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Paleovegetational Reconstruction Based on Modern and Fossil Pollen Data: An Application of Discriminant Analysis

Kam-biu Liu* and Nina Siu-Ngan Lam†

*Department of Geography and Anthropology, Louisiana State University, Baton Rouge, LA 70803

†Department of Geography, The Ohio State University, Columbus, OH 43210

Abstract. This paper introduces the use of discriminant analysis as an aid in paleovegetational reconstruction based on modern and fossil pollen data. We derived a set of discriminant functions that correctly classifies 95 percent of 121 surface samples collected from different vegetation regions in northeastern North America. These functions were then applied to the pollen-stratigraphic data from Jack Lake to reconstruct the postglacial vegetational history of northern Ontario. The discriminant analysis results are summarized in two indices. A "vegetation zonal index" directly translates each fossil pollen spectrum into its modern vegetational analogue. Paleovegetation types without modern analogue could be easily detected by computing the "probability of modern analogue." These results indicate explicitly that the early spruce-dominated boreal forest around Jack Lake does not have a modern analogue and that the boreal forest/Great Lakes–St. Lawrence Forest ecotone advanced far north of Jack Lake during the Hypsithermal (ca. 7,300–2,600 B.P.).

Key Words: discriminant analysis, pollen data, paleovegetational reconstruction, classification, vegetation zonal index, modern analogue, ecotone, Ontario.

A primary task for Quaternary palynologists is to reconstruct past vegetational changes from pollen-stratigraphic evidence. This is done by comparing fossil pollen assemblages with modern pollen assemblages collected from known vegetation regions. By assuming that the same pollen-vegetation relationships existing today also existed in the past, it is possible to infer that the paleovegetation that produced the fossil pollen assemblage is similar to the vegetation producing a similar modern pollen assemblage (i.e., its modern analogue). The increasing use of computers since the early 1970s has permitted fossil pollen assemblages to be related quantitatively to their modern analogues by means of a number of numerical techniques.

Several studies have shown that many late-glacial and early Holocene pollen assemblages (and hence the vegetation communities they represent) do not have modern analogues (M. B. Davis 1976, 1978; Birks 1981a, 1981b; Ritchie 1977; Ritchie and Yarranton 1978a, 1978b). For example, because of differential species migra-

tion rates and the prevalence of fresh soils, the late-glacial spruce forest in the American Midwest and west-central Canada differed from the modern boreal forest by lacking jack pine and containing an admixture of thermophilous hardwoods (Amundson and Wright 1979; Wright 1971; Ritchie 1976). A numerical technique is therefore needed not only to identify quantitatively a fossil pollen assemblage with its modern analogue from known vegetation regions, but also to detect objectively fossil pollen assemblages without modern analogues.

Several numerical techniques have been employed to compare modern and fossil pollen spectra. The first attempts involved Spearman rank correlation analysis (Ogden 1969; King 1973) and Pearson's product-moment correlation analysis (R. B. Davis et al. 1975). These techniques directly compare a fossil pollen sample with the modern pollen spectra; the similarity of each pair of samples is measured by their correlation coefficient. An apparent disadvantage of these correlation techniques is that

pollen spectra are compared pairwise, so that when both the modern and fossil pollen data sets are very large, the matrix of correlation coefficients will become too large to portray and interpret effectively. More important, Prentice (1980) has pointed out that these correlation coefficients are unsuitable for comparing pollen spectra because they are not true measures of similarity.

Principal component analysis (Webb 1974a; Ritchie 1977; Ritchie and Yarranton 1978a, 1978b; Birks and Berglund 1979) and canonical variate analysis (Adam 1970; Birks 1976, 1980) have been used to reduce the dimensionality of the pollen data. These multivariate numerical techniques seek to summarize the variation within the data into a few linear combinations of variables (i.e., principal components or canonical variates), which permit comparison between the modern and fossil pollen spectra in a multi-dimensional space. A common practice in this approach is to plot the scores of the pollen spectra along two dimensions or axes in the form of a scatter diagram. The similarity or dissimilarity between two pollen spectra or two groups of spectra is then measured by the distance between the two respective points in this coordinate system. Although the scatter diagram provides a useful visual aid for comparing modern and fossil pollen spectra, the assignment of a fossil spectrum to one of the groups of modern pollen assemblages (or to none in the case of no modern analogue) is still subjective. The decision is especially arbitrary when the fossil pollen spectrum is located between two or more groups of modern pollen spectra, because neither technique provides a quantitative criterion value to discriminate between groups of samples. The tasks of discrimination and classification can be more effectively and explicitly performed by discriminant analysis.

This paper introduces discriminant analysis as an alternative technique in paleovegetational reconstruction based on modern and fossil pollen data. Discriminant analysis differs from other numerical techniques (except canonical variate analysis) in that it requires an a priori grouping of samples based on vegetation types. Since Holocene vegetational changes usually involve temporal changes from one vegetation type to another, discriminant analysis is an effective means to depict major trends of vegetational changes from pollen-stratigraphic data. Discriminant analysis has not been a common numerical

technique in palynological research. One of its variants, canonical variate analysis, has been used as an ordination technique to discriminate among groups of modern pollen spectra from different vegetation regions (Birks 1977; Birks, Webb and Berti 1975; A.M. Davis 1980), and to compare modern and fossil pollen spectra (Adam 1970; Birks 1976, 1980). However, discriminant analysis can be used not only to classify samples into groups according to some a priori criteria, but also to assign group memberships to new samples with unknown identities. This unique property has recently been exploited by Birks and Peglar (1980) to discriminate between fossil pollen grains of white spruce (*Picea glauca*) and black spruce (*P. mariana*). Heide (1981) used a similar approach to classify fossil pollen spectra into boreal forest and conifer-hardwood forest assemblages based on their scores on a single discriminant function. Our study applies discriminant analysis to aid paleovegetational reconstruction from pollen-stratigraphic data in a different way.

In this paper, we illustrate an application of discriminant analysis by applying it to a Holocene pollen stratigraphy from Jack Lake, Ontario, to reconstruct the postglacial vegetational history of northern Ontario. The modern pollen data network, against which the fossil pollen spectra are compared for modern analogues, is derived from a large number of sites in different vegetation regions of northeastern North America. We shall demonstrate that, within the constraints imposed by its statistical assumptions, discriminant analysis can (1) reveal explicitly *whether* and *to what extent* a fossil pollen assemblage has modern analogues, based on an index called the probability of modern analogue; and, (2) if a modern analogue does exist, relate the fossil pollen assemblage quantitatively and objectively to the group of modern pollen spectra representing its modern analogue, based on a probability of group membership.

Discriminant Analysis

The mathematics of discriminant analysis has been reviewed by many authors (e.g., Lachenbruch 1975; Tatsuoaka 1970, 1971; Cooley and Lohnes 1971; J. C. Davis 1973). In palynological literature, the principles and procedures of discriminant analysis involving two groups have been discussed by Birks and Peglar (1980).

