such methods in examining upland boreal vegetation (e.g., Bergeron and Bouchard 1983; Foster 1984; Kenkel 1986) suggests their potential utility.

Previous studies have indicated that a number of environmental factors may be responsible for the floristic composition and physiognomy of wetland stands. Principal among these are pH, nutrient status, water table level, drainage, nature of the substratum (whether organic or inorganic), the nature and degree of groundwater flow, and the frequency and extent of flooding (Heinselman 1963, 1970; Jeglum 1973*b*; Jeglum *et al.* 1974; Bergeron and Bouchard 1983). Many of these environmental factors are thought to influence the ionic balance and cation exchange of wetland substrates (Schwintzer 1978; Bergeron and Bouchard 1983), suggesting that nutrient status may be of principal importance in boreal wetland ecosystems. However, accurate measurements of stand minerotrophy may be difficult to obtain (e.g., Gorham 1956; Sjörs 1961*a*, 1963; Ingram 1967; Jeglum 1973*b*; Jasieniuk and Johnson 1982). As an overall indicator of minerotrophic status in wetlands, pH may be a useful measure (DuReitz 1949; Sjörs 1963; Jeglum 1971; Moore and Bellamy 1974) since it reflects the availability of nutrients within the rooting zone (Heinselman 1963, 1970; Sims *et al.* 1982). In this regard the high correlation often found between pH and nutrient levels (e.g., Wells 1981; Glaser *et al.* 1981; Sims *et al.* 1982; Vitt and Slack 1984) is encouraging.

A number of boreal wetland studies have suggested that certain species are useful indicators of nutrient availability (Sjörs 1961*a*, 1963; Glaser *et al.* 1981; Glaser 1983). Vitt *et al.* (1975) and Slack *et al.* (1980) have suggested that bryophytes and carices may be particularly good indicators (see also Sjörs 1963). Recently, Persson (1981) suggested that species ecological indicator values may be useful in the interpretation of ordination scattergrams.

The objectives of this study were (*i*) to delineate, examine interrelationships among, and describe vegetation types from the diverse wetland habitats near Elk Lake, Ont., using multivariate methods; (*ii*) to delineate species ecological groups (Bergeron and Bouchard 1983), and examine the interrelationships among the vegetation types and these groups, again using multivariate methods; (*iii*) to determine the importance of selected environmental scalars on the floristics of the wetland habitats examined; and (*iv*) to assess the utility of ecological indicator values (Persson 1981) in determining trends in nutrient status within boreal wetland stands.

Study area

The study area (see map in Kenkel 1986) encompasses some 70 km² in east-central Ontario (47°50′ N, 80°30′ W). It occurs along the southern edge of the boreal forest (Rowe 1972) and lies within the low boreal wetland region of Zoltai and Pollett (1983). The terrain is typically flat to gently undulating, with occasional rocky hills and outcrops. The region is drained by the Montreal River and its tributaries, but many poorly drained areas of organic peat occur in low-lying regions. Granitic diabase and dikes are the predominant geological formations in the area (Boissoneau 1968).

The climate of the region is continental, characterized by short, warm summers and long, cold winters. Environmental data from the nearby Indian Chute meteorological station indicate an average annual precipitation of 780 mm, about half of which falls between May and September. The mean annual temperature is 2°C, with January and July means of −16 and 17°C, respectively. A more detailed account of the climate of the region can be found in Kenkel (1986).

Donnelly and Harrington (1978) indicate that an extensive, severe fire occurred in the region during the early 1920s. As a result, the upland stands are of uniform age, about 60 years. At least some of the wetland stands in the area must have been spared, however, as ring counts of some recently felled white cedars indicated ages greater than 250 years.

The Elk Lake region is characterized by a diversity of vegetation types. Upland stands are generally dominated by stands of jack pine, trembling aspen, or a mixed forest of balsam fir, black spruce, jack pine, trembling aspen, and white birch. Wetlands in the area are equally diverse. Black spruce stands and open bogs dominate poorly drained regions with considerable organic accumulation, while tamarack is characteristic of water tracks bordering boggy land. Black ash occurs on silty deposits along meanders of the Montreal River, while eastern white cedar or alder thicket is found along some riverbanks and lakeshores and in seepage areas. Grass and *Carex* marshes occur in inundated areas, and birch fens are of occasional occurrence. An account of the vegetation and landforms of the area can be found in Baldwin (1958).

Methods

Field sampling

A stratified random procedure was used in sampling the study area. Three sampling strata were defined based on relative elevation above the perceived water table. Stratal boundaries were delineated with the aid of aerial photographs and contour maps. Proportional allocation (Cochran 1977) was used, with random points marked on aerial photographs and subsequently located in the field. From a given point, a random direction (1 of 8 compass directions) and distance (ranging between 0 and 50 paces) were taken, and this final position became the centre of the stand. In some cases more than one stand was located within the same general area. Each stand was enumerated using a two-stage sampling strategy, in which four 3-m² (small) quadrats were located systematically within a 12-m² (large) quadrat. Trees and tall shrubs were enumerated within the large quadrat, while the small shrub and herb layers were examined within the small quadrats. The 431 stands enumerated were initially partitioned using two-way indicator species analysis (Hill *et al.* 1975). This divisive procedure led to the recognition of three major groupings: 132 wetland stands, 180 sandy upland stands, and 119 mixed forest stands. The sandy upland stands (mostly dominated by jack pine) are treated in a separate paper (Kenkel 1986). This study is concerned only with the 132 wetland stands.

