Structure and dynamics of jack pine stands near Elk Lake, Ontario: a multivariate approach

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Multivariate techniques were utilized to examine even-aged jack pine stands on upland sandy sites at the southern edge of the boreal forest near Elk Lake, Ontario. Cluster analysis of 180 stands led to the recognition of 10 vegetation types, each showing a unique combination of floristics, physiognomy, and environmental components. Classification of common species led to the recognition of five ecological groupings, which show varying degrees of association with the vegetation types. Nonmetric multidimensional scaling of the stands suggested a vegetational continuum in response to overall moisture availability. A corresponding ordination of common species indicated the development of interspecific associations related to soil moisture conditions. It is suggested that the vegetational composition of upland jack pine forests is determined by both probabilistic and deterministic effects, and this is discussed in the context of vegetation structure and dynamics.

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Les techniques d'analyse multivariée ont été utilisées pour étudier des bosquets de cyprès d'âge uniforme que l'on retrouve dans les sites sablonneux des hautes terres à la lisière méridionale de la forêt boréale près du Lac des Elans, en Ontario. Une analyse d'ensembles des 180 bosquets a démontré l'existence de 10 types de végétations, chacun avec une combinaison unique des composantes de la floristique, de la physiognomie et de l'environnement. La classification des espèces communes nous a amené à reconnaître cinq groupements écologiques auxquels sont associés à des degrés divers, les types de végétation. D'après une mesure non-métrique et multidimensionnelle des bosquets il y aurait un continuum dans la végétation, ceci en fonction du degré de l'humidité environnante. Une ordination correspondante des espèces communes a indiqué le développement d'associations interspécifiques liées aux conditions d'humidité du sol. L'auteur suggère que la composition de la végétation des forêts de cyprès des hautes terres est déterminée à la fois par les effets de la probabilité et du déterminisme et en discute dans le contexte de la structure et la dynamique de la végétation.

[Traduit par le journal]

Introduction

In any study of the composition and structure of vegetation, consideration must be given to both spatial variation, which reflects environmental divergence, and temporal influences, which include both successional sequences and considerations of the initial floristic composition of a site (Egler 1954). Large-scale vegetation surveys within the boreal forest undertaken to elucidate the relationship between floristics and environment are necessarily confounded by a temporal factor (Carleton and Maycock 1978, 1980; Johnson 1981; Bergeron and Bouchard 1983). There are two ways to overcome this problem. Johnson (1981) suggested a methodological approach in which the linear variation attributable to temporal differences is channeled out of a raw data matrix prior to its analysis. Such a strategy is predicated on the assumption that the temporal and environmental components of variation are completely independent. Otherwise variation is confounded and the method may partition out potentially useful information. Furthermore, the underlying linearity assumption renders the method ineffective in removing nonlinear temporal trends. The alternative strategy is to restrict the study to a uniform area of known stand age. While this does not permit examination of temporal sequences, it will allow the full range of vegetational variation within an area to be investigated. Temporal factors must of course still be considered, since stand history and the initial floristic composition can be expected to have some influence on the present-day vegetation. Nevertheless, the degree of confounding by temporal variation can be expected to be much reduced. The high degree of consistency in boreal vegetation over large areas (Raup 1946) suggests that a relatively small-scale survey can incorporate a considerable component of the full scale of vegetational variation in the population.

Recent papers which have examined *Pinus banksiana* Lamb. (jack pine) ecosystems have tended to concentrate on temporal variation. Studies of both species diversity, heterogeneity, and composition (Shafi and Yarranton 1973*a*, 1973*b*; Carleton 1982*a*) and biomass and nutrient status (MacLean and Wein 1976; Foster and Morrison 1976) have been undertaken. These studies have generally been restricted to the examination of "typical" monotypic stands on upland sandy flats. Few studies have elucidated the full range of vegetational variation in upland study sites in the boreal forest. The most intensive was undertaken by Mueller-Dumbois (1964, 1965), who examined upland sites in southeastern Manitoba. A more recent paper by Carroll and Bliss (1982) examined the extensive jack pine stands of northern Saskatchewan, which are characterized by regular, recurrent fires. Some recent surveys in the boreal regions of Ontario and Québec which have utilized multivariate techniques (Carleton and Maycock 1978, 1980; Bergeron and Bouchard 1983) have described jack pine stands in a much broader context, emphasizing their relationship to other forest types within the boreal region.

This study applies multivariate techniques to the analysis of spatial variation of upland sandy sites at the southern reaches of the boreal forest near Elk Lake, Ontario. To summarize variation in the data, classification of both sites and species is undertaken using cluster analysis. Site groups (termed vegetation types) are described and related to the species groups, using concentration analysis. Ordination of the sites is undertaken to examine relationships between vegetation and envi-

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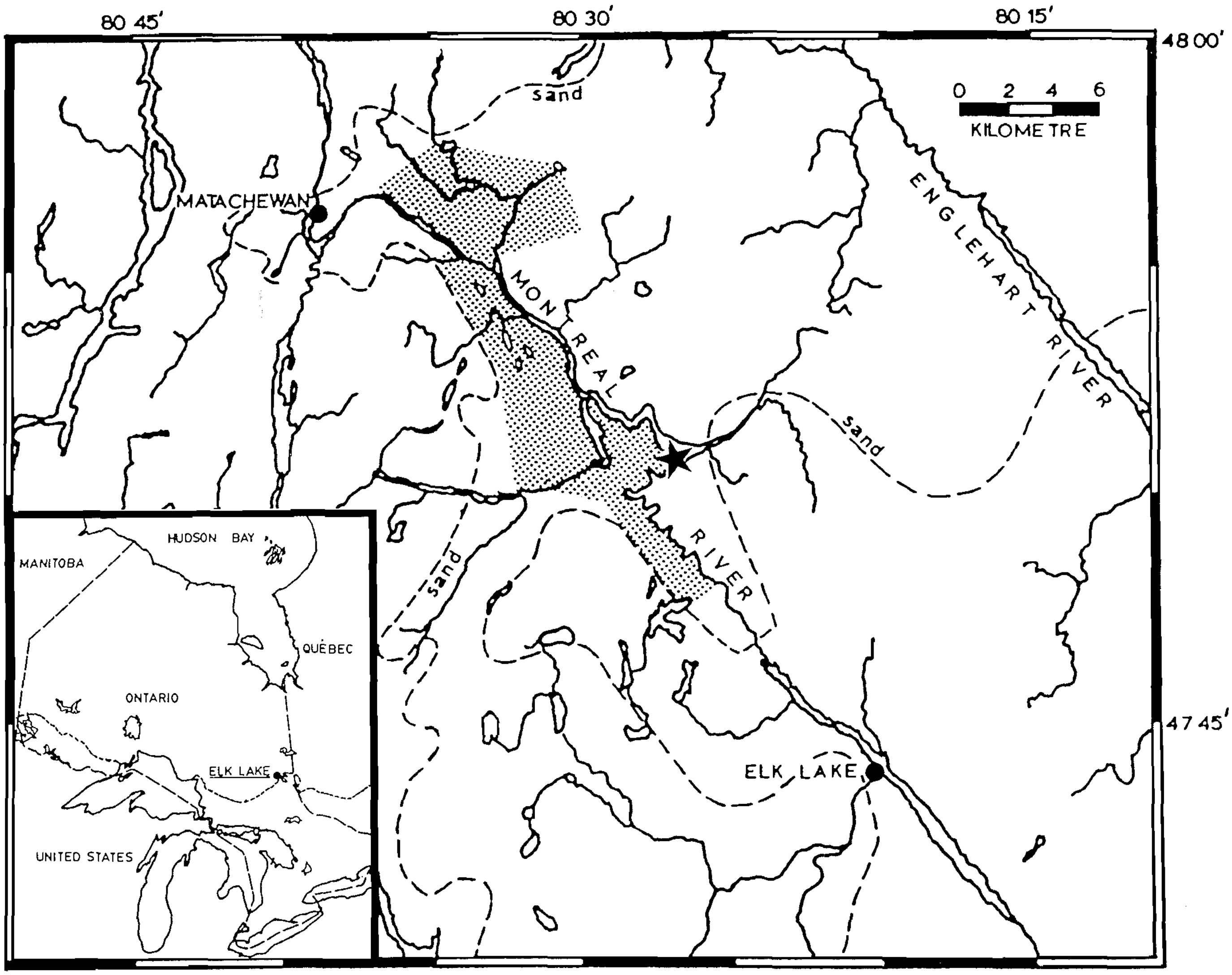

