Numerical Methods in Quaternary Pollen Analysis

H. J. B. BIRKS AND A. D. GORDON

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H. J. B. BIRKS
Botanical Institute
University of Bergen
Norway

A. D. GORDON
Department of Statistics
University of St. Andrews
Scotland

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Preface

In the last two or three decades, ecology has developed from a subject that was almost entirely qualitative and observational in outlook to a science in which investigators seek generalisations on the basis of observations that can be quantified and analysed statistically. More recently, the same trend has been evident in Quaternary palaeoecology. Quaternary pollen analysis has always had a quantitative basis, in that the primary data are the numbers of different types of pollen grains and spores counted in a sample, but there has recently been an increasing awareness of the potential contribution of statistical methodology to palynological investigations. There has also been some scepticism about the magnitude of this contribution, possibly fuelled by excessive claims for, and inappropriate uses of, statistical techniques. This book, which has arisen out of collaborative research by the two authors over more than a decade, describes and reviews numerical methods which we believe can assist an investigator in the analysis of Quaternary pollen analytical data. Many of the methods are of more widespread applicability, for example to palynological data from deposits of earlier ages, and to other quantitative palaeoecological variables, such as sediment chemistry, plant macrofossils, diatoms, cladocera, mollusca, foraminifers, ostracods, and dinoflagellates.

H. J. B. B. wishes to record his very great debt to the late J. B. Birks, E. J. Cushing, I. C. Prentice, R. A. Reyment, and T. Webb III for stimulating and encouraging his interests in quantitative methods of analysing Quaternary palynological data and for freely sharing ideas, insights, and experiences.

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All or part of the manuscript has been critically read by C. W. Barnosky, H. H. Birks, R. M. Cormack, F. S. Gilbert, I. C. Prentice, R. A. Reyment, and T. Webb III, who have contributed valuable suggestions for its improvement. To all these people and to others who, directly or indirectly, have influenced the contents of this book, we express our sincere thanks.

We should be most grateful to readers who draw our attention to any errors or obscurities in the text, or suggest other improvements.

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H. J. B. Birks
A. D. Gordon

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CHAPTER 1

The Nature of Quaternary Pollen Analytical Data

1.1 Pollen Analysis as a Quaternary Palaeoecological Technique

The primary aim of Quaternary palaeoecology is the reconstruction of the past environments and ecosystems of the last 1–2 million years of earth's history. As past environments and ecosystems cannot be observed directly, they must be reconstructed from the fossils and the sediments in which the fossils are found. Sediments of Quaternary age occur commonly in both continental and marine situations, and their palaeoecology attracts considerable scientific attention. This is because the Quaternary period is unique in earth's history as the period when man evolved and when the climate oscillated, in the latitude of Europe and North America, between temperate, so-called interglacial phases of 10,000 to 20,000 years duration and cold phases of 50,000 to 100,000 years duration during which glaciation commonly occurred.

The period of time represented by Quaternary deposits has been studied more intensively than any other time span of comparable magnitude. Quaternary palaeoecology can only consider and be based on those groups of organisms that are found as fossils—foraminifers, molluscs, arthropods, vertebrates, algae, bryophytes, and vascular plants, all of which contain compounds resistant to decay such as calcite, aragonite, chitin, silica, cutin, lignin, and sporopollenin (see Cushing and Wright, 1967; H. J. B. Birks and H. H. Birks, 1980). Pollen grains and spores of vascular plants are by far the most abundant type of fossil preserved in terrestrial Quaternary sediments, with the result that terrestrial Quaternary palaeoecology is largely dominated by the technique of stratigraphical pollen analysis (Cushing and Wright, 1967).

Pollen analysis, the principles of which we discuss in this chapter, provides a means of reconstructing the past flora (the distribution of individual plant taxa in time and space), the past plant populations (the abundance of plant taxa in time and space), and the past vegetation (the distribution of plant assemblages or communities in time and space) (see Cushing, 1963; H. J. B. Birks, 1973b). The reconstruction of past plant communities represents a major step towards the reconstruction of the past ecosystem, as the plant community is the most complex part of any ecosystem. After the community has been reconstructed, inferences can be made about the environment of the past ecosystem, assuming that the ecological requirements and tolerances of the species and the communities are known (see M. B. Davis, 1978; H. J. B. Birks and H. H. Birks, 1980; H. J. B. Birks, 1981c).