Discriminant analysis requires an a priori classification of samples into groups. The technique seeks to derive linear combinations of variables, called discriminant functions, that are independent of each other. These discriminant functions will ensure maximum separation among the a priori groups of samples. They could also be used to classify new samples with unknown group memberships into one of the a priori groups. It is the latter property that led to the selection of this numerical technique for the present research problem.

Probability of Group Membership

The subprogram DISCRIMINANT in SPSS (Statistical Package for the Social Sciences) (Nie et al. 1975) was used to perform the discriminant analysis. Two useful parameters could be computed by DISCRIMINANT. The first, here called the *probability of group membership*, is based on the distance between a sample and the centroid of each a priori group in a multidimensional space. Denoted as $P(H_k|X_i)$, the probability of sample i belonging to group k given the values in case i of the m variables ($X_{1i}, X_{2i}, \dots, X_{mi}$), is calculated in SPSS by first computing the quantity for each group:

$$g_{ik} = \log P_k - \frac{1}{2} (\log |D_k| + \chi_{ik}^2) \quad (1)$$

where P_k is the a priori probability for group k . If no a priori probability is specified before the calculation, equal probability for each group is assumed. $|D_k|$ represents the determinant of the within-group variance-covariance matrix of group k . χ_{ik}^2 is computed by:

$$\chi_{ik}^2 = d'_{ik} D^{-1} d_{ik} \quad (2)$$

where D^{-1} is the inverse of the pooled within-group variance-covariance matrix; d_{ik} is the vector containing the difference between sample i and the k^{th} group centroid for all variables, and d'_{ik} is its transpose. $P(H_k|X_i)$ is then determined by:

$$P(H_k|X_i) = \frac{\exp(g_{ik} - \max_k g_{ik})}{\sum_{k=1}^g \exp(g_{ik} - \max_k g_{ik})} \quad (3)$$

if $(g_{ik} - \max_k g_{ik}) > -46$, otherwise $P(H_k|X_i)$ is zero (Norušis 1979). For each sample, the sum of the

probabilities of group membership for all k groups is equal to one. A sample is assigned to the group to which its probability of group membership is the highest. As will be shown later, this probability is useful not only in assigning samples to a group, but also in identifying samples with transitional identities between two groups.

Probability of Modern Analogue

Classification of new samples (i.e., fossil pollen assemblages) solely on the basis of their probabilities of group membership may sometimes be misleading. This is because each new sample must be assigned to one of the a priori groups (i.e., vegetation regions), without allowing for any no-modern-analogue situations. This is a serious limitation in paleovegetational reconstruction, but the problem can be overcome by computing the second parameter, here conveniently called the *probability of modern analogue*. Denoted as $P(X_i|H_k)$, this probability represents the proportion of samples, among members of group k , that have values of the m variables in the vicinity of ($X_{1i}, X_{2i}, \dots, X_{mi}$) (Tatsuoka 1971). In SPSS, $P(X_i|H_k)$ is determined by first calculating the chi-square distance between a sample and its assigned group centroid by using Equation (2). If sample i is a member of group k , χ_{ik}^2 has a chi-square distribution with m degrees of freedom, where m is the number of variables. $P(X_i|H_k)$ is the significance level of such a χ_{ik}^2 . In other words, $P(X_i|H_k)$ measures the similarity of sample i in group k with other samples in the same group. This probability is particularly useful in correctly interpreting the discriminant result. It is possible that a sample may in fact be very dissimilar to all of the groups under consideration (i.e., have low probabilities of modern analogue) but still be classified to one of the groups, a necessary condition for computing the probability of group membership. It is therefore necessary to examine both probabilities for the present research problem.

In palynological terms, the probability of modern analogue compares a pollen assemblage with the "palynological signature" of its assigned vegetation region (as represented by its group centroid). This probability could be computed for both modern and fossil pollen samples. A low probability for a surface sample suggests

that this sample, though geographically derived from or statistically assigned to a vegetation region, in fact contains a pollen assemblage distinct from the palynological signature of this vegetation region. Some low probability values may occur in groups composed of highly variable surface samples. A low probability for a fossil pollen assemblage suggests that it does not resemble the palynological signature of its assigned modern vegetation region. This, however, does not preclude the possibility that this fossil sample may resemble an equally atypical modern sample in the same group (which would have been regarded as its modern analogue in the strict sense of the word). With this caution taken, it is possible to interpret a fossil pollen sample with low probability of modern analogue as belonging to none of the *a priori* groups, hence representing a paleovegetation without

modern analogue at the level of vegetation region or formation.

The Data Base

Modern Pollen Spectra

To establish the spatial and statistical relationships between modern pollen and vegetation, modern pollen spectra were obtained from 121 sites along a transect from Michigan to Baffin Island (Fig. 1). These include 63 surface samples collected from northern Ontario (Liu 1982) and 58 lake sediment and moss samples from a wider region of northeastern North America. The latter group of samples was selected from a large number of unpublished and published sources (e.g., Webb 1974b; Andrews, Mode and Davis 1980; McAndrews, unpublished pollen data), compiled by J. H. McAndrews and G. C. Manville at the Royal Ontario Museum.

These 121 surface samples generally lie along a broad transect between 70° and 90°W longitude and between 40° and 70°N latitude. This transect spans five major vegetation regions (corresponding to vegetation formations) as defined by Rowe (1972): (1) deciduous forest; (2) Great Lakes–St. Lawrence Forest (hereafter called mixed forest); (3) boreal forest; (4) forest and barren (hereafter called boreal woodland); and (5) tundra. Among these 121 surface samples, 18 are from deciduous forest, 24 from mixed forest, 53 from boreal forest, 12 from boreal woodland, and 14 from tundra. These constitute the five *a priori* groups for the discriminant analysis.

In all modern and fossil samples pollen percentages were calculated based on a sum of 25 taxa, including all trees and shrubs as well as Gramineae and Cyperaceae. Eighteen taxa were selected for the discriminant analysis. These included *Picea* (spruce), *Abies* (fir), *Thuja/Juniperus* (cedar/juniper), *Pinus banksiana/resinosa* (jack/red pine), *Pinus strobus* (white pine), *Betula* (birch), *Populus* (poplar), *Quercus* (oak), *Ulmus* (elm), *Carya* (hickory), *Acer* (maple), *Tsuga* (hemlock), *Fagus* (beech), *Alnus* (alder), *Salix* (willow), *Artemisia* (sage), Gramineae (grass), and Cyperaceae (sedge). Selection of these pollen taxa was based on their importance in characterizing the major vegetation regions in northeastern North America (Webb and McAndrews 1976). These 18 taxa do not add up to 100 percent in any sample.