FIG. 1. Location of the study area in east-central Ontario. The limits of surficial lacustrine sand deposits are also shown. ★, location of the Indian Chute weather station.

ronment, in an attempt to elucidate which factors are most important in accounting for vegetational variation. A species ordination is also performed to summarize trends in interspecific associations.

Study area

The study area lies between 47°45′ and 48°00′ N and between 80°25′ and 80°35′ W (Fig. 1), just south of both the height of land and the "clay belt" region (Baldwin 1958) and along the southern edge of the boreal forest as delineated by Rowe (1972). Elevation ranges between 300 and 400 m. A flat relief is characteristic, although occasional rocky hills rising 50 – 100 m above the surrounding terrain also occur. Surficial sand deposits predominate on the flat areas, while finer soils often occur in rocky and hilly areas. Local rock outcrops are also common. The region is drained by the Montreal River watershed which flows into the Ottawa River drainage basin. Nevertheless, some poorly drained areas occur, attributable primarily to the accumulation of peat in low-lying areas. Geologically the region is characterized by felsic and mafic intrusive rock, with granitic diabase and dikes predominating (Boissoneau 1968).

Climatic parameters for northern Ontario are given by Chapman (1953). In the Elk Lake area, the growing season (from when the mean daily temperature reaches 5.6°C until when it falls below this level) extends from May 3 to October 11, or an average of about 160 days. Potential evapotranspiration is in the range 48 – 50.5 cm, which is high for the boreal forest (Larsen 1980). Thunderstorms, which are important in igniting forest fires, average 15 per year. Climate data from Indian Chute (47°51′ N, 80°27′ W, elevation 293 m), which lies within the study area, are summarized in Fig. 2. The area is characterized by a rather short, warm summer and a long, cold winter. Precipitation is greatest in the summer months, with just over 50% falling between May and September.

An extensive and severe fire swept through the area in the early 1920s (Donnelly and Harrington 1978), and as a result the stands are of a uniform age of about 60 years. Some recently felled *Thuja occidentalis* individuals, however, were aged at greater than 250 years.

An analysis of aerial photographs and a general reconnaissance undertaken in the fall of 1980 suggested that drainage is of principal importance in determining vegetational composition and structure in the area. Flat sandy plains above the water table are generally dominated by jack pine or trembling aspen. On finer soils over rock, mixed forests of balsam fir, black spruce, jack pine, trembling aspen, and white birch occur. Lowland clay deposits along rivers, a rare habitat in the area, support stands of balsam poplar or white spruce along with some of the species mentioned above. Silty, periodically flooded terraces along the meanders of the Montreal River below Indian Chute are dominated by stands of black ash. Eastern white cedar occurs along riverbanks and some lakeshores and in seepage areas where considerable deposits of well-decomposed organic muck occur.

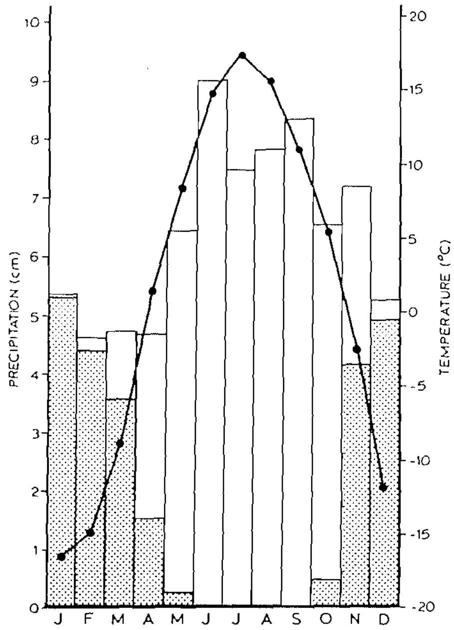

FIG. 2. Environmental data for Indian Chute, Ontario (means for the period 1941 – 1970). Shaded area represents proportion of precipitation falling as snow.

On poorly decomposed peat black spruce generally occurs, while tamarack is often present along water tracks in boggy areas.

Methods

Field sampling

Various strategies have been employed in sampling boreal vegetation. Carleton and Maycock (1978) (also Swan and Dix 1966) used plotless sampling for the enumeration of trees and tall shrubs, locating 30 points in each stand. The understory vegetation was examined at alternate points, using 1-m² quadrats. Plotless sampling has some advantages, primarily in removing edge effect problems. However, unbiased estimates are not obtained unless the trees are randomly distributed (Pielou 1977). Furthermore, plotless methods are useful only in broad-scale site descriptions, since at least 20 point are required to obtain an adequate description. Because interest in this study lies in small-scale variation (following Goodall 1970) and the obtaining of unbiased estimates, quadrats were used to enumerate both the tree and shrub – herb layers. A 12-m² quadrat was chosen for examining the overstory, and a 3-m² one for the understory. A two-stage strategy was used in which four understory quadrats were systematically placed within each of the large quadrats, giving a 25% enumeration. The two-stage systematic strategy yields unbiased estimates provided that the large quadrats are located at random (Cochran 1977). Each area enumerated by this two-stage strategy will henceforth be referred to as a stand.

Within the study area three sampling strata were defined on the basis of relative elevation (above the perceived water table). Stratal boundaries were delineated with the aid of aerial photographs and contour maps. The number of stands located within a given stratum was made proportional to stratal area. Stands were located at random, marked on aerial photographs and contour maps, and subsequently located in the field as well as possible. From this point, a random direction (one of eight compass-point directions) and distance (ranging between 0 and 50 paces) were taken, and this position was taken as the centre of the stand. If the area proved to be vegetationally heterogeneous, more than one stand was enumerated in the same general area.

A total of 400 stands were located in the manner outlined above. Of these, 19 occurred in disturbed areas and were therefore excluded from enumeration. At 44 of the positions, more than one stand was enumerated. In total, data from 431 stands were obtained. This large data set was initially partitioned using TWINSPAN, a polythetic divisive clustering technique (Hill 1979). The results suggested the recognition of three major groups: 132 wetland stands, 180 sandy upland stands dominated by jack pine and (or) black spruce, and 119 upland stands dominated by other tree species. This paper is concerned only with the 180 sandy upland stands.