Data collected

Percent cover of trees and tall shrubs and counts of the number of trees were obtained from each large quadrat. Measurements of diameter at breast height (DBH) and occasionally heights were also recorded for trees. Percent cover estimates were obtained for the remaining species within each of the four small quadrats. Values from these four quadrats were subsequently pooled to obtain the mean cover for each species in the stand. Species nomenclature follows Gleason (1968) for vascular plants, Ireland *et al.* (1980) for mosses, Schuster (1966−1974) for hepatics, and Hale (1979) for lichens.

Depth to the water table, obtained by digging a pit when necessary, was recorded at selected stands in late July 1982. At each stand, degree of organic matter decomposition was recorded using the ordinal scale: 1, poorly decomposed (plant parts readily discernable); 2, moderately decomposed (only some plant parts discernable); 3, well decomposed (plant parts not discernable). At many of the stands, a water sample was taken (late July 1982) and a pH measurement obtained the same day, using a Radiometer pH meter. Drainage class

TABLE 1. Physiognomic–environmental characterization of the

	I	II	III	IV
Dominant species	*Picea mariana, Ledum groenlandicum*	*Chamaedaphne calyculata, Sphagnum* species	*Picea mariana, C. calyculata*	*Larix laricina, Alnus rugosa*
Physiognomy	Shrub-rich treed bog	Low shrub bog	Graminoid-rich treed bog	Thicket–conifer swamp
Nature of substrate	Poorly decomposed peat	Poorly decomposed peat	Poorly decomposed peat	Poorly to moderately decomposed peat
Terrain type	Irregularly flat, hummocks	Irregular flat, high hummocks	Irregular, high hummocks	Hummocky, with water courses and pools
Depth to water table*	0.5–1.0	0–0.25	0–0.5	0–0.25
Drainage class	Topogenous–soligenous	Ombrogenous	Ombrogenous–topogenous	Soligenous
Flooding periodicity	—	—	—	Intermittent; some surface flow
Nutrient status	Oligotrophic	Very oligotrophic	Very oligotrophic – oligotrophic	Mesotrophic
pH	Acidic	Highly acidic – acidic	Highly acidic – acidic	Acidic – slightly acidic
Productivity	*Picea mariana* DBH: 15–25 cm Height: 9–12 m	*Picea mariana* DBH: 10–15 cm Height: 4–6 m	*Picea mariana* DBH: 10–20 cm Height: 5–10 m	*Larix laricina* DBH: 20–35 cm Height: 10–15 m

*Metres, late summer 1982.

(based on drainage patterns suggested by aerial photographs) was recorded before visiting a stand using the four principal classes of Jeglum (1973*a*). Flooding periodicity, based on field observations at various times of the year, was also recorded. Finally, general physiognomy, substrate type, nature and degree of variability of the surrounding vegetation, and disturbance features were noted.

Ecological indicator species values (Persson 1981) were used to obtain an estimate of nutrient availability within stands. Each of the 114 most commonly occurring species in the 132 stands was assigned to one of the five nutrient status categories suggested by Jeglum (1971): 1, very oligotrophic; 2, oligotrophic; 3, mesotrophic; 4, eutrophic; 5, very eutrophic. Species indicator value assignments were based on previous Canadian wetland studies, in particular Jeglum (1971) and Jeglum *et al.* (1974). Additional assignments for species of more localized distribution were made based on the studies of Gaudreau (1979) and Bergeron and Bouchard (1983), while values for *Sphagnum* were obtained from Vitt and Slack (1984). Stand nutrient status was calculated as

$$N_j = \text{INT}\left[\frac{\Sigma C_{ij} Z_i}{\Sigma C_{ij}}\right] \text{i} = 1, \ldots, p$$

where C_{ij} = cover of the ith species in the jth stand, Z_i = nutrient indicator value of the ith species, and N_j = estimated nutrient status of the jth stand. INT indicates rounding to the nearest integer.

Data analysis

Cluster analysis was used to classify stands into vegetation types (after Orlóci and Stanek 1979) and species into ecological groups (after Bergeron and Bouchard 1983). In both cases a chord distance matrix (Orlóci 1967) was used as input into sum of squares agglomerative cluster analysis (Ward 1963). Plots of the fusion sum of squares versus the number of groups (after Goodall 1978) were used in choosing the number of groups to recognize. A "classification efficiency" (the ratio of the between groups to the total sum of squares) was then calculated.

A two-dimensional ordination of stands was obtained using non-metric multidimensional scaling (Kruskal 1964*a*, 1964*b*), based on a chord distance matrix. The potential advantages of this ordination algorithm over methods which use eigenanalysis are discussed by Prentice (1977, 1980), Austin (1985), and Kenkel and Orlóci (1986). For comparative purposes, ordinations using principal components analysis (PCA; Orlóci 1978), correspondence analysis (CA; Hill 1974), and detrended correspondence analysis (DCA; Hill and Gauch 1980) were also performed.

Concentration analysis was used to examine relationships within and among the vegetation types and ecological species groups imposed by cluster analysis. This method orders the original data matrix according to the species and stand groups and records for each block of the resultant table the number of occurrences for species of a given group within a vegetation type. This results in a $q \times t$ contingency table (q = number of species groups; t = number of vegetation types), which is examined as in correspondence analysis (Lancaster 1949) after adjustment to equal block size (Feoli and Orlóci 1979). The result is a simultaneous ordination of vegetation types and species ecological groups through a partitioning of the total contingency chi-squared.