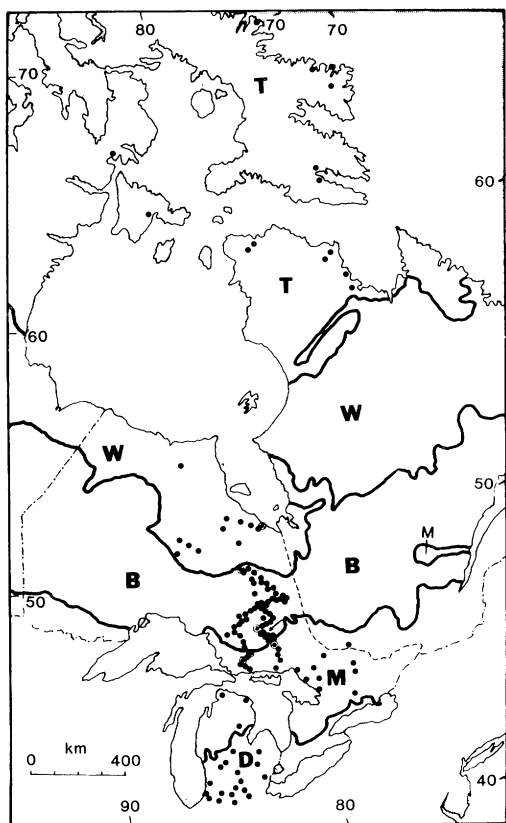


Figure 1. Distribution of the 121 surface samples in relation to Rowe's vegetation regions. Circled dots are samples misclassified by discriminant analysis. Jack Lake is indicated by an arrow. D = deciduous forest, M = mixed forest, B = boreal forest, W = boreal woodland, T = tundra.

The mean percentages and standard deviations of the 18 pollen taxa in each vegetation region are listed in Table 1. It is clear that each vegetation region is characterized by a distinctive pollen assemblage. The pollen of *Quercus*, as well as *Ulmus*, *Carya*, *Acer*, and *Fagus*, reach highest percentages in the deciduous forest. The mixed forest is characterized by maximum frequencies of *Pinus strobus*, *Betula*, and *Tsuga*. *Pinus banksiana/resinosa* is most abundant in the boreal forest, and *Picea* most abundant in the boreal woodland. The tundra contains very high percentages of Cyperaceae, Gramineae, and *Salix*. The large standard deviations associated with these pollen types, however, suggest great variability among these pollen spectra from the tundra.

Pollen Stratigraphy from Jack Lake

Jack Lake (47°19'N, 81°46'W) occupies a small basin in the boreal forest region of northern Ontario (Fig. 1). It is, however, only about 20 km north of the boreal forest/Great Lakes–St. Lawrence Forest ecotone (Rowe 1972). The pollen stratigraphy from this site was

chosen for testing the application of discriminant analysis because it is expected to contain a sensitive record of ecotonal displacements and vegetational changes during the Holocene.

The pollen stratigraphy from Jack Lake is 4.80 m long and is divided into four local pollen assemblage zones including four subzones (Liu 1982) (Fig. 2). (1) The basal *Picea* pollen zone (Zone JL-1) contains large percentages of spruce pollen. It is divided into two subzones, JL-1a and JL-1b, based on relatively high frequencies of herb pollen (e.g., Cyperaceae, *Artemisia*, *Pteridium*) and *Populus* and *Larix* pollen, respectively. (2) The *Pinus banksiana/resinosa* pollen zone (Zone JL-2) above is characterized by a peak in jack/red pine pollen and declining frequencies of *Picea*. (3) The *Pinus strobus* pollen zone (Zone JL-3), dominated by the pollen of white pine, is divided into two subzones. Subzone JL-3a contains maximum percentages of *Pinus strobus*, which declines steadily in subzone JL-3b and is replaced by *Betula*. (4) The *Pinus banksiana/resinosa*-*Betula* pollen zone (Zone JL-4) is marked by an increase in the pollen of *Pinus banksiana/resinosa* and *Picea*, and *Betula* pollen remains relatively abundant. Three C-14 dates provide the time

Table 1. Summary Statistics of Modern Pollen Rain in Different Vegetation Regions^a

| Pollen taxon | Vegetation region | | | | |
|-------------------------------|-------------------------------------|--------------|-----------------------|-----------------------|------------|
| | Deciduous forest | Mixed forest | Boreal forest | Boreal woodland | Tundra |
| <i>Picea</i> | 0.3 ^b (0.3) ^c | 5.4(5.8) | 12.9(10.9) | 37.4(14.8) | 7.2(9.7) |
| <i>Abies</i> | 0.0(0.1) ^d | 1.9(1.6) | 1.7(2.3) | 1.0(0.9) | 0.0(0.0) |
| <i>Thuja/Juniperus</i> | 0.9(0.5) | 1.8(1.7) | 1.5(1.8) | 0.1(0.2) | 0.1(0.3) |
| <i>Pinus bank/res</i> | 2.6(1.8) | 24.5(17.9) | 44.4(16.8) | 4.1(9.8) | 6.2(5.3) |
| <i>Pinus strobus</i> | 6.8(7.3) | 20.3(11.7) | 3.6(3.9) | 0.1(0.2) | 0.1(0.2) |
| <i>Betula</i> | 3.5(2.4) | 21.8(10.9) | 16.1(7.8) | 10.0(3.6) | 7.9(8.5) |
| <i>Populus</i> | 2.5(2.2) | 0.4(0.6) | 0.9(1.2) | 0.2(0.2) | 1.1(3.8) |
| <i>Quercus</i> | 43.7(10.9) | 3.7(3.4) | 1.2(0.8) | 1.3(0.9) | 0.0(0.0) |
| <i>Ulmus</i> | 8.1(3.0) | 1.1(1.1) | 0.3(0.3) | 0.1(0.2) | 0.1(0.2) |
| <i>Carya</i> | 3.6(2.0) | 0.2(0.2) | 0.0(0.1) ^d | 0.0(0.0) | 0.0(0.0) |
| <i>Acer</i> | 3.9(1.8) | 3.0(2.4) | 0.2(0.2) | 0.0(0.1) ^d | 0.0(0.0) |
| <i>Tsuga</i> | 0.6(0.7) | 3.7(4.1) | 0.1(0.2) | 0.0(0.0) | 0.1(0.2) |
| <i>Fagus</i> | 5.5(5.0) | 1.1(1.5) | 0.1(0.2) | 0.0(0.0) | 0.0(0.0) |
| <i>Alnus</i> | 1.3(1.4) | 2.8(2.2) | 8.5(6.5) | 7.2(4.5) | 4.7(5.5) |
| <i>Salix</i> | 2.6(1.9) | 0.5(0.7) | 0.7(1.0) | 3.4(8.0) | 14.5(22.0) |
| <i>Artemisia</i> ^e | 0.6(0.4) | 0.5(0.7) | 0.5(0.4) | 0.9(0.7) | 1.0(1.0) |
| Gramineae | 5.0(0.8) | 2.6(1.9) | 2.9(2.0) | 1.5(3.2) | 22.5(24.2) |
| Cyperaceae | 1.3(1.1) | 0.8(1.1) | 1.6(2.0) | 7.0(5.5) | 41.3(22.2) |

^a Pollen percentages are based on a sum of all tree and shrub pollen taxa together with Gramineae and Cyperaceae. Only the 18 taxa selected for the discriminant analysis are presented.

^b Mean pollen percentage

^c Standard deviations are in brackets.

^d Mean pollen percentages of <0.05 are rounded to 0.0.

^e *Artemisia* percentages are calculated outside the pollen sum.