Data collected

For the overstory (large quadrat), percent cover and number of each tree species were recorded, and their height and diameter at breast height (DBH) were measured. At 38 of the stands, sample cores (at 1.0 m height) of at least two jack pine individuals (overstory members only) were taken to verify the assumption of stand age uniformity. Values ranged between 53 and 60 years, with a mean of 56.2 years. This was later checked by aging stumps from a portion of the study area which was logged during the winter of 1982 – 1983. Age counts of over 30 stumps ranged between 56 and 61 years. This clearly establishes the uniformity of postfire stand ages. However, it does not preclude the possibility that later localized surface fires may have affected the structure and composition of the understory, implying that the stands may not all be at the same stage of successional development.

Within each of the four understory quadrats, percentage cover estimates were made for each species. The data for these quadrats were subsequently pooled to obtain a mean cover value for each species in the stand. Species nomenclature follows Gleason (1968) for vascular plants, Crum and Anderson (1981) for mosses, Schuster (1966 – 1974) for hepatics, and Hale (1979) for lichens.

A soil pit was dug near the centre of each large quadrat. Depth of the organic layer and the leached A-horizon, colour and texture of the soil, and the amount of gravel and (or) rock were recorded. In addition, a soil sample was taken from just below the leached layer and air dried for later determination of particle size. This was quantified by first passing the sample through a series of sieves with mesh diameters of 1.0, 0.5, 0.212, 0.105, and 0.053 mm. The resulting five fractions have mean particle size diameters: *1* = 0.75 mm, *2* = 0.356 mm, *3* = 0.1585 mm, *4* = 0.079 mm, and *5* = 0.039 mm. Note the multiplicative nature of this series, each value approximately half the previous one. Each fraction was weighed to the nearest 0.1 g and converted to a proportion of total sample dry weight. Particle size was calculated by linearizing the multiplicative scale of the mean diameter values: $X = (p_1(\log_2 0.75 \text{ mm}) + \ldots + p_5(\log_2 0.039 \text{ mm}))$, where p_i is the proportional weight of fraction i. Soil particle size is then given by $Y = 2^X$.

At all sites, the general physiognomy, topography, and substrate type of the area were recorded, and slope and aspect were noted. Drainage class was also recorded, using the scale *1*, very xeric; *2*, xeric, *3*, mesic – xeric; *4*, mesic; *5*, mesic – hydric; *6*, hydric. Assignment was initially made on the basis of relative elevation (height above water table, determined from the examination of aerial photographs and topographic maps) before visiting the site. At the site, modifications were made if necessary using topographic and soil criteria (texture, presence of rock and (or) gravel). Nutrient status (using the five-point scale of Jeglum *et al.* 1974) estimates were made based on the results of previous workers (particularly Mueller-Dumbois 1964; Bergeron and Bouchard 1983) and considerations of stand drainage, depth of water table, and nature of the groundwater. Finally, the nature and degree of variability of vegetation in the immediate area and disturbance features were also noted.

Data analysis

The overall analytical strategy of this study reflects the generally accepted viewpoint that maximal information in survey studies results from a dual strategy of ordination and classification (Anderson 1965; Orlóci 1978; Green 1979). Stand classification is undertaken as a utilitarian strategy for delineating vegetation types. Stand ordination is used to examine and summarize trends of variation in the vegetation. Ordination and classification of the common species is also undertaken, with the objective of recognizing trends and groupings of interspecific relationships. A combined analysis of the vegetation types and species groups derived from the classifications is performed to summarize trends and relationships within and among the groupings.

Cluster analysis was utilized in the classification of both stands and species. Sum of squares agglomerative clustering (Ward 1963; Orlóci 1967) was performed on a chord distance matrix (Orlóci 1966). The advantages of this clustering algorithm are discussed by Kuiper and Fisher (1975), Goodall (1978), and Milligan (1980). In cluster analysis the decision of a cutoff level for group recognition is necessarily subjective. In this study a plot of the fusion sum of squares versus the number of groups (as suggested by Ward 1963; Goodall 1978; Orlóci 1978) was used. A "classification efficiency," which is the ratio of the between groups to the total sum of squares, was then calculated.

Nonmetric multidimensional scaling (Kruskal 1964*a*, 1964*b*), using a chord distance matrix as input and specifying a two-dimensional solution, was used to obtain ordinations of both stands and common species. The method attempts to find an arrangement of individuals in a reduced Euclidean space such that the interspecific distances are as closely monotonic as possible to the distances calculated in variable space. Though rarely utilized by ecologists, this ordination method has a number of theoretical and practical advantages over eigenanalysis strategies (Prentice 1977, 1980). A major theoretical advantage is that the method is not limited to summarizing linear variation. Practical advantages include a greater choice of resemblance coefficients and the ability to specify the dimensionality of the final solution (Shepard 1974). Principal components analysis and correspondence analysis were also employed for comparative purposes, but the results proved to be less interpretable and are not presented here.

The relationship between vegetation types and species groups defined by cluster analysis was examined using concentration analysis (Feoli and Orlóci 1979). This method begins with an ordered (site and species groupings) table. Within each block of the table, the number of occurrences of the species of a given group within a vegetation type is recorded. This results in a q by t contingency table, where q is the number of species groups and t the number of vegetation types. The table is then examined as in correspondence analysis (Lancaster 1949; Hill 1974) after adjustment to equal block size. The result is a simultaneous ordination of vegetation types and species groups through the partitioning of the total contingency chi-squared.

Results

Stand classification

The cluster analysis dendrogram is given in Fig. 3. A plot of the fusion sum of squares versus the number of groups, together with ecological considerations, suggested the recognition of 10 vegetation types, giving a classification efficiency of 53.6%. The types are described below with respect to their species composition, physiognomic structure, and habitat characteristics. Types are named by their major constituent species.

(I) *Vaccinium angustifolium* – *Arctostaphylos uva-ursi*

This type is characteristic of coarse, loose, sometimes shifting sand, typically on south-facing dune slopes. Soil development is poor to nonexistent. *Pinus banksiana* occurs with an average cover of less than 10%, and the type is dominated by lichens and low shrubs adapted to highly xeric, oligotrophic conditions. The dominant shrubs are *Arctostaphylos uva-ursi, Vaccinium angustifolium*, *Comptonia peregrina*, *Prunus pumila*, *Pteridium aquilinum*, and *Gaultheria procumbens*. An extensive lichen mat occurs, which includes *Cladina rangiferina*, *C. mitis*, *C. stellaris*, *C. arbuscula*, *Lecidea granulosa*, and a number of species of the genus *Cladonia*. There is little accumulation of surface organic matter. In very dry, sloping areas, the sand is often covered by a thin crust of the lichen

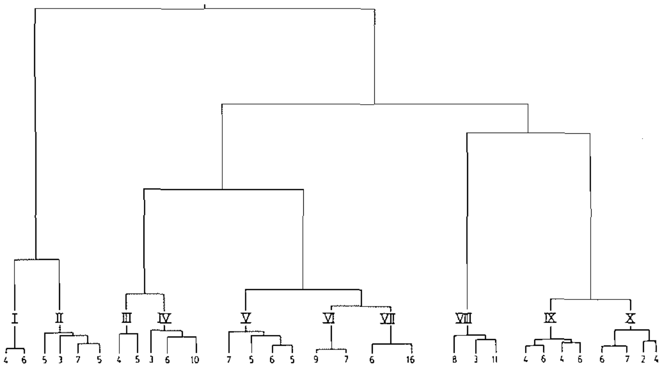

FIG. 3. Sum of squares agglomeration dendrogram of the 180 stands. The 10 vegetation types (I–X) described in the text are indicated. Arabic numerals along the bottom of the dendrogram indicate the number of stands belonging to corresponding branches; lower level bifurcations are not shown.