Interpretations of Quaternary pollen analytical data are derived almost entirely from the extrapolation of present-day ecological observations backwards in time. Past communities, environments, and ecosystems are reconstructed by analogy with present-day communities and ecosystems and with known ecological preferences of the taxa and communities involved (D. Walker, 1978). Implicit in all Quaternary pollen analytical studies, as in all palaeoecology, is the assumption and philosophical principle of methodological uniformitarianism (*sensu* Gould, 1965), or actualism, which states that the nature of modern processes is the same as in the past and thus that modern laws of nature can be extended backwards in time and used to reconstruct and explain past events (see Rymer, 1978, for a critical review of uniformitarianism in relation to Quaternary pollen analysis). As H. J. B. Birks and H. H. Birks (1980) discuss, there is no way to prove or disprove methodological uniformitarianism ('the present is the key to the past'), as it is the basic logic and methodology of all historical sciences, including Quaternary palaeoecology; all reconstructions of the past require some application and extrapolation in time of modern ecological or geological knowledge.

Quaternary pollen analysis closely parallels descriptive plant ecology in its scientific development. Qualitative, often rather generalised, descriptions of fossil pollen assemblages preserved in peats were prevalent in the 1880s and 1890s (Erdtman, 1943; Manten, 1967; Faegri and Iversen, 1975), just as qualitative, broad-scale descriptions of modern vegetation were common at that time (Whittaker, 1962). Quantitative descriptions of vegetation were first attempted in the 1910s and 1920s, and quantification in descriptive plant ecology developed rapidly (McIntosh, 1974, 1975). In 1916, the potentialities of the quantitative analysis of pollen grains preserved in Quaternary sediments such as peats were first demonstrated by the Swedish geologist Lennart von Post (1918, reprinted in English in 1967). Following the work of Gustaf Lagerheim, von Post counted samples of fossil pollen preserved at different levels in a peat profile and presented his counts as percentages of the sum of pollen grains counted (Manten, 1967). He displayed his results as stratigraphical diagrams with pollen percentages plotted against depth through the stratigraphical column (see Fries, 1967). Von Post demonstrated strong similarities in pollen profiles from sites within the same region and marked differences between sequences from sites in different parts of Sweden. He was thus able to add the fourth dimension, namely, time, to the study of vegetation and to the elucidation of such problems as the nature of past vegetation, the history of major vegetation formations, the patterns of vegetation change over long periods of time, and the timing and magnitude of post-glacial climatic change. As Deevey (1967, p. 65) so aptly comments, 'Von Post's simple idea, that a series of changes in pollen proportions in accumulating peat was a four-dimensional look at vegetation, must rank with the double helix as one of the most productive suggestions of modern times.'

The basic principles of Quaternary pollen analysis or palynology are as follows (Godwin, 1934; Erdtman, 1943; West, 1971; Faegri and Iversen, 1975: H. J. B. Birks and H. H. Birks, 1980):

1. Pollen grains and spores are small (10–100 microns) and are produced in great abundance by vascular plants (flowering plants and ferns), but only a few of these ever fulfil their natural function of fertilisation. Most eventually fall to the ground.
2. Before reaching the ground, pollen and spores are well mixed by turbulence in the atmosphere, resulting in a more or less uniform pollen rain within an area.
3. The organic compounds (sporopollenin, cellulose, pectins, callose, proteins, etc.) that comprise pollen grains and spores rapidly decay unless the processes of biological decomposition are inhibited in some way. This inhibition occurs where there is a lack of oxygen, for example in permanently waterlogged areas such as bogs, fens, lake bottoms, and the ocean floor. The sporopollenin of the outer wall or exine of pollen and spores is well preserved in non-oxidising sediments that accumulate in these areas.
4. The taxonomy of pollen grains and spores is relatively well known, at least in the Northern Hemisphere (see, e.g., McAndrews *et al.*, 1973; Faegri and Iversen, 1975; P. D. Moore and Webb, 1978). The major types are identifiable to various taxonomic levels (family, genus, species) using the transmitted-light microscope.
5. As the composition of the pollen rain depends on the composition of the vegetation that produced it, the pollen rain is a function of the vegetation of the area. A sample of the pollen rain will thus be a reflection of the vegetation, both local or lowland (aquatic and wetland communities) and regional or upland (forest, grassland, heathland communities, etc.), at that point in space and time.
6. If a sample of the pollen rain preserved in peat or mud of known age is examined and the various pollen and spore types preserved are identified and counted, the pollen spectrum is a reflection of the vegetation surrounding the site of deposition at the time the sediment and its contained pollen and spores were deposited. Because pollen grains and spores are small and very abundant (up to 10^6 grains cm^{-3}), only small amounts (0.5–1 cm^3) of

sediment are needed for detailed pollen analysis. This small sample volume contrasts with the requirements for studies of fossils such as seeds and fruits, molluscs, insects, and vertebrates, where relatively large amounts of sediment are needed to provide an adequate sample of the fossil population.