Results

Classification of stands

The cluster analysis dendrogram of the 132 stands is presented in Fig. 1. Nine vegetation types have been recognized, based on both ecological considerations and a plot of the fusion sum of squares versus number of groups, giving a classification efficiency of 71.7%. These types have been named for their major constituent species, while physiognomic descriptions (e.g., marsh, bog) follow Jeglum *et al.* (1974). Table 1 presents a physiognomic–environmental characterization of the nine types. The results suggest that each is characterized by a unique combination of environmental factors which can be expected to influence overall species composition, physiognomy, and site productivity. Periodicity and degree of flooding, water table levels, drainage, nutrient status, and nature of the substratum all appear to be important factors.

Ordination of stands

The results of both CA and DCA (not shown) were disappointing, separating out one vegetation type while obscuring nine vegetation types recognized by cluster analysis (Fig. 1)

V	VI	VII	VIII	IX
Alnus rugosa	*Fraxinus nigra*	*Thuja occidentalis, Sphagnum* species	*Betula pumila, C. calyculata*	*Carex aquatilis, Carex rostrata, Calamogrostis canadensis*
Tall shrub thicket swamp	Hardwood swamp	Conifer swamp	Low shrub fen	Graminoid meadow–marsh
Highly decomposed organic matter, some silt accumulation	Silt and clay	Well-decomposed peat	Poorly to moderately decomposed peat	Well-decomposed peat, silt accumulation
Level, occasionally hummocky	Level floodplain, occasional ditches	Irregular, hummocky with water courses and pools	Level or slightly hummocky	Level, with small hummocks, occasional water courses
0.5–1.5	1–1.5	0–0.25	0–0.5	0–0.1
Limnogenous	Limnogenous	Soligenous–limnogenous	Topogenous–soligenous	Limnogenous
Spring; occasionally after heavy rain	Spring	Continuous percolation	Spring	Spring, after heavy rains
Eutrophic	Eutrophic – very eutrophic	Mesotrophic–eutrophic	Oligotrophic–mesotrophic	Mesotrophic–eutrophic
Slightly acidic	Neutral – slightly basic	Slightly acidic	Acidic – slightly acidic	Slightly acidic
Alnus rugosa Height: 2–5 m *Salix discolor* Height: 8–12 m *Larix laricina* DBH: 20–40 cm Height: 10–20 m	*Fraxinus nigra* DBH: 20–30 cm Height: 10–15 m	*Thuja occidentalis* DBH: 25–50 cm Height: 9–12 m	Low shrubs Height: 1–2 m	Grasses and sedges Height: to 1 m

trends in the remaining stands. PCA results (not presented) indicated that at least three dimensions were necessary to summarize the data structure indicated by the classification. Since nonmetric multidimensional scaling (NMDS) was the only method that give results which were readily interpretable in two dimensions, the results of this ordination technique are summarized (Fig. 2). Although the stress value, at 17.3%, is high (Kruskal 1964*a*), the ordination configuration suggests that the result is a parsimonious one. Convergence to this same general configuration was obtained using different random starting configurations, indicating that the solution is a global rather than local minimum (Shepard 1974).

Examination of the scattergram confirms the strength of the groups (nine vegetation types) produced by cluster analysis and reveals some interesting trends. The *Fraxinus* swamp (type VI) stands form a distinctive group at the upper right. The *Betula* fen (type VIII) and *Carex–Calamogrostis* marsh (type IX) stands each form distinctive groups at the lower right. The *Thuja–Sphagnum* swamp (type VII) stands form a relatively distinct group at the upper left, though some affinity to both the *Larix–Alnus* swamp (type IV) and *Alnus* thicket (type V) stands is indicated. These latter two types are also quite distinctive, though some degree of intergradation is apparent. The three bog groups (types I–III) show more or less continuous intergradation, indicating that the three groups produced by cluster analysis, while ecologically meaningful, may be somewhat arbitrary. There is also evidence of intergradation between types I (*Picea–Ledum* dry bog) and IV (*Larix–Alnus* swamp).

Trends in the scattergram were examined by superimposing selected measured variables on the ordination scattergram and by calculating multiple correlation values between axis scores and the variable in question (Fig. 3). Nutrient status (derived from species indicator values) is the most highly correlated of the six variables examined, showing a strong trend from the lower left to upper right. Depth to water table (late summer)

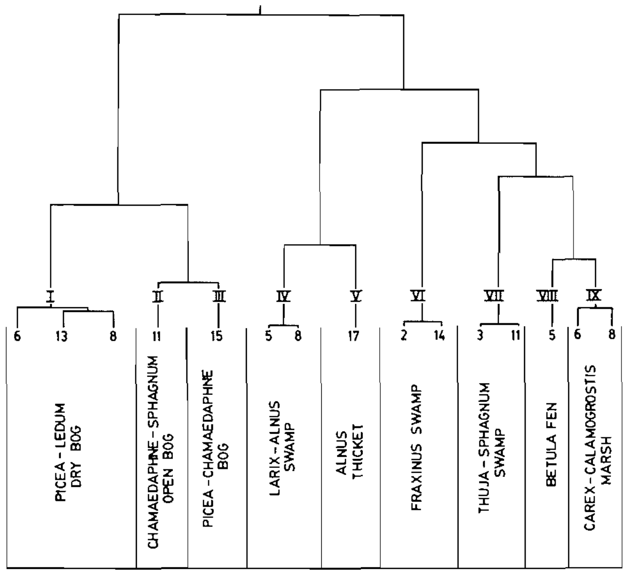

FIG. 1. Sum of squares agglomeration dendrogram, based on chord distance, of the 132 stands. Nine vegetation types (I–IX) are indicated and named. Arabic numerals along the bottom of the dendrogram indicate the number of stands associated with corresponding branches; lower level bifurcations are not shown.