Lecidea granulosa, which may stabilize the sand and prevent erosion. This type bears some resemblance to both the "very dry *Cladonia*" and "dry *Arctostaphylos*–*Cladonia*" types described by Mueller-Dumbois (1964).

(II) *Pinus banksiana* – *Vaccinium angustifolium* – *Cladina rangiferina*

This type occurs either on dry rock outcrops or on coarse sand flats overlying a loose stone–gravel mix. As in type I, very xeric and oligotrophic conditions prevail. Organic accumulation is generally greater in these stands, however, particularly on rock where pockets of poorly decomposed humus are characteristic. The flat, coarse sand sites typically have a continuous poorly decomposed humus layer 1–2 cm in depth.

Pinus banksiana is the characteristic tree of this type, reaching almost 40% mean cover. On the rock outcrops, *Picea mariana* may also occur, and occasionally saplings of *Pinus strobus* were noted. The characteristic shrub is *Vaccinium angustifolium*, with *V. myrtylloides* and *Comptonia peregrina* occurring with much lower frequency and cover. The lichen *Cladina rangiferina* is the most common forest floor constituent, although the mosses *Pleurozium schreberi* and *Dicranum polysetum* also occur. Other species characteristic of the ground layer include *C. mitis*, *C. stellaris*, *Ptilidium ciliare*, and a number of species of the genus *Cladonia*.

The stands occurring on rock are similar to those described by Jones *et al.* (1983). Trees generally root in fissures and cracks in the rock, and windthrows are common. The sites occurring on very coarse sands show some affinity with the "dry *Arctostaphylos*–*Cladonia*" type of Mueller-Dumbois (1964). Commercial gravel excavations near these sites revealed that below a 2 to 3-m layer of coarse sand a layer of boulders and gravel occurs, indicating excessive site drainage.

(III) *Pinus banksiana* – *Kalmia angustifolia* – *Populus tremuloides*

These stands are characterized by a gravelly–bouldery substratum intermixed with small pockets of silty soil. They all occur near the Montreal River, suggesting that they may have originated during riparian remodelling phases. Trees are fairly widely spaced, with large specimens of *Pinus banksiana* predominating. *Populus tremuloides* occurs as small, depauperate, actively resprouting individuals. A number of dead trunks of this species are also evident, suggesting that it is here at its limit of tolerance. These trees may have died following a

TABLE 1. Physiognomic–environmental characterization of the 10 vegetation types I–X described in the text

	I	II	III	IV	V
Dominant species	*Vaccinium angustifolium*, *Arctostaphylos uva-ursi*	*Pinus banksiana*, *Vaccinium angustifolium*, *Cladina rangiferina*	*Pinus banksiana*, *Kalmia angustifolia*, *Populus tremuloides*	*Pinus banksiana*, *Comptonia peregrina*, *Vaccinium angustifolium*	*Pinus banksiana*, *Pleurozium schreberi*, *Cladina rangiferina*
Physiognomy	Low shrub–cryptogam, scattered trees	Low shrub, open coniferous forest	Low shrub, open conifer forest with deciduous component	Low shrub–cryptogam, conifer parkland	Low shrub, open conifer forest
Substrate type	Coarse sand	Rock or coarse sand over boulder layer	Boulder with gravel, pockets of silt accumulation	Coarse, often gravelly sand deposits	Coarse to fine sand deposits
Terrain type	High dunes and dune slopes, south facing	Local rock outcrops, or level sand plains	Gently sloping to level	Level to moderately steep slopes	Level or very gently rolling
Drainage class	Very xeric	Very xeric to xeric	Xeric–mesic	Xeric	Xeric to xeric–mesic
Nutrient status (estimated)	Very oligotrophic	Very oligotrophic – oligotrophic	Mesotrophic – oligotrophic	Oligotrophic	Oligotrophic
Particle size class	Very coarse	Coarse	Medium to fine	Coarse–medium	Coarse
Soil	Sandy O*: 0–1 cm A*: none Weak soil development	Rock outcrops or sandy O: 1–3 cm A: 6–10 cm Weak podzolization	Bouldery, silt O: 1–2 cm A: none Small soil pockets	Sand, some gravel O: 1–6 cm A: 8–12 cm Strong podzolization	Sandy O: 4–8 cm A: 12–16 cm Strong podzolization
Productivity	Tree cover: 10% *Pinus banksiana* DBH: 10–20 cm Height: 10–12 m	Tree cover: 40% *Pinus banksiana* DBH: 15–20 cm Height: 10–16 m	Tree cover: 40% *Pinus banksiana* DBH: 15–25 cm Height: 12–16 m *Populus tremuloides* DBH: 15–20 cm Height: 10–14 m	Tree cover: 20% *Pinus banksiana* DBH: 10–20 cm Height: 12–18 m	Tree cover: 30% *Pinus banksiana* DBH: 15–22 cm Height: 12–16 m

*Depth of the organic layer (O) and the leached A-horizon (A).

particularly dry summer (see discussion in Yarranton and Yarranton, 1975). Shrub species include *Kalmia angustifolia*, *Vaccinium myrtylloides*, *Aster macrophyllus*, *Cornus canadensis*, *Comptonia peregrina*, *Maianthemum canadense*, *Salix humilis*, and *Linnaea borealis*. Lichens are rare, but the mosses *Pleurozium schreberi* and *Dicranum polysetum* do occur. This is an interesting combination of species, indicating relatively xeric but somewhat less oligotrophic conditions than types I and II. This is probably attributable to the fine silt and clay deposits found here. However, the bouldery–gravelly nature of the site leads to excessive drainage, favouring species adapted to xeric conditions.

(IV) *Pinus banksiana – Comptonia peregrina – Vaccinium angustifolium*

This type includes steep, stable dune faces with high cover of *Pteridium aquilinum*, flat, coarse sand plains dominated by *Comptonia peregrina*, and very gravelly, coarse sandy soils resulting from lacustrine sorting of fluvioglacial deposits. It is characterized by low jack pine cover (averaging less than 20%) and an almost continuous shrub layer dominated by the low shrubs *Kalmia angustifolia*, *Vaccinium angustifolium*, *Comptonia peregrina*, and *V. myrtylloides*. *Populus tremuloides* also occurs in the overstory, though it is generally small and depauperate in form, much as in type III. *Cladina rangiferina*, *Pleurozium schreberi*, and *Dicranum polysetum* are characteristic of openings in the shrub layer, while *Salix humilis* and *Prunus pensylvanica* are the most common tall shrubs. *Diervilla lonicera* and the small annual *Melampyrum lineare* occur in about half the stands.

(V) *Pinus banksiana – Pleurozium schreberi – Cladina rangiferina*

This type occurs on coarse sandy flats or occasionally on coarse sand over rock. *Pinus banksiana* is the dominant tree species, achieving a mean cover of just over 30%. The understory is dominated by the low shrubs *Kalmia angustifolia*, *Vaccinium angustifolium*, *V. myrtylloides*, *Diervilla lonicera*, *Comptonia peregrina*, and *Gaultheria procumbens*. *Pleurozium schreberi* is the dominant species of the ground layer, although *Cladina rangiferina* and *Dicranum polysetum* also occur. The tall shrubs *Prunus pensylvanica*, *Alnus crispa*, and *Salix humilis* often occur in more open areas of the canopy.