7. If samples of the pollen rain preserved at several levels throughout the sediment are examined, the fossil pollen assemblages provide stratigraphical records of the past vegetation and its development through the time period represented by the sedimentary record.
8. If two or more series of stratigraphical pollen assemblages are obtained from several sites, it is possible to compare the pollen spectra and to detect similarities and differences in vegetation through time at different points in space.

A Quaternary palaeoecological study involving pollen analysis usually proceeds along the following lines. After the aims of the investigation and the hypotheses to be tested have been defined, the site(s) of interest and relevance to the study is visited. The selection of suitable sites for pollen analysis is of critical importance; it will depend on the aims of the study, the spatial and temporal scales of interest, and the availability of suitable sites. Jacobson and Bradshaw (1981) discuss the question of site selection in detail. Cores of sediment are collected from the site, after a series of trial borings has been made to establish the gross sediment stratigraphy and morphometry of the basin. If the sediments are exposed, for example, in gravel pits, eroding peat hags, or sea cliffs, samples can be conveniently collected from the exposed face. The lithology and sediment characteristics of the samples, either from the cores or from the exposures, are then described (see H. J. B. Birks and H. H. Birks, 1980).

H. J. B. Birks and H. H. Birks (1980) discuss ways in which investigators select the positions in sediment cores or sedimentary sections at which samples of material are extracted for analysis. In Quaternary pollen analysis, the most commonly used sampling strategy is search sampling (*sensu* Krumbein and Graybill, 1965), in which the core or section is initially sampled fairly sparsely. The results of analysing this first set of samples indicate the positions where subsequent more detailed investigation would be advisable. Gordon (1974) describes sequential sampling strategies for use in the uncommon situation in which one has fairly precise information about some feature of the preserved pollen record (e.g., the rise of *Ambrosia*-type pollen in eastern North America some 80–150 years ago) and one wishes to identify rapidly the position in the core at which this occurs.

Samples extracted from the core are prepared for pollen analysis using a standard laboratory procedure, which aims to concentrate the pollen and to remove as much of the sediment matrix as possible. Details of field and laboratory techniques are given by Faegri and Iversen (1975), West (1977), and H. J. B. Birks and H. H. Birks (1980).

After the sample has been prepared for pollen analysis, the residue is mounted on a microscope slide and pollen identification and counting can begin. Identification of pollen and spores can reliably be done only by careful comparison between fossil material and modern reference material of pollen and spores collected from plants of known identity and prepared in the same way as the fossil material (see Hansen and Cushing, 1973, and H. J. B. Birks and H. H. Birks, 1980, for a discussion of identification procedures in Quaternary pollen analysis). Problems of deteriorated pollen and of unknown grains can arise in some samples (e.g., Cushing, 1967a; H. J. B. Birks, 1973b, 1981a).

Pollen counting is carried out along regularly spaced traverses of the microscope slide at a magnification of ×300–400. The number of grains counted depends on the problem being investigated. A sufficient number of grains should be counted to obtain reliable estimates, that is, to achieve broadly constant percentages of the pollen types of interest when their counts are expressed as percentages of the pollen sum. In general, a total of 300 to 500 grains is usually adequate (Bowman, 1931; Crabtree, 1968; Maher, 1972b), but in certain studies counts of 1000 or more grains per sample are essential to obtain the precision required to answer particular questions. Traverses should be positioned evenly over the whole slide (and not concentrated near the edge) to avoid any effects of non-random distribution of pollen and spores on the slide (Brookes and Thomas, 1967). Questions of the statistical reliability of pollen counts and of confidence intervals for pollen percentage data are discussed in Section 2.2.