shows a much lower correlation; presumably the fluctuation of water levels, and degree of groundwater flow, must also be taken into account in assessing hydrological influences on the vegetation. The trend in tree cover suggests a physiognomic gradient from lower right (open bog, marshes, fens, and thickets) to upper left (treed sites). Species richness tends to be greatest in nutrient-rich treed stands. The cover of *Sphagnum* species, which serves as an overall indicator of the accumulation of organic peat, is greatest in the more acidic, oligotrophic stands at the left of the scattergram. The cover of ericaceous

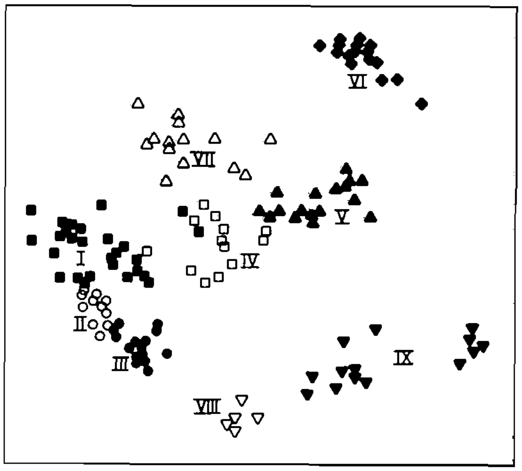

FIG. 2. Nonmetric multidimensional scaling ordination (two-dimensional solution, global order equivalence) of the 132 stands. Symbols correspond to the nine vegetation types I–IX (Fig. 1).

species shows a similar trend, reflecting the physiological and morphological adaptations of many members of this family to oligotrophic conditions (Small 1972*a*, 1972*b*).

Trends in factors not readily quantifiable (periodicity and extent of flooding, nature of the substratum, and drainage) can be inferred by reference to Table 1. Oligotrophic, acidic bogs with negligible groundwater flow on undecomposed organic substrates (types I–III) occur at the left of Fig. 2. To the right of these occur the larch stands (type IV), which are also acidic but show greater decomposition of the organic substrate and some groundwater flow. Above the larch stands are the white cedar swamps (type VII), which have still greater groundwater flow and occur on moderately to well decomposed organic muck. Alder thickets (type V), which are to the right of the larch stands, are characteristic of well-decomposed muck that is subject to regular and recurrent flooding. At the far right are the eutrophic black ash swamps (type VI), which occur in seasonally flooded silty habitats. The birch fen stands (type VIII) occur to the right of the open bog sites. Physiognomically these stands are similar, but they differ in that the fen substrates tend to be more decomposed and are somewhat less acidic. The *Carex*–grass marsh stands (type IX) form a distinctive group at the lower right, showing little affinity with the other groups except the birch fens. These graminoid marshes are characterized by a high water table, regular flooding, and some silt accumulation.

Classification of species

The cluster analysis dendrogram is presented in Fig. 4, with the corresponding species list given in Table 2. Before performing the analysis, species occurring with a frequency of less than 10 were removed, because it was felt that they contained insufficient information as to their interspecific affinities. In total, 114 species were classified. The recognition of seven species ecological groups, based on a plot of the sum of squares versus number of groups and ecological considerations, resulted in a classification efficiency of 36.1%. The groups are described briefly as follows. (A) These 18 species, which show a high association with black spruce, occur on poorly decomposed, oligotrophic and acidic peat. (B) This group of 11 species is characteristic of open bog habitats. The water table is nearer the surface than group A, but otherwise conditions are similar. (C) The 9 species of this group are characteristic of poorly to moderately decomposed organic substrates with some nutrient enrichment through groundwater flow. They show a high association with tamarack. (D) These 17 species are characteristic of riparian areas subject to periodic flooding (intermittent water courses) and are usually associated with a dense tall shrub *Alnus rugosa* overstory. The substratum is typically a black, well-decomposed organic muck overlying mineral soil. (E) This large group of 27 species is characteristic of annually flooded low alluvial silty mineral soils, typically associated with a black ash overstory. (F) These 20 species are characteristic of seepage areas or riverbanks, typically on well-decomposed organic muck in association with eastern white cedar. (G) These 12 species are characteristic of marsh and fen habitats, typically on moderately decomposed organic soil or well-decomposed organic muck subject to regular flooding.

The species ecological groups suggest the development of interspecific associations in response to nutrient availability, substrate type, degree and periodicity of flooding, and depth to water table. The development of strong canopy–understory affinities is also apparent.

Ecological relationships

Three-dimensional scattergrams resulting from concentration analysis are presented in Fig. 5. Note that these scattergrams have a one-to-one correspondence (Gittins 1985). Partitioning of the total contingency chi-squared (Table 3) revealed that 85.5% of the total is accounted for by the first three canonical axes.

The trends represented by the ordination of vegetation types were examined by correlating the first three sets of canonical scores with selected quantifiable environmental factors (Table 4). The results indicate that the first axis reflects a strong nutrient gradient, from types II and III (very oligotrophic) to type VI (very eutrophic). Depth to the water table and, particularly, pH are also highly correlated with the first axis. The second axis is most highly correlated with depth to water table and serves primarily to separate marshes (type IX) and fens (type VIII) from the other stands. Correlations with the third axis, which serves primarily to distinguish black ash stands (type VI) from those dominated by speckled alder (type V) and eastern white cedar (type VII), are quite low.