(VI) *Pinus banksiana – Pleurozium schreberi – Kalmia angustifolia – Ledum groenlandicum*

This type is characterized by a dense jack pine overstory (averaging just over 70% cover) and saplings or small individuals or *Picea mariana*. These are sandy stands with a well-developed podzol, occurring along the fringe of black spruce bogs 0.5–2 m above the water table. Thus the conditions are somewhat more mesic than types I–V, although oligotrophic conditions still prevail. *Kalmia angustifolia* is the dominant shrub, although *Ledum groenlandicum* is also typical. This latter species, along with *Coptis groenlandicum*, *Gaultheria hispidula*, and *Maianthemum canadense*, are good indicators of the more mesic status of this type. The forest

VI	VII	VIII	IX	X
Pinus banksiana, *Pleurozium schreberi,* *Kalmia angustifolia,* *Vaccinium myrtylloides*	*Pinus banksiana,* *Kalmia angustifolia,* *Vaccinium myrtylloides,* *Pleurozium schreberi*	*Picea mariana,* *Pleurozium schreberi,* *Ledum groenlandicum,* *Kalmia angustifolia*	*Pinus banksiana,* *Pleurozium schreberi,* *Alnus crispa*	*Pinus banksiana,* *Corylus cornuta,* *Alnus crispa*
Low shrub, closed conifer forest	Low shrub, closed conifer forest	Low shrub, closed mixed conifer forest	Tall shrub, mixed conifer forest	Tall shrub, conifer forest
Coarse to fine sand	Finely textured sand	Relatively coarse to fine sand (variable)	Fine sand, occasional rock	Fine sand, some silt
Very gently sloping	Level	Gently sloping to level	Level or gently sloping	Level or very gently sloping
Mesic	Xeric–mesic to mesic	Mesic	Xeric–mesic to mesic	Mesic
Oligotrophic–mesotrophic	Oligotrophic	Oligotrophic–mesotrophic	Oligotrophic–mesotrophic	Mesotrophic
Medium	Medium–fine	Generally medium	Medium–fine	Medium–fine
Sandy O: 6–12 cm A: 8–12 cm Strong podzolization	Sandy O: 8–12 cm A: 12–18 cm Strong podzolization	Sandy O: 4–6 cm A: 4–8 cm, weak Poor profile development	Sandy O: 4–10 cm A: 8–16 cm Variable, poor to good podzolization	Sandy O: 10–14 cm A: 8–10 cm, weak Moderate podzolization
Tree cover: 70% *Pinus banksiana* DBH: 20–30 cm Height: 15–20 m	Tree cover: 70% *Pinus banksiana* DBH: 15–25 cm Height: 15–18 m	Tree cover: 70% *Picea mariana* DBH: 10–16 cm Height: 10–14 m *Pinus banksiana* DBH: 12–20 cm Height: 12–17 m	Tree cover: 60% *Pinus banksiana* DBH: 15–22 cm Height: 14–18 m	Tree cover: 60% *Pinus banksiana* DBH: 16–24 cm Height: 15–20 m

floor is dominated by thick mats of *Pleurozium schreberi*, with occasional clumps of *Dicranum polysetum*. *Sphagnum* species do occur but are uncommon. Other shrubs occurring in this type include *Vaccinium myrtylloides*, *V. angustifolium*, and *Cornus canadensis*.

The prevalence of black spruce saplings in the lower tree strata is probably attributable to the relatively high water table, the oligotrophic conditions, and the proximity of black spruce bog, which provides a ready seed source. In the absence of fire it seems likely that black spruce would come to dominate jack pine in these stands.

(VII) *Pinus banksiana – Pleurozium schreberi – Kalmia angustifolia – Vaccinium myrtylloides*

This type is typical of flat upland sandy areas. The soil consists of strongly podzolized and finely textured sand. Monospecific jack pine stands are characteristic, attaining just over two-thirds mean cover. The understory is dominated by *Kalmia angustifolia*, although the shrubs *Vaccinium myrtylloides*, *Cornus canadensis*, *Linnaea borealis*, *V. angustifolium*, *Maianthemum canadense*, *Gaultheria procumbens*, and *Diervilla lonicera* are also common. The ground layer is dominated by *Pleurozium schreberi*. The tall shrubs *Prunus pensylvanica*, *Salix humilis*, and *Amelanchier sanguinea* each occur with about 50% frequency though low cover. Seedlings or small trees of both *Abies balsamea* and *Picea mariana* are occasional though uncommon.

This type is a more upland, less mesic version of type VI, physiognomically similar though lacking some species characteristic of a higher water table. The more mesic conditions here compared with types I–V are indicated by the increased dominance of jack pine, the higher cover of small ericaceous species, and the decreased abundance of lichens, particularly *Cladina rangiferina*. Also, the presence of *Linnaea borealis*, *Diervilla lonicera*, and *Cornus canadensis*, and the increased importance of *Prunus pensylvanica*, *Salix humilis*, *Amelanchier sanguinea*, and occasionally *Alnus crispa* are all good indicators of less xeric conditions.

(VIII) *Picea mariana – Pleurozium schreberi – Ledum groenlandicum*

This type is characteristic of flat or gently sloping sandy substrates just above the water table, typically bordering boggy land. Some of these stands are characterized by rock overlain with sandy soil 0.5–1 m in depth. Soils generally show poor podzolization, and the sand is often saturated at depths greater than about 50 cm. *Picea mariana* is the dominant species of the tree stratum, achieving an average cover of over 55%. *Pinus banksiana* also occurs, with an average cover of just under 25%. Because of the active layering and consequent local shading and smothering by black spruce, the understory is of relatively low cover. *Ledum groenlandicum* and *Kalmia angustifolia* predominate in the shrub layer, although *Cornus canadensis*, *Vaccinium myrtylloides*, and *Gaultheria hispidula* are also characteristic. The ground layer is dominated by thick carpets of *Pleurozium schreberi*, interspersed with small

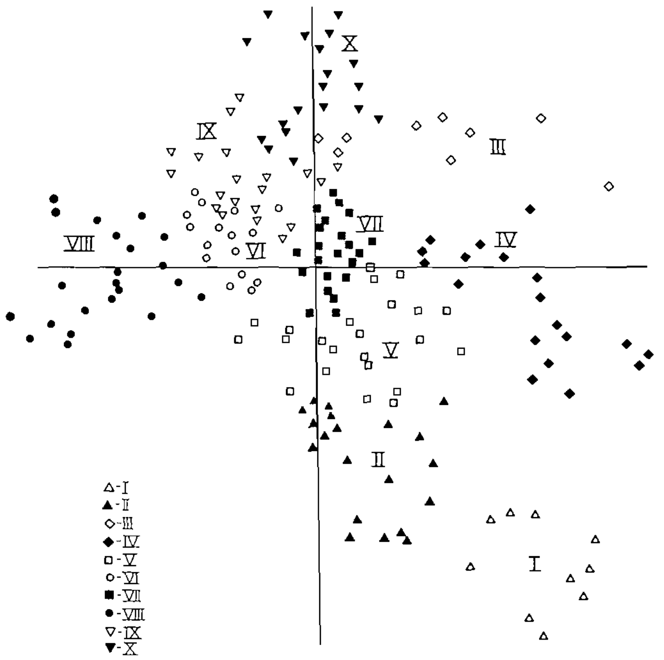

FIG. 4. Nonmetric multidimensional scaling (two-dimensional solution, utilizing chord distance) of the 180 stands. Symbols correspond to the 10 vegetation types I−X as indicated. The stress value is 21.3%.

clumps of *Cladina rangiferina* and *Dicranum polysetum*. Species of *Sphagnum* are of rare occurrence.