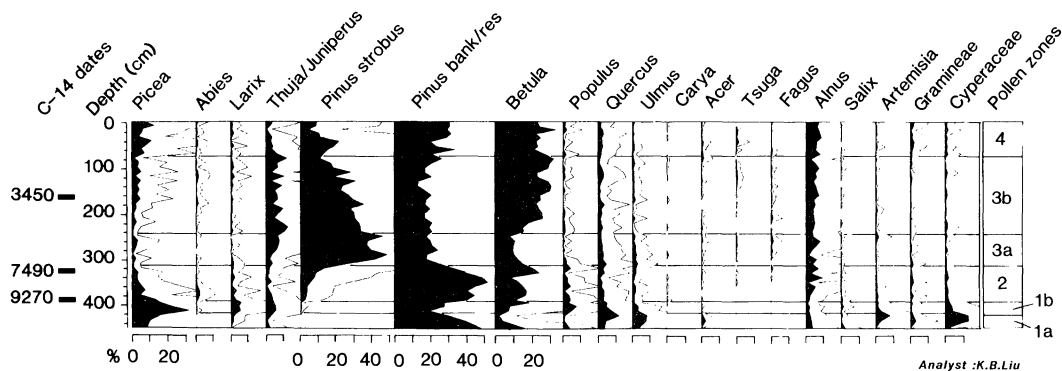


Figure 2. Abbreviated pollen percentage diagram for Jack Lake. All curves are plotted to the same scale. The scale of the unshaded silhouettes has been exaggerated five times. Pollen percentages are based on a sum of at least 300 grains derived from trees, shrubs, and herbs, excluding pteridophytes and aquatics.

control for this pollen stratigraphy (Liu 1982). All dates mentioned in this paper are obtained by linear interpolation between C-14 dates.

Ecological and Statistical Assumptions

The application of discriminant analysis to paleovegetational reconstruction from modern and fossil pollen data is constrained by a number of ecological and statistical assumptions. The ecological assumptions are: (1) the modern pollen samples selected for the analysis adequately represent the palynological signatures of their parent vegetation regions; (2) no evolutionary or physiological change has occurred over the time period considered that would alter a species' pattern of pollen production and dispersal or its ecological amplitudes in the environment; (3) the same set of climatic and physical factors that governs pollen dispersal and deposition today also operated in the past. The first assumption depends on the number and spatial distribution of the modern pollen spectra used in the analysis in relation to the spatial and statistical variability of the pollen rain in these vegetation regions. Given the limited availability of surface samples in some vegetation regions, the spatial distribution of our modern pollen data points is uneven. The boreal forest and mixed forest regions are more well-represented in the modern data set than are the other three vegetation regions. However, since much of the variation contained in the fossil pollen data is expected to fall within the range of the boreal forest and mixed forest regions, the unequal representation among the

vegetation regions should not seriously affect the results of the analysis.

The second and third assumptions are difficult to test but are probably valid, within limits, for the time scale being considered (i.e., the Holocene). These assumptions, underlining the principle of uniformity, apply to any paleoecological reconstruction based on micro-paleontologic data and are not unique to discriminant analysis (Webb and Clark 1977; Birks 1981a; Webb and Bryson 1972).

Five statistical assumptions have to be made in using discriminant analysis for statistical inference (J. C. Davis 1973). (1) The samples in each a priori group are randomly chosen. (2) The probabilities of an unknown sample belonging to any group are equal, unless some a priori probability is specified. (3) The samples used to derive the discriminant functions are correctly classified with respect to the a priori groups. (4) The variance-covariance matrices of the groups are statistically equal. (5) The variables are normally distributed within each group. The first two assumptions can be justified with some reservations. In some vegetation regions (e.g., boreal woodland and tundra), selection of surface samples was limited by their availability, resulting in fewer samples and an uneven sampling network. Assumption (3) can be justified only if the vegetation regions are discrete entities with clear-cut boundaries or if all the surface samples are sufficiently remote from the ecotones so that misplacement in the field or on the map is highly unlikely. The latter condition is probably met for the deciduous forest, boreal woodland, and tundra groups, but is less certain for the diffuse ecotone between the mixed forest and the boreal

forest in northern Ontario, where samples are densely spaced along two transects. This assumption, however, could be evaluated empirically. The classification results by discriminant analysis (discussed later) indicate that 95 percent of the 121 surface samples are correctly classified with respect to their a priori groups, suggesting that each of these vegetation regions has a distinct palynological signature as represented by the surface samples.

Assumptions (4) and (5) can be tested statistically. In testing assumption (4), the equality of within-group variance-covariance matrix, the Box's M statistic was used (Norušis 1979; Cooley and Lohnes 1971). The DISCRIMINANT subprogram provides an option to calculate the Box's M statistic. In the present set of modern pollen data, the variance-covariance matrices are singular for the deciduous forest, boreal woodland, and tundra groups partly because of zero values of some variables throughout these regions (e.g., *Abies* in deciduous forest, *Carya* and *Fagus* in boreal woodland and tundra). Therefore, the test could only be performed by excluding the variance-covariance matrices of these groups.¹ The Box's M statistic for the mixed forest and boreal forest was found to be 3,098.2, and the corresponding F-value was 12.2. With 171 and 6,700.4 degrees of freedom, the Box's M statistic is significant at the 0.0 level, implying no significant difference between the two variance-covariance matrices tested.

The measures of multivariate skewness and kurtosis proposed by Mardia (1970, 1974) were used to test Assumption (5). Compared with the ordinary univariate tests of normality (e.g., Kolmogorov-Smirnov test), Mardia's measures have the advantage of taking into account interrelationships among variables. A computer program was written to calculate these measures and to perform their corresponding significance tests.² Again, Mardia's measures of skewness

and kurtosis cannot be calculated for the deciduous forest, boreal woodland, and tundra groups because of singularities in their variance-covariance matrices. The results of the test show that the assumption of multivariate normality holds for the mixed forest group, but does not hold for the boreal forest group at the 0.05 significance level (Table 2).

Although the statistical assumptions of the technique are not fully met—a problem that is commonly encountered in many types of geological and biological data (Reyment 1971)—several authors have suggested that discriminant analysis is a robust technique (J. C. Davis 1973; Nie et al. 1975). Limited departures from multivariate normality or from equality of variance-covariance matrices would not seriously affect the classification results. Melton (1963) has suggested that meeting these two assumptions is not really necessary for applying the technique successfully and that such deviations, especially with respect to unequal variance-covariance matrices, could even aid in discrimination. Moreover, most numerical tests for these assumptions would be affected by sample size. For example, in the case of Mardia's measures of multivariate skewness and kurtosis, Reyment (1971) showed that smaller samples tend to produce unstable values. Effective testing of these statistical assumptions, therefore, must await the availability of a larger set of modern pollen data.