Having obtained a stratigraphical sequence of pollen counts, the next stage in a palynological investigation is to present the results in the form of a graph or other diagram, prior to the interpretation of the data. Pollen analytical data are invariably complex and are most effectively presented in the form of a pollen diagram (see Section 1.3). This is a series of graphs of the values for different pollen and spore types plotted against their stratigraphical depth or, more rarely, against their age. Nearly all pollen analytical data are relative proportions of the different pollen and spore types (the proportions being with respect to some specified pollen sum). In some studies, estimates are made of the 'absolute' numbers of pollen grains per unit volume or unit weight of sediment, or per unit area of sediment deposited per unit time. In such studies the counts of the different pollen and spore types are independent of each other (which is not the case with relative percentage data) and, in the estimation of number of grains per unit area per unit time, are also independent of changes in the sediment-accumulation rate within the sequence (see Section 1.2).

For percentage data, a critical decision is the specification of the taxa which will be included in the pollen sum. Cushing (1963), H. J. B. Birks (1973b), and H. J. B. Birks and H. H. Birks (1980) argue that the choice should be based on the principle that all members of the 'universe' of interest and under study should be included. In general, the main interest is usually centered on regional vegetational history, and in this case all pollen and spores which could have originated from the upland vegetation should be included in the pollen sum. Pollen and spores of plants confined to the lowland local aquatic and mire vegetation (e.g., obligate aquatic plants and bog and fen species) should be excluded from the pollen sum because they are locally produced from a different vegetation from that with which the investigation is primarily concerned. Special pollen sums can be used for selected taxa only, and for specific palaeoecological problems (see Wright and Patten, 1963; H. H. Birks, 1972; Janssen, 1981b; Cwynar, 1982). The question of pollen sums is discussed further in Section 2.5.

Pollen diagrams (e.g., Figures 1.2 and 1.3) are often complicated and difficult to comprehend rapidly because they present a large amount of data in a graphical form. Prior to interpretation of the data, it is often useful to subdivide each pollen stratigraphical sequence into smaller units, so-called pollen zones, for ease in description, discussion, comparison, interpretation, and correlation. A variety of numerical methods can be used for zoning single pollen sequences, and these methods are described in Chapter 3. Numerical methods can also be used for comparing two or more pollen sequences, and these techniques are discussed in Chapter 4. Comparisons permit the detection of similarities among pollen sequences and hence the delimitation of regional pollen zones. Comparisons can also emphasise differences between profiles, and such differences may be of considerable palaeoecological interest, particularly at a local scale.

Once the pollen sequence has been divided into pollen zones and compared with other sequences, the task of interpretation can begin. In general, interpretation should follow the logical sequence of reconstruction of past flora, reconstruction of past populations, reconstruction of past vegetation, and reconstruction of past environments. H. J. B. Birks and H. H. Birks (1980; see also H. J. B. Birks, 1973b) present six basic questions of interpretation which can be asked of a pollen diagram.

1. What taxa were present in the past flora?
2. What were the relative abundances of the taxa present in the past?
3. What plant communities were present in the past?
4. What space did each community occupy in the past?
5. At what time did each community occur in the past?
6. What was the past environment of the plant communities at that time and space?

The answer to the first question can never be complete because the fossil pollen and spore record is never complete. Some plants produce pollen that is rarely, if ever, preserved (e.g., *Juncus, Luzula, Naias flexilis*) or produce pollen in such small amounts (e.g., *Linum*) that the probabilities of its pollen ever becoming incorporated in sediments and being detected by a pollen analyst are extremely low. In addition, some plants, such as grasses and sedges, produce abundant pollen, but the pollen is not specifically or generically distinct from pollen of other members of the same family. Clearly, the degree of floristic information that can be extracted from the pollen stratigraphical record depends on the quality and reliability of the pollen identifications and on the taxonomic level to which the identifications are carried out. Numerical methods can assist the pollen analyst in separating mixtures of pollen grains of similar morphology but which differ in size and/or shape (see Section 2.4).

An additional problem in reconstructing the past flora from pollen stratigraphical data is that some pollen may have been transported long distances by air masses or other currents. There is a non-zero probability of finding a pollen grain that originates from a plant anywhere in the world (Cushing, 1963). Some pollen types (e.g., *Pinus* and *Ephedra*) are notorious for their long-distance transport, and allowance should be made for this in any floristic reconstruction. H. J. B. Birks (1981b) has applied the theory of point processes (Cox and Lewis, 1966; Reyment, 1969b, 1976b, 1980b) to the occurrences of 27 pollen and spores of presumed long-distance transport in sediments of late-Wisconsin age in Minnesota and has demonstrated that the occurrences of some types (e.g., *Carya* and *Platanus occidentalis*) show significant trends in the rate of occurrences between 8400 and 20,500 years B.P. (before present), whereas such trends were not evident for other species (e.g., *Acer negundo* and *Sarcobatus vermiculatus*).