Ledum groenlandicum and *G. hispidula* are indicative of the mesic conditions prevailing at these stands. The occurrence of *P. schreberi* and *C. rangiferina* is probably attributable to the physiognomic structure of the stands. Unlike jack pine, black spruce tapers strongly and branches profusely near the base. As a result the canopy is more open, leading to greater insolation and evapotranspiration at the surface. These conditions may favour species adapted to xeric conditions.

(IX) *Pinus banksiana* − *Pleurozium schreberi* − *Alnus crispa*

This type is characteristic of coarse to relatively fine sandy soils which are often associated with rock. While jack pine forms the major component of the tree stratum, black spruce also occurs with high frequency (often as small trees), and *Betula papyrifera* and *Acer rubrum* occur in some stands. *Alnus crispa* is the common tall shrub. The understory is of relatively low cover and not strongly dominated by any one species. The most commonly encountered shrubs are *Kalmia angustifolia*, *Vaccinium myrtylloides*, *Cornus canadensis*, *V. angustifolium*, and *Diervilla lonicera*. The ground layer is dominated by *Pleurozium schreberi*, although *Dicranum polysetum* also occurs.

(X) *Pinus banksiana* − *Corylus cornuta* − *Alnus crispa*

This type is characteristic of riparian stands on coarse sand along the Montreal River. The type is therefore mesic and probably mesotrophic, the water table normally occurring no more than a metre below the surface. Jack pine is the dominant tree, although *Betula papyrifera* also occurs with high frequency but lower cover. The tall shrubs *Alnus crispa* and *Corylus cornuta* occur with high frequency and cover, often forming dense impenetrable thickets. The shading of this tall shrub layer inhibits the development of a dense lower understory. Understory constituents include *Diervilla lonicera*, *Aster macrophyllus*, *Vaccinium myrtylloides*, *V. angustifolium*, *Maianthemum canadense*, and *Kalmia angustifolia*. *Pleurozium schreberi* occurs in the ground layer with relatively low cover.

The occurrence of *D. lonicera* and *A. macrophyllus* in the understory is interesting, as these species are more characteristic of a canopy dominated by *Populus tremuloides*. It seems likely that the two dominant tall shrubs may produce the necessary shade and deciduous litter for the establishment and persistence of these species. The relatively mesic, mesotrophic conditions undoubtedly have some influence also. The occurrence of *A. crispa* and *C. cornuta* are reflective of a high water table and more mesotrophic conditions (Mueller-Dumbois 1964; Gleason 1968).

Environmental characterization of the vegetation types

Table 1 presents a physiognomic−environmental characterization of the 10 vegetation types. Dominant species are defined as those contributing the greatest biomass and (or) cover. Substantial environmental divergence of the types is indicated, particularly with regard to substrate type, drainage class, and soil particle size. The depth of the organic layer and the extent of podzolization also show considerable variation among types. These results suggest the importance of substrate type and overall moisture availability in determining the constituent vegetation of sandy upland boreal regions.

Ordination of stands

The ordination scattergram (Fig. 4) suggests that, in general, the group structure imposed on the stand data by cluster analysis is reproduced well by the ordination. A continuum is suggested, however, implying that the 10 vegetation types may in fact represent a continuum in vegetational (and presumably environmental) space and that the subdivisions imposed, while objective, are perhaps somewhat arbitrary. Nonetheless, the types described do serve the utilitarian purpose of providing a comprehensive description of the vegetation, and the ability to interpret the results in an environmental context suggests that they are ecologically meaningful.

Since many of the environmental factors measured in this study were not quantifiable across all stands, analytical techniques such as canonical correlation could not be used to examine trends in environmental variation. Instead, selected environmental factors were superimposed on the scattergram. The results (Fig. 5) suggest a number of interesting trends. Soil particle size and particularly drainage class show a scattergram trend from the lower right (large particle size, very xeric) to the upper left (small particle size, mesic), indicating increased moisture availability. Degree of organic accumulation also increases in this direction, though the trend is poorly developed in the upper left portion. Assuming that organic accumulation reflects overall site productivity, a positive correlation between moisture availability and productivity is indicated. Podzolization is greatest near the centre of the scattergram (vegetation types V, VI, VII, and IX), corresponding to good but not excessive stand drainage.

Species classification

The cluster analysis dendrogram is presented in Fig. 6. Species occurring with a frequency of less than 10 were first removed from the data set. A plot of sum of squares versus number of groups, and ecological considerations, suggested the recognition of five groups, giving a classification efficiency of 27.2%. These are discussed below.

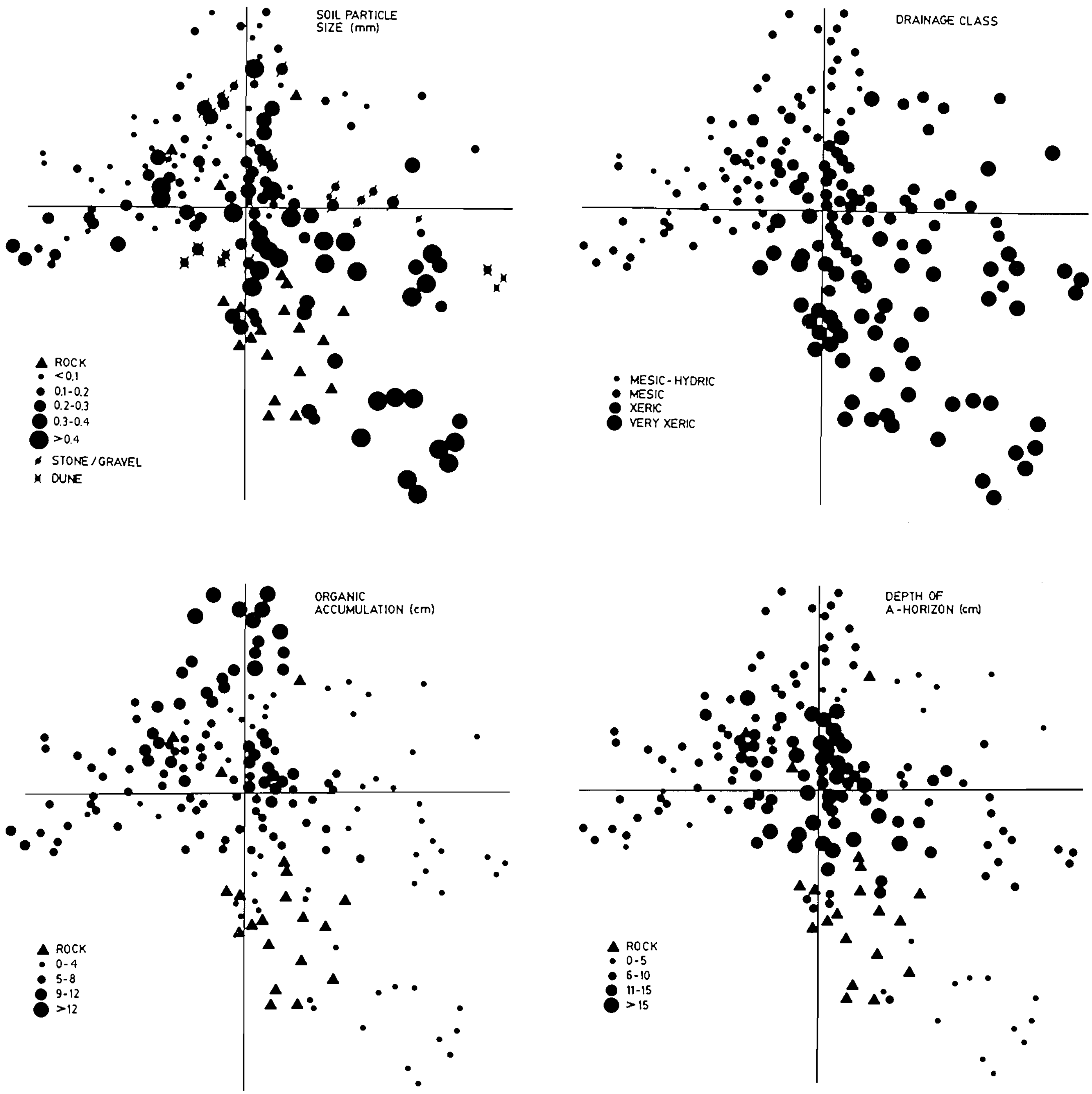

FIG. 5. Selected environmental factors superimposed on the scattergram of Fig. 4.