Results and Interpretation

Modern Pollen-Vegetation Relationships

The variance contained in the modern pollen data is completely accounted for by four discriminant functions. They account for 69.2 percent, 22.0 percent, 5.9 percent, and 2.9 percent of the total variance, respectively. This shows

Table 2. Summary Statistics of Mardia's Test of Multivariate Skewness and Kurtosis^a

| Group | $b_{1,m}$ | A | d.f. ^b | $\chi^2_{\alpha=.05}$ ^c | $b_{2,m}$ | B |
|---------------------------|-----------|---------|-------------------|------------------------------------|-----------|-------|
| Mixed forest (n = 24) | 237.33 | 949.32 | 1140 | 1234.99 | 311.81 | -1.77 |
| Boreal forest (n = 53) | 203.10 | 1794.05 | 1140 | 1234.99 | 392.30 | 4.38 |

^a See Note 2 for an explanation of notation.

^b degrees of freedom

^c the χ^2 value at 0.05 significance level

Table 3. Standardized Discriminant Function Coefficients

| Taxa | Function 1 | Function 2 | Function 3 | Function 4 |
|---------------------------|------------|------------|------------|------------|
| <i>Picea</i> | -0.09 | 0.22 | 0.08 | 0.35 |
| <i>Abies</i> | 0.09 | -0.41 | 0.70 | 0.39 |
| <i>Thuja/Juniperus</i> | -0.09 | -0.10 | 0.14 | 0.31 |
| <i>Pinus banklres</i> | 0.23 | -0.52 | 1.45 | 1.06 |
| <i>Pinus strobus</i> | 0.48 | -0.15 | 0.80 | -0.22 |
| <i>Betula</i> | 0.11 | -0.24 | 0.72 | 0.09 |
| <i>Populus</i> | 0.23 | 0.09 | 0.11 | 0.12 |
| <i>Quercus</i> | 1.11 | 0.12 | 0.33 | 0.32 |
| <i>Ulmus</i> | 0.50 | 0.08 | 0.12 | 0.24 |
| <i>Carya</i> | 0.06 | -0.03 | 0.19 | -0.09 |
| <i>Acer</i> | 0.56 | -0.05 | 0.25 | -0.25 |
| <i>Tsuga</i> | -0.46 | -0.28 | 0.39 | -0.10 |
| <i>Fagus</i> | 0.51 | 0.10 | 0.10 | 0.32 |
| <i>Alnus</i> | 0.04 | -0.14 | 0.51 | 0.60 |
| <i>Salix</i> | -0.07 | 0.18 | -0.22 | -0.15 |
| <i>Artemisia</i> | -0.14 | 0.24 | 0.30 | 0.10 |
| <i>Gramineae</i> | -0.22 | 0.90 | 1.21 | 0.53 |
| <i>Cyperaceae</i> | -0.27 | 1.09 | 1.07 | 0.40 |
| Percent of total variance | 69.2 | 22.0 | 5.9 | 2.9 |

that the discriminating power of the first two discriminant functions is very high, although all four functions are used by SPSS in the analysis. The standardized discriminant function coefficients for the 18 taxa on each function are listed in Table 3.

The discriminant scores of the 121 surface samples are plotted along the first two discriminant functions (Fig. 3). It shows that the five group centroids are clearly separated from each other. The deciduous forest and the tundra groups are palynologically most distinct, but this could be partly a function of the spatial segregation of these two groups of samples from the

others. Some overlapping occurs between the boreal woodland, boreal forest, and mixed forest groups. This overlapping reflects the transitional character of the vegetation regions and their palynological signatures in the study region.

Each of the 121 surface samples is classified into one of the five vegetation regions by the discriminant functions. A comparison of the objectively predicted group memberships with the a priori group memberships shows that 115 (or 95 percent) of the 121 samples are correctly classified (Table 4). Among the five groups, all samples from the deciduous forest and the tundra are correctly classified. Only two out of the 53

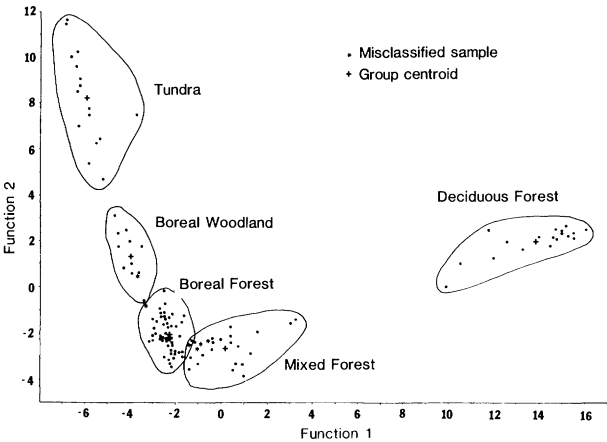


Figure 3. Ordination of 121 surface samples along discriminant functions 1 and 2.

Table 4. Classification Results of the Surface Samples

| Actual group | No. of samples | Predicted group membership | | | | |
|---|----------------|---------------------------------------|--------------|---------------|-----------------|-------------|
| | | Deciduous forest | Mixed forest | Boreal forest | Boreal woodland | Tundra |
| Deciduous forest | 18 | 18 ^a (100) ^b | 0 (0) | 0 (0) | 0 (0) | 0 (0) |
| Mixed forest | 24 | 0 (0) | 21 (87.5) | 3 (12.5) | 0 (0) | 0 (0) |
| Boreal forest | 53 | 0 (0) | 1 (1.9) | 51 (96.2) | 1 (1.9) | 0 (0) |
| Boreal woodland | 12 | 0 (0) | 0 (0) | 1 (8.3) | 11 (91.7) | 0 (0) |
| Tundra | 14 | 0 (0) | 0 (0) | 0 (0) | 0 (0) | 14 (100) |
| Total number of samples: 121 | | | | | | |
| Number of misclassified samples: 6 | | | | | | |
| Percentage of samples correctly classified: 95.04 | | | | | | |

^a Number of samples classified as that group^b Percentage of samples classified as that group

boreal forest samples are misclassified into adjacent vegetation regions (i.e., boreal forest and mixed forest), and one of the boreal woodland samples is misclassified as boreal forest. The mixed forest group has 87.5 percent correctly classified, with four samples misclassified as boreal forest. Most of the misclassified samples occur near the ecotones (see Fig. 1). This is explained by the ecotonal character of the vegetation at these sampling sites.

Vegetation Zonal Indices

The probabilities of membership in the predicted group and in the second most probable group are calculated for each surface sample. In all cases, the second most probable group is always the vegetation region that is geographically adjacent to the predicted vegetation region. For instance, the second most probable group for all samples classified by discriminant analysis as boreal forest is always either mixed forest or boreal woodland. This reflects the zonal pattern of the vegetation along a north-south gradient. It is possible, therefore, to convert these probabilities of group membership (in the predicted and the second most probable groups) into a single "vegetation zonal index" for each surface sample.³ Samples classified as "typical" (i.e., with 100 percent probability of group membership) deciduous forest, mixed forest, boreal forest, boreal woodland, and tundra are assigned vegetation zonal indices of 1.0, 2.0, 3.0, 4.0, and

5.0, respectively. Samples classified as transitional (i.e., having intermediate probabilities) between two adjacent vegetation regions are then assigned intermediate zonal indices relative to the two probabilities of group membership. For example, a sample classified as 90 percent mixed forest (i.e., the predicted group) and 10 percent boreal forest (i.e., the second most probable group) would have a vegetation zonal index of 2.1. Similarly, a vegetation zonal index of 1.8 indicates an 80 percent probability of belonging to the mixed forest and 20 percent probability of belonging to the deciduous forest. Therefore, samples classified as deciduous forest will have vegetation zonal indices ranging from 1.0 to 1.5, mixed forest from 1.5 to 2.5, boreal forest from 2.5 to 3.5, boreal woodland from 3.5 to 4.5, and tundra from 4.5 to 5.0.