Similar trends are indicated by the species groups ordination. The first axis reflects nutrient availability, with species groups at the right characteristic of more oligotrophic stands.

Interesting trends in the relationships between vegetation types and species groups are also apparent. Types II and III show a strong affinity with group B, indicating oligotrophic conditions, a high water table, and a poorly decomposed organic substrate. Type I shows very high association with species group A, again reflecting oligotrophic conditions and an undecomposed organic substrate but with a somewhat lower water table. Type IV shows highest affinity with species group C, characteristic of poorly to moderately decomposed organic peats and increased minerotrophy. Close one-to-one correspondence occurs between the following vegetation types and species groupings: VII (cedar swamp) and F (species of mesotrophic to eutrophic, seepage areas); V (alder thicket) and D (species on well-decomposed organic muck, eutrophic riparian sites); and VI (black ash swamp) and E (species of low alluvial silt deposits, eutrophic). The fen and marsh stands (types VIII and IX) show strong association with species group G (species adapted to a high water table and recurrent, regular

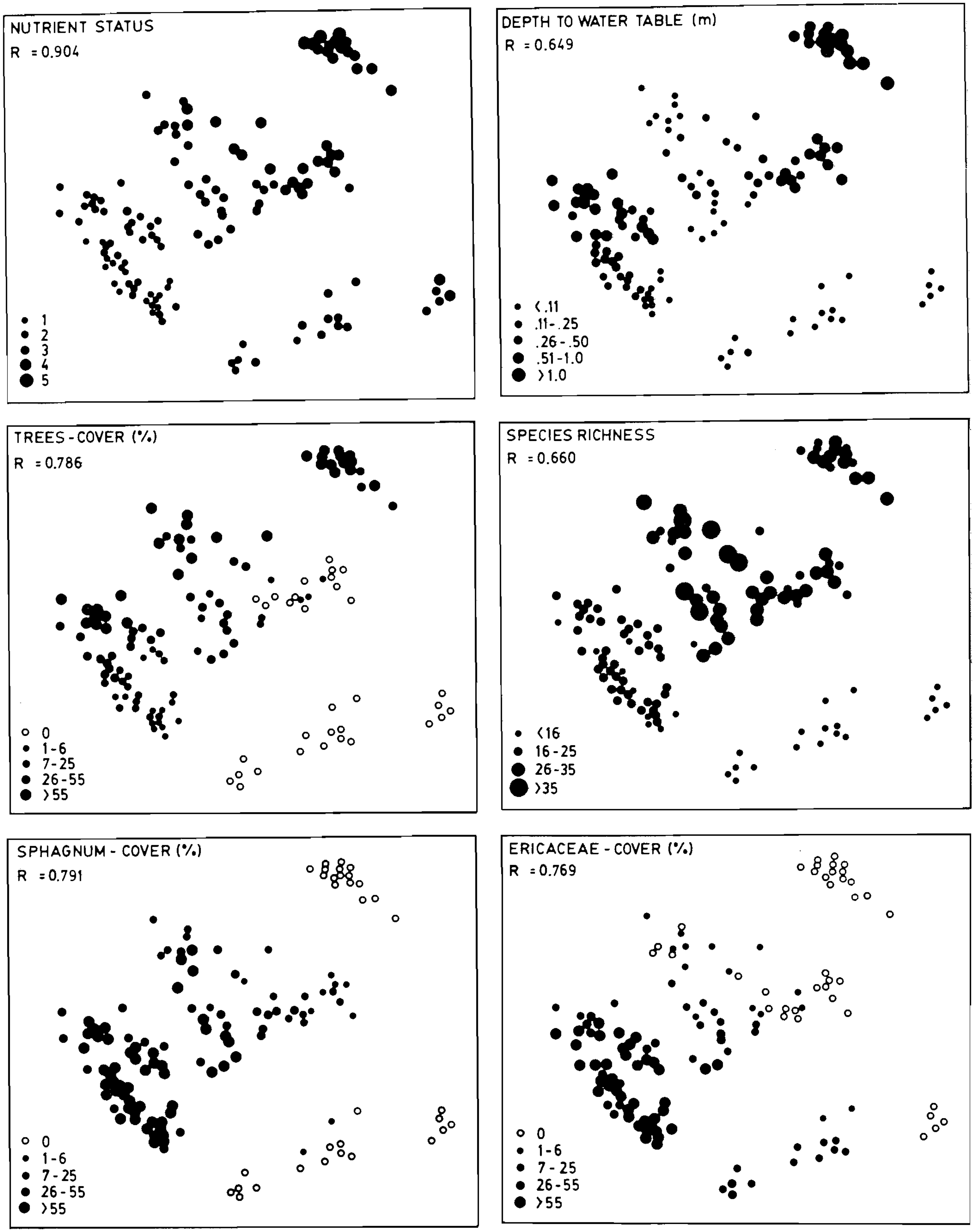

FIG. 3. Selected variables superimposed on the ordination scattergram of Fig. 2. Nutrient status codes are given in the text. The *R* values are multiple correlations.