Group A

These eight species form a distinctive group restricted to dune slopes of unstable, coarse sand. Such stands are highly xeric and oligotrophic. These species characteristically grow directly on sand, since surface organic accumulation is virtually nonexistent.

Group B

These 15 species occur in very xeric, oligotrophic habitats, either on dry rock outcrops or coarse sandy flats. Such areas generally have some accumulation of poorly decomposed humus. Species may grow directly on rock (*Stereocaulon paschale*, *Cladina*, and *Cladonia* species), on humus layers over rock (*Dicranum polysetum*, some *Cladonia* species), on humus layers over rock (*Dicranum polysetum*, some *Cladonia* species), or in pockets of mixed organic and inorganic matter (*Vaccinium angustifolium*, *Ptilidium ciliaire*, *Potentilla tridentata*, *Oryzopsis pungens*, *Polytrichum juniperinum*).

Group C

The 12 species of this group require more mesic and mesotrophic conditions, occurring on sand or gravelly sand in riparian habitats. In such areas the water table is no more than a metre or so from the surface, providing some nutrient enrichment through groundwater flow.

Group D

These six species are characteristic of mesic, oligotrophic habitats, occurring in upland sites bordering acidic black

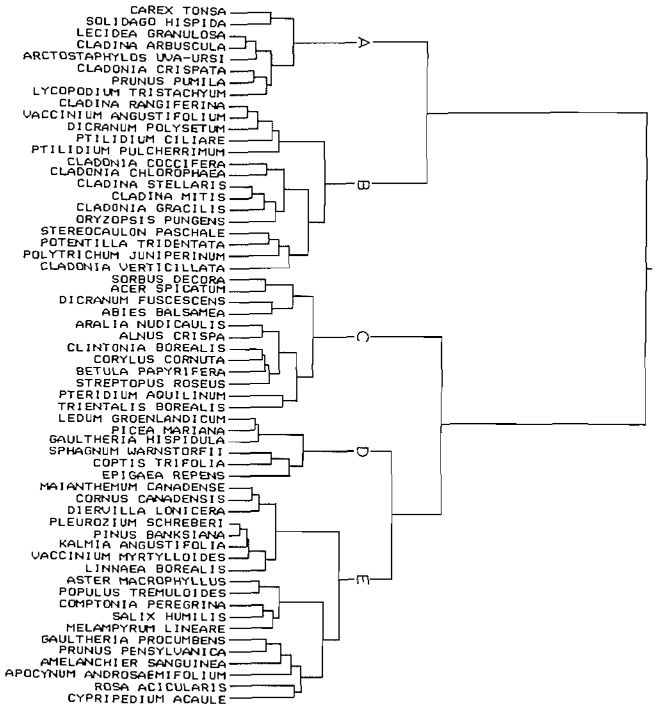

FIG. 6. Sum of squares agglomeration dendrogram of the 60 most common species encountered in the study. The five species ecological groupings (A–E) are also indicated.

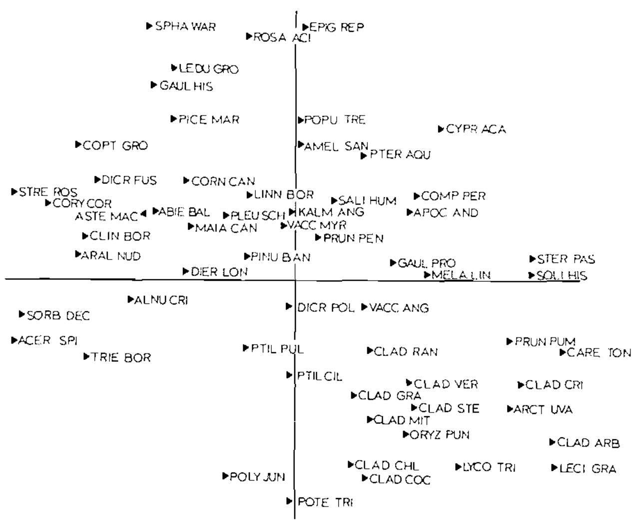

FIG. 7. Nonmetric multidimensional scaling (two-dimensional solution, utilizing chord distance) of the 60 most common species encountered in the study. Codes correspond to species names (the first four letters of the genus, and the first three of the species epithet, see Fig. 6). The stress value is 16.2%.

spruce bogs. The water table is generally no more than a metre or so from the surface.

Group E

This is a large group of 12 species characteristic of flat upland sandy sites dominated by jack pine. The vegetation represents a pyric–edaphic climax, the species forming a distinct ecological group adapted to the xeric to xeric–mesic, oligotrophic conditions. These species are typically well adapted to fire, with many having the ability to resprout from underground parts after a relatively light fire, or to rapid colonization of more severely burned areas.

TABLE 2. Results of the partitioning of total contingency chi-squared into additive components in concentration analysis. See also Fig. 8

Canonical variate	Canonical correlation	Chi-square	Percent
1	0.634	1252.48	60.8
2	0.349	379.04	18.4
3	0.302	285.06	13.8
4	0.214	142.95	7.0
Total		2059.3	100.0

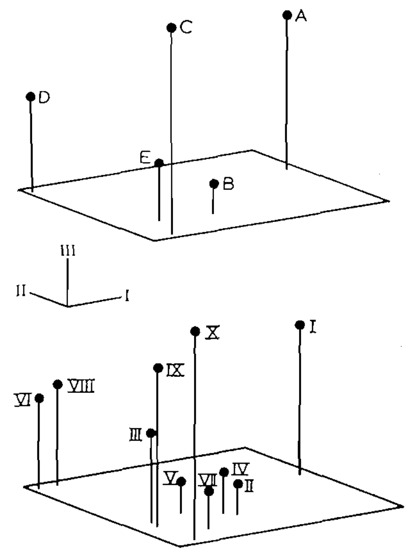

FIG. 8. Three-dimensional concentration analysis ordinations of the 10 vegetation types (I–X) and five species ecological groupings (A–E). These ordinations have a one-to-one correspondence.

Species ordination

The ordination scattergram is shown in Fig. 7. *Pinus banksiana* occurs near the centre of this ordination, with various trends emanating from it. Species adapted to highly xeric, oligotrophic conditions (species group A) occur at the lower right. Those species characteristic of rock outcrops (group B) occur in the same area of the scattergram, but slightly to the left. Species characteristic of mesic, mesotrophic riparian sites (species group C) occur in the middle left, while those adapted to mesic, oligotrophic conditions (species group D) are found at the upper left of the scattergram. Members of species group E, adapted to growing under a jack pine canopy on sand flats, occur near the centre of the scattergram.