The vegetation zonal indices and the probabilities of modern analogue are plotted for the 121 surface samples arranged latitudinally (Fig. 4). The boundaries between vegetation regions generally correspond to abrupt changes in the vegetation zonal indices.

Probabilities of Modern Analogue

For most surface samples the probability of modern analogue is high (>0.50) (Fig. 4), as would be expected from these modern pollen assemblages. Several samples within the tundra group have very low probability values (<0.1). This attests to the high variability in these tundra

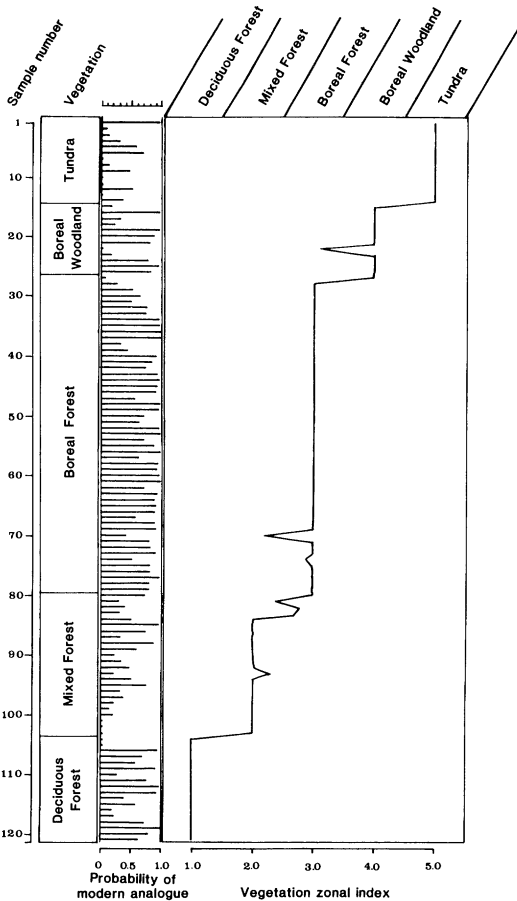


Figure 4. Results of discriminant analysis for the 121 surface samples.

pollen spectra, which are derived from moss polsters over a wide geographical area. Groups characterized by greater dispersion of data would tend to have a higher proportion of samples with very low probability values because these samples would be relatively far away from the group centroid.

There seems to be a slight decline in probability values for samples near the ecotones (e.g., between the boreal forest and mixed forest). This is probably due to the fact that, under the assumption of a normal distribution of samples and variables within a group, ecotonal samples would be farther away from their group centroid than most of the other samples of the same group. These values, however, are only moderately low (e.g., 0.2–0.5). Some very low values (<0.1) occur in several samples near the mixed forest/deciduous forest ecotone. These values are probably too low to be explained by the

“ecotone effect” alone and suggest that the surface samples they represent are unique among members of their own groups. Moreover, the fact that the vegetation zonal indices for these samples are not transitional also suggests that these pollen assemblages are not truly ecotonal in character.

Postglacial Vegetational Changes around Jack Lake

The probability of modern analogue and the vegetation zonal index are calculated for each fossil pollen spectrum in the same way as for the surface samples. These values are then plotted stratigraphically for the pollen sequence from Jack Lake. The stratigraphic changes in these probabilities and indices could then be easily interpreted in terms of vegetational changes (Fig. 5).

A vegetation zonal index of 4.0 at the lowest stratigraphic level indicates that the initial vegetation around Jack Lake is best described as a boreal woodland. The vegetation zonal indices change to about 3.0 in the rest of pollen zone JL-1. This suggests a succession toward a vegetation with boreal forest affinities. However, the probabilities of modern analogue are extremely low (<0.05) throughout this pollen zone, suggesting that this early boreal woodland/forest in fact does not have a modern analogue. Further evidence of this no-modern-analogue situation comes from an anomalous classification result for a sample at 423 cm. This sample, having a probability of modern analogue of zero, is classified as boreal forest but has tundra as its second most probable group, a condition clearly unmatched in any of the 121 surface samples. The vegetation zonal index for this sample was calculated as if the second most probable group were from the boreal woodland.

In order to substantiate further the interpretation that pollen zone JL-1 represents a vegetation without modern analogue, the discriminant scores for the fossil pollen spectra from Jack Lake were plotted along the first two discriminant functions and compared with those of the surface samples (Fig. 6). The pollen zone JL-1 samples clearly lie outside the ranges of the modern samples comprising the five vegetation regions.

The interpretation of pollen zone JL-1 by discriminant analysis as boreal woodland and bo-

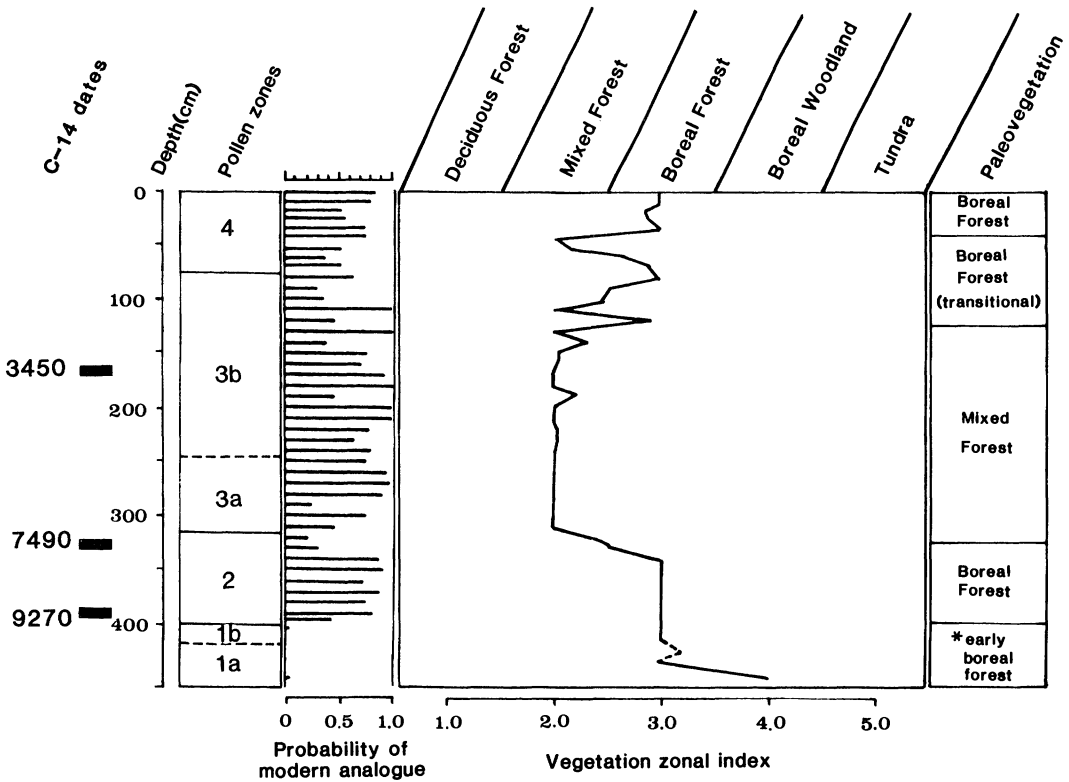


Figure 5. Results of discriminant analysis for the pollen stratigraphy from Jack Lake. The dotted line connects a sample whose vegetation zonal index was calculated by ignoring the anomalous probability of membership to the second highest group. Paleovegetation type without modern analogue is marked with an asterisk.