The second question involves interpretation of the numerical data of the pollen spectra in terms of the past abundances or population sizes of the plants present in the past. Unlike many fossil groups (e.g., trilobites, brachiopods, belemnites, and diatoms) where one fossil reflects one living individual, in pollen analysis, one individual plant may produce many millions of pollen grains. Before the fossil pollen values can be interpreted in terms of past abundances of plants, the pollen production and representation of modern plants must be studied. Modern pollen-representation factors (e.g., *R* values *sensu* M. B. Davis, 1963) can be derived and applied to the fossil pollen counts to derive estimates of past plant abundance.

Modern pollen-representation factors for taxon k can be estimated by collecting surface samples, such as the top 1–2 cm of mud accumulating in a lake, and by comparing p_{0k}, the observed proportions of pollen type k in the surface sample 0, with v_k, the observed proportions of taxon k in the surrounding modern vegetation (see Figure 1.1). (In Section 5.4 we discuss an appropriate manner of defining v_k). The modern representation factor for taxon k is estimated by

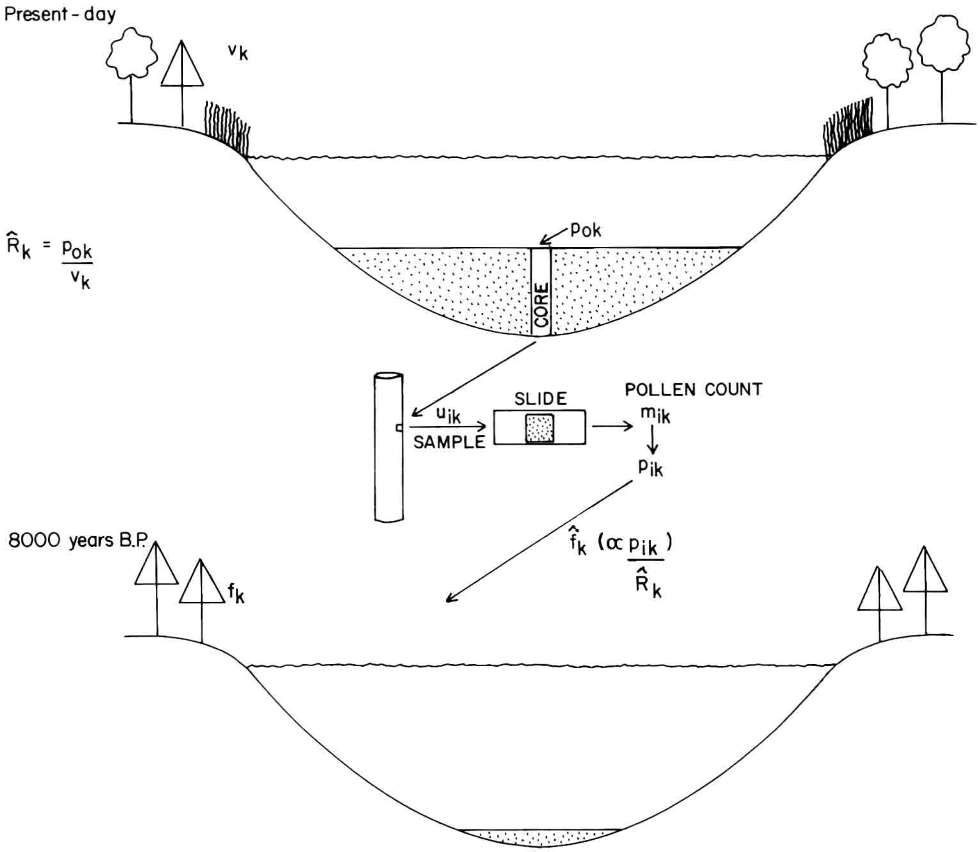
$$\hat{R}_{\mathrm{k}} = p_{0\mathrm{k}}/v_{\mathrm{k}}$$

The R values vary between taxa by several orders of magnitude (M. B. Davis, 1963; Andersen, 1970) because abundant species in the vegetation may produce little or no pollen whereas rare species may produce abundant pollen.