TABLE 2. List of the 114 most commonly encountered species in the study (frequency greater than 10). Ordering of species corresponds to the dendrogram in Fig. 4, from left to right

Group A	Group B	Group C	Group D	Group E	Group F	Group G
Sphagnum wulfianum	*Carex paupercula*	*Equisetum fluviatile*	*Viola pallens*	*Elymus virginianus*	*Fragaria vesca*	*Scuttelaria lateriflora*
Polytrichum juniperinum	*Sarracenia purpurea*	*Larix laricina*	*Rubus strigosus*	*Rosa acicularis*	*Aralia nudicaulis*	*Lysimachia terrestris*
Dicranum polysetum	*Drosera rotundifolia*	*Sphagnum squarrosum*	*Solidago rugosa*	*Lonicera canadensis*	*Mitella nuda*	*Carex rostrata*
Cladina rangiferina	*Carex oligosperma*	*Drepanocladus aduncus*	*Gymnocarpium dryopteris*	*Cinna latifolia*	*Clintonia borealis*	*Calamogrostis canadensis*
Nemopanthus mucronatus	*Eriophorum spissum*	*Sphagnum russowii*	*Lycopodium lucidulum*	*Streptopus roseus*	*Dryopteris austriaca*	*Campanula aparinoides* var. *uliginosa*
Cornus canadensis	*Sphagnum fuscum*	*Menyanthes trifoliata*	*Hypnum lindbergii*	*Viburnum edule*	*Trientalis borealis*	*Betula pumila*
Coptis trifolia	*Kalmia polifolia*	*Smilacina trifolia*	*Alnus rugosa*	*Fraxinus nigra*	*Sphagnum warnstorfii*	*Carex aquatilis*
Sphagnum magellanicum	*Chamaedaphne calyculata*	*Andromeda glaucophylla*	*Climacium dendroides*	*Ulmus americana*	*Sphagnum girgensohnii*	*Spiraea alba*
Gaultheria hispidula	*Vaccinium oxycoccus*	*Carex canescens*	*Athyrium felix-femina*	*Viola incognita*	*Carex leptonervia*	*Glyceria striata*
Carex trisperma	*Carex pauciflora*		*Mnium punctatum*	*Galium triflorum*	*Lonicera villosa*	*Hypericum ellipticum*
Ptilium crista-castrensis	*Sphagnum rubellum*		*Onoclea sensibilis*	*Acer spicatum*	*Aulacomnium palustre*	*Potentilla palustris*
Pleurozium schreberi			*Thalictrum dioicum*	*Pyrola asarifolia*	*Carex leptalea*	*Myrica gale*
Vaccinium myrtilloides			*Eupatorium maculatum*	*Prunus pensylvanica*	*Rhamnus alnifolius*	
Sphagnum nemoreum			*Ribes glandulosum*	*Abies balsamea*	*Lycopus uniflorus*	
Picea mariana			*Galium asprellum*	*Maianthemum canadense*	*Hylocomium splendens*	
Kalmia angustifolia			*Salix discolor*	*Petasites frigidus*	*Salix pedicellaris*	
Sphagnum angustifolium			*Caltha palustris*	*Lonicera hirsuta*	*Carex disperma*	
Ledum groenlandicum				*Aster umbellatus*	*Thuja occidentalis*	
				Lycopodium annotinum	*Iris versicolor*	
				Ribes hirtellum	*Carex brunnescens*	
				Equisetum sylvaticum		
				Rubus pubescens		
				Brachythecium salebrosum		
				Calliergon cordifolium		
				Carex intumescens		
				Cornus stolonifera		
				Aster puniceus		

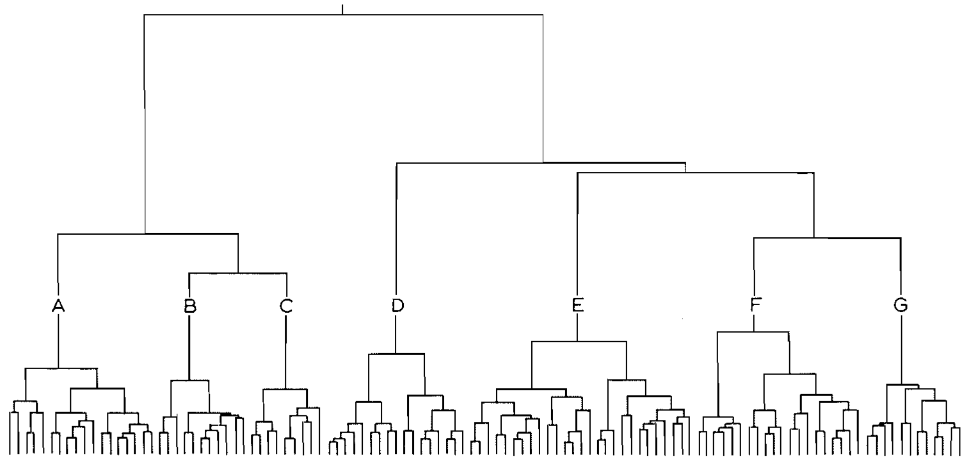

FIG. 4. Sum of squares agglomeration dendrogram of the 114 most commonly encountered species (frequency greater than 10) in the study. The seven ecological groups (A–G) are indicated. Species names associated with these groups are given in Table 2.