real forest is compatible with the high pollen percentages of *Picea* and *Pinus banksiana/resinosa*, both of which are representative taxa of these vegetation regions. The percentages of *Quercus* (4–12 percent) and *Ulmus* (4–8 percent), however, are unusually high for this late-glacial pollen assemblage zone. Both are typical species of the deciduous forest; their pollen rarely exceeds 3 percent in modern boreal forest samples. Moreover, the percentages of *Populus* (5–8 percent), *Artemisia* (3–8 percent), and *Cyperaceae* (up to 13 percent) also exceed their characteristic modern values in the boreal forest or boreal woodland. The lack of modern analogue for zone JL-1 probably can be attributed to this admixture of boreal and thermophilous pollen taxa at relatively high percentages.

The reason for this admixture of boreal and thermophilous pollen taxa in these late-glacial sediments is unclear. Similar admixtures also occur in the late-glacial sediments of several sites in Ontario south of Jack Lake (Liu 1982; Karrow et al. 1975). This possibly suggests co-

existence of these boreal and thermophilous tree species in an early spruce-dominated forest. A periglacial climate—characterized by frequent katabatic winds, by milder, drier winters and cooler, windier summers than prevail today, as well as by the abundance of fresh soil on a newly deglaciated landscape—could have favored the growth of thermophilous hardwoods (Amundson and Wright 1979). Alternatively, these thermophilous tree pollen might have been redeposited from older sediments or from melting ice blocks (McAndrews 1982). The abundance of degraded pollen in this pollen zone lends support to this explanation.

The probability of modern analogue increases across the boundary between pollen zones JL-1 and JL-2 (Fig. 5), suggesting that the vegetation became more modern in character. This corresponded with a decline in the abundance of spruce and an expansion of jack pine around the site about 9,200 years ago, probably in response to climatic warming and an increase in continentality. The vegetation zonal indices remain at

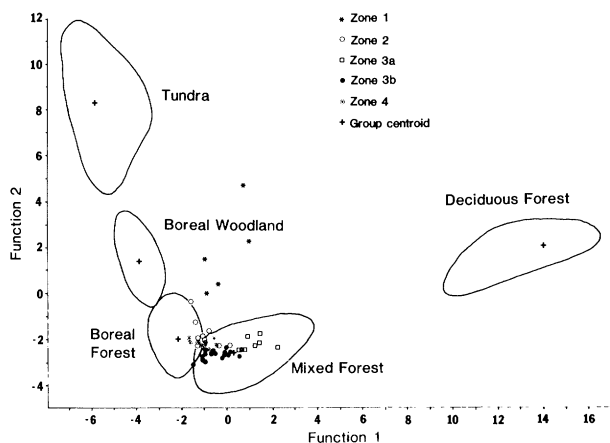


Figure 6. Ordination of the fossil pollen samples from Jack Lake along discriminant functions 1 and 2. Samples from different pollen assemblage zones are designated by different symbols. The ranges of the surface samples from the five vegetation regions are superimposed for comparison.

about 3.0 throughout pollen zone JL-2, indicating that a boreal forest similar to the modern one was established around Jack Lake from 9,200 to 7,300 B.P. This boreal forest was dominated by jack pine, with abundant spruce, white birch, poplar, and balsam fir.

The vegetation zonal indices decline from 3.0 to 2.0 through a brief transition at the top of pollen zone JL-2. This signals a major vegetational change from a boreal forest to a mixed forest about 7,300 years ago, when white pine (*Pinus strobus*), a typical species of the mixed forest, immigrated to Jack Lake from the south. From 310 to 130 cm (pollen subzone JL-3a and the lower part of subzone JL-3b), the vegetation zonal indices remain at or near 2.0, accompanied by high probabilities of modern analogue. This indicates that a mixed forest prevailed around Jack Lake during the mid-Holocene (ca. 7,300–2,600 B.P.). During the Hypsithermal (Deevey and Flint 1957), the ecotone between the boreal forest and the Great Lakes–St. Lawrence Forest was probably displaced far north of Jack Lake.

In the pollen diagram, the percentages of *Pinus strobus* pollen decline steadily throughout subzone JL-3b, accompanied by increasing values of *Betula* and *Picea* pollen. *Pinus banksiana/resinosa* pollen also begins to increase toward the top of this subzone. The higher vegetation zonal indices at 190 cm and 140 cm could be regarded as prologue to a major vegetational change in the late-Holocene. At 120 cm (dated at about 2,600 B.P. by interpolation), the vege-

tation zonal index shifts again to about 3.0, signifying a shift from a mixed forest to a boreal forest. From 43 to 120 cm, encompassing the pollen zone JL-3/JL-4 boundary, the vegetation zonal indices fluctuate between 2.0 and 3.0. This could be interpreted as a transitional phase between a mixed forest and a boreal forest, resulting from the ecotone's retreat southward across Jack Lake from its Hypsithermal position.

At the uppermost levels of pollen zone JL-4, the vegetation zonal indices become stabilized at values slightly lower than 3.0, indicating establishment of the modern boreal forest. These values are compatible with the proximity of Jack Lake to the modern boreal forest/mixed forest ecotone.

Discussion and Conclusion

This paper illustrates an application of discriminant analysis in paleovegetational reconstruction with the Holocene pollen stratigraphy from Jack Lake. The results highlight two important aspects in the vegetational history of northern Ontario that may not be clearly evident upon an intuitive, subjective interpretation of the pollen diagram. First, we have shown explicitly that from 7,300 B.P. to about 2,600 B.P. the modern boreal forest around Jack Lake was completely replaced by mixed forest, implying a northward displacement of the ecotone during the Hypsithermal. Second, the early postglacial

spruce-dominated boreal forest around Jack Lake, represented by the basal *Picea* pollen assemblage zone, does not have a modern analogue.