To estimate the relative abundance of taxon k 8000 years ago (see Figure 1.1), we examine the core of sediment from the same place as our surface sample, sample the core at the appropriate depth, and estimate u_{ik}, the proportion of pollen of taxon k at the time period represented by sample i, by preparing the sample i for pollen analysis and counting an appropriate number of pollen grains m_{ik} on the microscope slide. The proportion of pollen type k in sample i is p_{ik}, and by assuming that our modern pollen-representation factor is invariant in time and space, we can estimate f_k, the proportion of taxon k in the past vegetation, by

$$\hat{f}_k \propto p_{ik}/\hat{R}_k,$$

where the constant of proportionality can be evaluated by noting that the past vegetation proportions must sum to 1. A fuller discussion of the assumptions



v_k = estimated proportion of modern vegetation which belongs to taxon k

u_{ik} = proportion in the underlying sediment of pollen of taxon k at the period of time being investigated by spectrum i

m_{ik} = number of pollen grains of taxon k in sample count i

p_{ik} = proportion of pollen spectrum i belonging to taxon k

p_{ok} = proportion of the surface pollen spectrum belonging to taxon k

f_k = proportion of past vegetation belonging to taxon k, estimated by $\hat{f}_k$

$\hat{R}_k$ = estimated R-value for taxon k $\left(= \frac{p_{ok}}{v_k}\right)$

Figure 1.1 Stages in the quantitative reconstruction of the relative abundance of taxon k in the vegetation around a lake 8000 years ago using estimates of modern pollen-representation factors $\hat{R}_k$ to transform fossil pollen spectra into past abundances f_k of the taxon. See text discussion of variables and equations.

involved in this approach is given in Chapters 5 and 6, which describe mathematical methods for deriving pollen-representation factors from modern pollen counts and the use of such factors in estimating past abundances and population sizes of plants (see Sections 5.4 and 6.3).

The reconstruction of past vegetation and of past plant communities involves comparisons of the fossil pollen spectra with modern pollen spectra from areas of known vegetation (Wright, 1967; H. J. B. Birks and H. H. Birks, 1980). If the modern and fossil spectra are similar, it can be concluded that they were produced by similar vegetation. A modern analogue can thus be suggested for the past vegetation. If, however, no analogue can be found, it may either be concluded that the past vegetation has no modern analogue or that modern spectra should be sought elsewhere. Numerical methods for analysing modern pollen spectra are described in Section 5.3, and the use of quantitative techniques for comparing modern and fossil pollen spectra and thus for reconstructing past vegetation is discussed in Section 6.4.

Other approaches to vegetational reconstruction involve the extension backwards in time of known sociological and ecological preferences of individual taxa, the so-called indicator-species approach (see Janssen, 1967b, 1970, 1981b; H. J. B. Birks, 1973b; D. Walker, 1978; H. J. B. Birks and H. H. Birks, 1980) and the search for groups of fossils that are significantly associated together in a series of samples within and between stratigraphical sequences, so-called recurrent groups (H. J. B. Birks and H. H. Birks, 1980). Recurrent groups can, in some instances, suggest which taxa grew together in the past; the approach is described in Section 6.5.

Answers to the question of where particular plant communities grew in the past are critically dependent on our knowledge and understanding of the complex processes of pollen transport and dispersal and on the choice of site, particularly its size and potential pollen source area (Janssen, 1981b; Jacobson and Bradshaw, 1981). Pollen sequences from several sites within a small geographical area are required to detect patterns of vegetational differentiation related, for example, to altitude (Turner and Hodgson, 1979, 1983), soils (D. Walker, 1966; Brubaker, 1975; Jacobson, 1975, 1979), and climate and topography (McAndrews, 1966, 1967). Alternatively, transects of pollen diagrams across a site either in one (Turner, 1965) or two (Turner, 1970, 1975) dimensions may permit the detection of spatial differentiation in the occurrence of particular pollen assemblages and hence of particular plant communities (see H. J. B. Birks and H. H. Birks, 1980).

Detailed, independent chronologies are required to answer the question of when particular communities occurred in the past. In ideal circumstances, radiocarbon dating of organic sediments can give an exact answer (within the precision of the radiocarbon dating technique). However, large errors can arise in the dating of a range of organic materials (peats, wood, charcoal, lake muds), (Broecker, 1965; Ogden, 1967; Godwin, 1969), in laboratory procedures (Pardi and Marcus, 1977), in systematic bias between laboratories (International Study Group, 1982), in the radiocarbon assay of sediments low in organic content (Shotton, 1967;