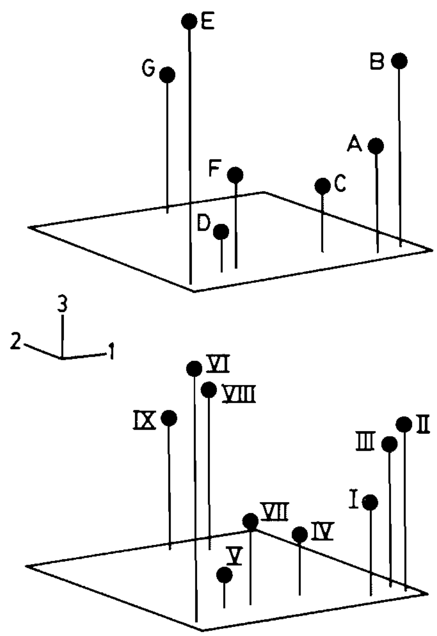

FIG. 5. Three-dimensional concentration analysis ordinations of the nine vegetation types (I–IX; Fig. 1) and seven species ecological groups (A–G; Fig. 4). These two ordinations have a one-to-one correspondence.

flooding), although type VIII (birch fen) also shows some affinity with species group C on the third axis.

Discussion

The results of this study indicate an overall high affinity between species ecological groups and vegetation types, suggesting a group structure reflecting unique combinations of environmental factors within a given stand. This in turn indicates that boreal wetlands may represent a series of discontinuous environments in which synergistically interacting environmental factors lead to the development of characteristic species assemblages (Goodall 1963). Indeed, the strong interspecific associations among the species and, in particular, the development of strong canopy–understory affinities are suggestive of the development of discrete plant communities. However, the ordination results also indicate that the bog stands show continuous intergradation, and there is some indication of vegetational overlap among the bog, fen, conifer swamp, and tall shrub thicket vegetation types.

Recent wetland studies (Vitt and Bayley 1984; Vitt and Slack 1984) have suggested, after Sjörs (1948), that the three principal environmental factors important to the development of bog and fen vegetation are minerotrophy, height above the water table, and degree of shading. In addition to these, Bergeron and Bouchard (1983) mention nature of the substratum (organic or mineral), drainage, flooding, fire perturbation, and microclimate. Nonetheless, the overriding importance of nutrient status on boreal vegetation is generally recognized (see reviews by Jeglum *et al.*, 1974, and Zoltai and Pollett, 1983). The present study, in which stand nutrient status was determined indirectly using species composition, appears to support this view. A number of additional factors which appear from this study to be important, particularly the extent and frequency of flooding, water table levels, and stand drainage, may directly or indirectly influence stand minerotrophy. In this respect nutrient status in wetlands represents a complex environmental gradient *sensu* Whittaker (1967).

The bog vegetation types described in this paper (types I–III) show considerable affinity with those discussed in previous studies. Type I (*Picea–Ledum* dry bog) is similar to the "shrub-rich treed bog" of Jeglum *et al.* (1974), who suggest that such stands are influenced by some mineral water (see also Glaser 1983; Heinselman 1963). At Elk Lake, these stands invariably occur in low-lying, gently sloping basins indicative of slow downslope drainage. The presence of *Kalmia angustifolia* and *Ledum groenlandicum* and the high cover of *Picea mariana* are good indicators of a water table lower than the other two bog types (Jeglum *et al.* 1974). Type III (*Picea–Chamaedaphne* bog) is a less minerotrophic form of Type I, with the water table at or near the surface. Plant indicators of these conditions include *Chamaedaphne calyculata, Kalmia polifolia,* and *Andromeda glaucophylla* (Segadas-Vianna 1955; Janssen 1967; Jeglum 1971). This type shows some affinity with the "graminoid-rich treed bog" of Jeglum *et al.* (1974), while similar plant communities are described by Hustich (1957), Dansereau (1959), Janssen (1967), and Jeglum (1973*a*). The final bog type (II; *Chamaedaphne–Sphagnum* open bog) is most similar to the second variant of the "low-shrub bog" of Jeglum *et al.* (1974; see also Jeglum 1973*a*; Gaudreau 1979; Glaser *et al.* 1981; Glaser 1983).

TABLE 3. Results of partitioning of the total contingency chi-squared into additive components in concentration analysis (Fig. 5)

Canonical variate (i)	Canonical correlation (R_i)	χ^2	Percent
1	0.7327	1432.40	40.78
2	0.6592	1159.51	33.01
3	0.3923	410.53	11.69
4	0.3057	249.41	7.10
5	0.2409	154.87	4.41
6	0.1992	105.91	3.01
Total		3512.63	100.00

TABLE 4. Simple (r) and multiple (R) correlations of concentration analysis scores for the vegetation types with selected environmental variables

	r_1	r_2	r_3	R
Nutrient status	−0.992*	0.075	−0.052	0.980*
pH	−0.794*	−0.297	0.307	0.879*
Depth to water table	−0.606	−0.450	0.348	0.793*

*Significant at $\alpha = 0.01$.

These stands are characteristic of nutrient-poor organic substrates isolated from mineral deposits. Indicators of this situation include *Eriophorum* species and *Carex pauciflora* (Glaser 1983).

Larix–Alnus swamp (type IV) may represent a primary or secondary successional stage on moderately well decomposed, water-saturated organic substrates (Raup 1946; Glaser *et al.* 1981; Bergeron and Bouchard 1983). Heinselman (1963) found that *Larix laricina* in Minnesota was typically found on mesotrophic organic substrates bordering swamps or uplands, generally along slow drainageways. The high shade intolerance of larch (Moss 1953; Beeftink 1960) has led some workers to hypothesize that such stands may be succeeded by black spruce given sufficient time (Jeglum 1973*a*). However, recurrent fires may perpetuate larch swamp habitats (Raup 1946; Vitt and Slack 1975). Compared with black spruce, larch seedlings show higher tolerance to growth in areas where the water table is at or near the surface, through rising water levels may kill established seedlings (Conway 1949).