A Hypsithermal northward displacement of the boreal forest/Great Lakes–St. Lawrence Forest ecotone has been inferred from macrofossil evidence of a range extension of white pine in northwestern Quebec during the mid-Holocene (Terasmae and Anderson 1970). The pollen evidence of a mid-Holocene maximum in *Pinus strobus* pollen also implies ecotonal movements (Saarnisto 1974, 1975; Vincent 1973; Richard 1980; Liu and Davis 1981), but this has not been pointed out explicitly in previous studies. The difficulty in interpreting these pollen-stratigraphic data in terms of ecotonal movements is partly due to the paucity of modern pollen spectra from this region (e.g., see surface sample networks in Webb and McAndrews (1976), R. B. Davis and Webb (1975), and Ogden (1977)) and partly due to the difficulty in relating fossil pollen assemblages directly to the palynological signatures of different modern vegetation regions or plant communities. This problem is overcome by means of discriminant analysis, particularly through the calculation of the vegetation zonal indices. These indices quantitatively summarize the predicted group memberships (hence modern analogues) of the fossil pollen spectra and, since they are based on a continuous probability distribution between adjacent groups, are effective in detecting transitional vegetation types. Plotting the vegetation zonal indices stratigraphically against depth or age clearly documents the prevalence of a mid-Holocene mixed forest around Jack Lake and objectively delimits its stratigraphic or chronological extent at 7,300–2,600 B.P. The late-Holocene transitional phase in the vegetation and the establishment of the modern boreal forest, brought about by a southward retreat of the ecotone presumably in response to Neoglacial cooling, is also clearly reflected in the vegetation zonal indices. These more subtle vegetational changes, by contrast, cannot be so clearly depicted by means of conventional ordination techniques (e.g., see Fig. 6).

Paleovegetational reconstruction based solely on the vegetation zonal indices could be misleading without examining the fossil pollen data for possible no-modern-analogue situations. In the case of Jack Lake the vegetation zonal indices for both the *Picea* pollen zone and the

Pinus banksiana/resinosa pollen zone (i.e., pollen zones 1 and 2) suggest boreal forest, but the probabilities of modern analogue indicate that the vegetation represented by the *Picea* pollen zone, though essentially boreal in character, lacks a modern analogue. Although the unique character of the fossil pollen assemblage in zone 1 is suspected from the unusual admixture of *Picea* with relatively high percentages of *Quercus*, *Ulmus*, *Populus*, and *Artemisia*, discriminant analysis permits this to be detected explicitly and objectively through the calculation of the probability of modern analogue.

Discriminant analysis is a useful tool in palynological research, and the results could have important paleoecological implications. During the past decade much research has been done on the use of transfer functions to derive quantitative estimates of the past climates directly from fossil pollen data, thus bypassing the need to reconstruct the past vegetation as an intermediate linkage between pollen and climate (e.g., Webb and Bryson 1972; Webb and Clark 1977; Andrews, Mode, and Davis 1980; Andrews and Nichols 1981; Andrews and Diaz 1981; Andrews et al. 1981; Kay 1979; Kay and Andrews 1983; Bryson and Kutzbach 1974; Sachs, Webb, and Clark 1977). Although this approach holds much promise as a tool in paleoclimatic reconstruction, other authors have stressed Gleason's individualistic concept of vegetation and have expressed serious reservations about the applicability of this approach, particularly to late-glacial and early postglacial conditions where no-analogue situations are expected (Birks 1981a, 1981b; M. B. Davis 1976, 1978; Wright 1976; Richard 1981). Richard (1981) has argued that a detailed reconstruction of the ancient vegetation cover is a prerequisite to any paleoclimatic reconstruction from fossil pollen data. Pollen evidence from Jack Lake and from other sites in northern Ontario (Liu 1982) suggests that many late-glacial and early postglacial pollen assemblages indeed lack modern analogues, thus supporting the caution that these no-analogue situations be detected and interpreted carefully before paleoclimatic transfer functions are applied (e.g., Hutson 1977). Discriminant analysis can be a useful tool in revealing these no-analogue situations.

Compared with principal component analysis and canonical variate analysis, discriminant analysis has the advantage of being more explicit and more objective in detecting no-ana-

logue situations and in assigning fossil pollen spectra directly to their modern analogues, thereby minimizing the subjectivity involved in the application of the ordination techniques. Like all other multidimensional scaling techniques (Prentice 1980), discriminant analysis is superior to correlation coefficient techniques because it reduces the dimensionality of the pollen data and thus yields more easily interpretable results. Because it requires an assumption of a specified probability distribution of the data, it enables the use of statistical inference. A disadvantage of discriminant analysis is that it requires that several statistical assumptions be satisfied. Owing to the nature of pollen data, vigorous testing or justification of some of these statistical assumptions may not always be possible (Howe and Webb 1977). Nevertheless, the classification results of the modern pollen spectra provide an empirical measure of the discriminating power of the discriminant functions with respect to the palynological signatures of the vegetation regions. A high percentage of correct classification in the surface samples, such as 95 percent in this study, should imply high reliability in the paleovegetational reconstruction from the fossil pollen data. More research, both theoretical and empirical, involving larger pollen data sets is needed to evaluate the effects of these statistical assumptions on the results of the discriminant analysis.

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Notes

1. Another alternative is to exclude all taxa with zero values in one or more regions (e.g., *Abies*, *Carya*, *Acer*, *Tsuga*, *Fagus*, *Quercus*) from the data base. However, we did not choose this option because these are important taxa in some forests and their exclusion would therefore be ecologically unsound.
2. Mardia's (1970, 1974) measure of multivariate skewness, $b_{1,m}$, is calculated by:

$$b_{1,m} = (1/n^2) \sum_{i=1}^n \sum_{j=1}^n \{(X_i - \bar{X})' S^{-1} (X_j - \bar{X})\}^3 \quad (2)$$

where m denotes the number of variables, $(X_i - \bar{X})$ and $(X_j - \bar{X})'$ represent respectively the vector and its transpose containing the deviation of sample i from its group mean for all variables. S^{-1} is the inverse of the variance-covariance matrix of the individual group. The significance of $b_{1,m}$ is tested by calculating:

$$A = n b_{1,m}/6 \quad (3)$$

which has a chi-square distribution with $m(m+1)(m+2)/6$ degrees of freedom. Significant large values of A will lead to the rejection of the null hypothesis $b_{1,m} = 0$, suggesting multivariate skewness in the distribution of the samples.

The measure of multivariate kurtosis, $b_{2,m}$, is calculated by:

$$b_{2,m} = 1/n \sum_{i=1}^n \{(X_i - \bar{X})' S^{-1} (X_i - \bar{X})\}^2. \quad (4)$$

The significance of $b_{2,m}$ for large sample is tested by:

$$B = \{b_{2,m} - m(m+2)\}/\{8m(m+2)/n\}^{1/2} \quad (5)$$

which is asymptotically distributed as $N(0,1)$. For small sample, B is slightly adjusted by:

$$B = \{b_{2,m} - m(m+2)(n-1)/(n+1)\}/\{8m(m+2)/n\}^{1/2}. \quad (6)$$

3. A similar approach of converting membership probabilities into standardized scores has been used by urban geographers, for example, to delimit rural-urban fringes (e.g. Fesenmaier, Goodchild, and Morrison 1979).

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