A xeric–mesic trend in the species ordination, from lower right to upper left, is clearly apparent, underlying the importance of soil moisture conditions to the development of interspecific associations.

Ecological relationships

Concentration analysis was performed to summarize trends in the 10 vegetation types and five species groupings, and to examine the relationship between the two classifications. The results are summarized in Table 2, while Fig. 8 presents the three-dimensional scattergrams. These scattergrams have a one-to-one correspondence.

The results for the vegetation types suggest four major

TABLE 3. Simple (r) and multiple (R) correlations of concentration analysis scores for the vegetation types with selected environmental parameters

	r_1	r_2	r_3	R
Drainage class	−0.903*	0.152	0.336	0.945*
Nutrient status	−0.916*	−0.054	0.389	0.977*
Soil particle size	−0.866*	−0.235	0.212	0.926*

*Probability less than 0.01.

groupings. Vegetation type I forms its own group. It shows very high affinity with species group A, underlying the characteristic highly xeric and oligotrophic conditions prevailing on these unstable sand dune systems. Types VI and VIII, both of which are characteristic of low-lying areas on coarse sand adjacent to boggy land, show a high affinity with species group D. Conditions here are more mesic than the upland jack pine forests, though they remain oligotrophic. A third general category includes types II, III, IV, V, and VII. These are all jack pine dominated ecosystems of xeric to xeric−mesic, oligotrophic habitats. Types II and IV show highest affinity with species group B, indicating xeric conditions on rock or very coarse sand. By contrast, types III, V, and VII are more highly associated with species group E, indicating somewhat less xeric conditions (medium to coarse, well-drained sands). The final category (to which type III shows some affinity) consists of types IX and X, which are characteristic of more nutrient rich jack pine dominated stands.

Overall trends in the scattergram of the 10 types were summarized by correlating quantifiable environmental factors (drainage, estimated nutrient status, and soil particle size) with the axis scores. The results, presented in Table 3, indicate a strong moisture−nutrient gradient along the first axis (which accounts for over 60% of the total chi-squared). The multiple correlation values further reinforce this. The second and third axes are rather poorly correlated with these factors, however. These axes may indicate trends in unmeasured environmental factors or may represent trends in floristic variation attributable to biotic and (or) historical factors.

Discussion

The results have demonstrated the importance of soil moisture status in dictating species composition and interspecific associations of upland, jack pine dominated boreal habitats. There is some evidence that nutrient status is also important, though more data would be required to substantiate this claim.

Pinus banksiana on coarse sand deposits is generally considered to be an edaphic−pyric climax, with recurrent fires perpetuating the ecosystem (Eyre 1938; Ahlgren and Ahlgren 1960; Ritchie 1956; Heinselman 1973). Rowe and Scotter (1973) have attributed the success of jack pine in a pyric ecosystem to cone serotiny, early seed production, rapid seedling growth under full light, and frost hardiness of seedlings. Seedlings also require an inorganic substrate and are highly shade intolerant, suggesting that a stand of jack pine may be succeeded by other species given sufficient time. Many of the jack pine stands (with the exception of the very xeric stands) had *Picea mariana* and occasionally *Abies balsamea* saplings or small trees in the understory, which lends credence to the hypothesis that either or both of these species will eventually dominate the tree stratum (Ritchie 1956; Heinselman 1973; Cayford and McRae 1983). Alternatively, Dix and Swan 1971 (also, Carleton and Maycock 1978) have suggested that the vegetation may become "parklike." Such open areas do occur within the Elk Lake study area, particularly within types IV and V. Whether these sites are the result of xeric conditions, surface fires, or a true successional sequence is not apparent; however, a combination of xeric conditions and a fire some years after the severe fire of the early 1920s seems the most likely candidate. Such a light fire would kill the young jack pine saplings but would not severely damage the underground perennating organs of fire-adapted shrubs which would have also established at the sites. This, coupled with the lack of a seed source for jack pine, could lead to an open parkland dominated by ericaceous shrubs and *Pleurozium schreberi*, with occasional scattered jack pine and black spruce (Rowe and Scotter 1973).

There is some evidence of overlapping habitat preferences between jack pine and trembling aspen, particularly on the less coarse sands of upland plains (vegetation type VII). Past history seems to be important in determining which of these species occurs in such areas. Trembling aspen, once established, may be difficult to eradicate because of its ability to resprout from root suckers following all but the most severe fires. Conversely, jack pine will generally reestablish itself following a severe fire because of cone serotiny; seedlings will have a chance to become well established in the same season, thereby outcompeting other species (Rowe and Scotter 1973).

Dix and Swan (1971) (also Rowe 1961; Carleton and Maycock 1978) have evoked the "pulse strategy" of Odum (1969) to explain temporal dynamics in boreal ecosystems. By this strategy fire maintains healthy, productive stands near the early stages of a hypothetical successional sequence. Similarly, Loucks (1970) cites the high incidence of fire as resulting in a randomly perturbed cyclical pattern of development in boreal ecosystems. The degree of occurrence and severity of fire is important in determining, quite independently of deterministic factors such as substrate conditions, the vegetation of a given stand. The observation of Ritchie (1956) that upland stands of apparently identical topographic and substrate conditions may be floristically different is undoubtedly attributable to historical factors related to fire. Thus in addition to substrate and related influences, which are deterministic in nature, the vegetation at a given stand is also determined by a probabilistic or chance component related to fire and fire history. On balance, the nature of the substratum, soil moisture conditions, fire history (including both severity and frequency of occurrence), the nature of the vegetation before a fire, and the adjacent vegetation (as a diaspore source) all appear to be important determinants of the vegetation of a given stand.

Muich (1970) has hypothesized that species of pyric ecosystems have adapted by increasing their flammability, sacrificing the individual for the benefit of the species as a whole. In addition, pyric species are adapted to survival and competition in the presence of recurrent fires. Carleton and Maycock (1978) have termed a fire ecosystem an unpredictable environment, but this is somewhat misleading. While the exact timing of a fire is largely unpredictable, fire is a recurrent phenomenon to which pyric boreal species are well adapted. Thus, in an evolutionary context recurrence implies that a fire ecosystem is a predictable one (Johnson 1979). Species adaptations to recurrent fires include effective regeneration following a fire, rapid growth and reproduction within the span of mean fire recurrence, rapid diaspore establishment (favouring opportunistic species), the ability to colonize open exposed sites and mineral soils, and fire-stimulated seed germination.

Carleton and Maycock (1978; after Dix and Swan 1971) have suggested that upland boreal vegetation may be held in "check," with succession arrested after an initial invasion of tree species. This may be attributable to the lack of a seed source of shade-tolerant species, edaphic factors (Ritchie 1956), or competition from understory shrubs. There is good evidence for this at Elk Lake, as many stands show poor tree regeneration in the understory. This is not true at all sites, however, and it would be misleading to make any generalizations regarding overstory replacement (or lack of it) without examining the question in greater detail and over a wider range of sites. A study by Carleton (1982*b*) has shown that the pattern of establishment beneath jack pine stands is complex. It appears to be dictated both by the proximity of a seed source and surface fires, which expose the mineral soil required for successful germination and establishment. These results suggest that it is misleading to infer a common successional sequence on upland jack pine dominated sites.

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