Alnus rugosa thicket (type V) is characteristic of oxygen-rich organic mucks, occurring along streams and lakes and in areas where drained bogs have resulted in oxidation of the peat surface (Curtis 1959). This vegetation type is maintained by periodic flooding, though Jeglum *et al.* (1974) have suggested that it is a successional stage leading to the development of hardwood or coniferous swamp. Janssen (1967) has suggested that thicket swamps may arise either from the clear-cutting of hardwood swamps or as an initial stage following bog destruction. Many of the stands at Elk Lake occur behind abandoned beaver dams, suggesting that the flooding of land and its later drainage may be important to the development of these thicket stands. The present study also concurs with Janssen's (1967) observation that the understory species composition of alder stands is most closely aligned with that of hardwood swamp forest (type VI). This latter vegetation type, which is dominated by black ash, is characteristic of seasonally flooded, eutrophic, mesic sites (Baldwin 1958; Janssen 1967; Jeglum *et al.* 1974; Bergeron and Bouchard 1983). Stands at Elk Lake are restricted to the meandering portions of the Montreal River, which are subject to strong spring flooding and silt deposition. A number of dead *Ulmus americana* trunks were present in some areas, probably the victims of Dutch elm disease. A number of saplings of this species were present, however, suggesting that it may in future become a more important component of these hardwood swamps.

Thuja–Sphagnum swamp (type VII) is characteristic of drainage areas with high oxygen and nutrient status, typically on highly decomposed organic deposits (Hustich 1957; Jeglum *et al.* 1974; Vitt and Slack 1975; Bergeron and Bouchard 1983). At Elk Lake these stands occur in seepage areas, and locally along slow-moving streams and lakeshores where the lake drains into boggy land. Nutrient-demanding *Sphagnum* species (Vitt and Slack 1984) are often characteristic of these habitats.

Betula fens (type VIII) are not well represented at Elk Lake. The five stands enumerated show some affinity with the "low-shrub fen" of Jeglum *et al.* (1974), which they characterize as mesotrophic to oligotrophic sites with at least 30 cm of moderately to poorly decomposed peat (see also Ritchie 1960). The presence of *Salix* species in some of the Elk Lake stands suggests the paludified bog type discussed by Jeglum *et al.* (1974). Recent discussions of the relationships between bogs and fens, in terms of vegetation and environment, can be found in Vitt *et al.* (1975), Slack *et al.* (1980), Sims *et al.* (1982), and Glaser (1983).

The final vegetation type (IX; *Carex–Calamogrostis* marsh) is similar to both the "meadow marsh" and "graminoid fen" of Jeglum *et al.* (1974), which they describe as being physiognomically similar (see also Baldwin, 1958). These stands, which are characteristic of frequently flooded areas, consist primarily of tussocky graminoids. The high, fluctuating water table likely precludes the establishment of trees in these stands.

While the dynamics of boreal wetland vegetation was not specifically examined in this study, some apparent patterns have emerged from the above descriptions of the vegetation types. In particular, the present study lends support to the idea that stochastic processes are important determinants of vegetational variation in boreal wetlands (Heinselman 1970; Jasieniuk and Johnson 1982). Sjörs (1961*a*, 1963) suggested that both fire effects and changes in water levels tend to lead to the development of multidirectional, irregular cycles of vegetational change in boreal wetlands. Indeed, the important effect of fire on wetland vegetation has been recognized in black spruce bogs and larch swamps (Raup 1946; Moss 1953; Sjörs 1961*a*, 1963; Jeglum 1973*a*, 1973*b*; Jasieniuk and Johnson 1982; Vitt and Slack 1975), while intermittent changes in vegetational composition in response to changing water levels are also documented (Sjörs 1963; Ingram 1967; Schwintzer and Williams 1974; Schwintzer 1978). Variation in water levels may reflect temporal variability in total precipitation, paludification (Heilman 1966; Zoltai and Pollett 1983), or changes in drainage patterns through beaver damming (Sjörs 1963), man-made diversions, or the gradual accumulation of organic matter in low-lying areas (Heinselman 1963; Heilman 1966; Jeglum 1973*b*). Recent stratigraphic studies have indicated that change in wetland vegetation is far from deterministic, being instead strongly dependent upon a number of largely unpredictable perturbatory influences (Heinselman 1963, 1970; Walker 1970; Tallis 1983).

This study also indicates the potential utility of indicator species values (Persson 1981) in assessing stand nutrient status within boreal wetlands. Further research should be undertaken to obtain more accurate data as to the indicator status of North American boreal wetland species, similar to those available for much of Europe (Ellenberg 1974). Such information would permit the estimation of stand minerotrophy in survey studies without the need to resort to the collection of nutrient data, which may be difficult to obtain (e.g., Rycroft *et al.* 1975*a*, 1975*b*) and possibly quite inaccurate (Jasieniuk and Johnson 1982). Furthermore, the high degree of intercorrelation typical of nutrient data collected from wetland stands (e.g., Wells 1981; Glaser *et al.* 1981; Sims *et al.* 1982) indicates that this information is highly redundant. Given that accurate, objectively defined indicator species values are available for the area being investigated and provided that the investigator is fully aware of the possibility of circularity in argument (Persson 1981), the indicator species approach may be of considerable utility in wetland studies where the objective is the exploratory analysis of data for the purpose of establishing vegetation–environmental relationships (Whittaker 1954; Persson 1981). The wide use of indicator species in discussions of North American boreal wetlands (e.g., Sjörs 1963; Wells 1981; Sims *et al.* 1982; Vitt and Slack 1984) offers strong empirical evidence for the utility of such an approach.

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