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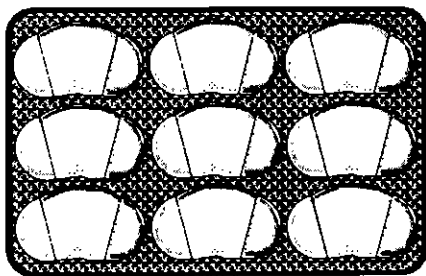
Methods in Quaternary Ecology #2. Palynology

Glen M. MacDonald

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Article abstract

Palynology is the study of organic-walled microfossils which include pollen, spores, dinoflagellates, acritarchs, tasmantids, and chitinozoa. Quaternary palynology is concerned predominantly with the paleoecological analysis of fossil pollen and spores. Palynology is one of the most widely used technique in Quaternary paleoecology. Fossil pollen and spores (palynomorphs) can befound in a wide variety of deposits. Recovery of the fossils from sediment samples is relatively easy. Transmitted light microscopy is sufficient for routine identification and counting of palynomorphs. Their occurrence in large quantities makes fossil pollen and spores amenable to numerical and statistical analysis. Interpretation of fossil samples in North America is aided by a large data-base of modern pollen and spore samples taken from various depositional environments and different vegetation types. Despite the long history and wide application of fossil pollen analysis in Quaternary studies, significant methodological and interpretive problems remain to be resolved. In this paper, I outline the basic principles and methods of Quaternary palynological analysis and review some representative examples of contemporary research in Canada.

Methods in Quaternary Ecology #2. Palynology

Glen M. MacDonald
Department of Geography
McMaster University
Hamilton, Ontario L8S 4K1

Summary
Palynology is the study of organic-walled microfossils which include pollen, spores, dinoflagellates, acritarchs, tasmantids, and chitinozoa. Quaternary palynology is concerned predominantly with the paleoecological analysis of fossil pollen and spores. Palynology is one of the most widely used technique in Quaternary paleoecology. Fossil pollen and spores (palynomorphs) can be found in a wide variety of deposits. Recovery of the fossils from sediment samples is relatively easy. Transmitted light microscopy is sufficient for routine identification and counting of palynomorphs. Their occurrence in large quantities makes fossil pollen and spores amenable to numerical and statistical analysis. Interpretation of fossil samples in North America is aided by a large data-base of modern pollen and spore samples taken from various depositional environments and different vegetation types. Despite the long history and wide application of fossil pollen analysis in Quaternary studies, significant methodological and interpretive problems remain to be resolved. In this paper, I outline the basic principles and methods of Quaternary palynological analysis and review some representative examples of contemporary research in Canada.

Introduction
To the layman, the study of fossil pollen and spores may appear esoteric at best and a singular waste of time and money at worst! However, palynology is one of the most widely used research tools in Quaternary studies (Edwards, 1983). A quick tabulation indicates that fossil pollen analysis was incorporated in approximately 25% of all research papers published in English and French language Quaternary journals in 1986. Indeed, palynology has a long history as an integral part of Quaternary research. Although descriptions of fossil pollen assemblages were made in the last century,

the Swedish geologist Lennart von Post is recognized as the father of quantitative pollen analysis. In a paper first published in 1916 (von Post, 1967), he put forward the concept of presenting pollen data as percentages of the sum of pollen grains in a sediment sample plotted against stratigraphic position. This method remains the standard technique used by palynologists. Furthermore, von Post demonstrated the usefulness of pollen analysis for environmental reconstruction and stratigraphic correlation by showing that pollen diagrams from the same region were similar to one another but were different from pollen diagrams of other areas.

From the time of von Post to the present, Quaternary pollen analysis has been predicated upon the following general principles (Birks and Birks, 1980): (1) Pollen and spores are produced in large numbers during the natural reproductive cycle of many plants; (2) The proportion of pollen and spores released in the environment depends on the number of parent plants and therefore reflects vegetation composition; (3) Most of the grains never fulfill their reproductive function and some of these are deposited in environments where they may be preserved as fossils; (4) The grains can be extracted from sediment and identified to taxonomic levels ranging from family to species; (5) Pollen and spores from different statigraphic levels provide information on vegetation at specific periods in the past; (6) Palynological data from different sites provide information on differences in vegetation at the sites.

Several important methodological advances have been made in Quaternary palynology since von Post's time. Szafer (1935) introduced the widely used technique of presenting palynological data from many sites in the form of isopollen maps. Radiocarbon dating was developed in the late 1940s and is now routinely used to provide direct chronological control of pollen stratigraphies. Mathematical transfer functions were developed to provide quantitative estimates of plant species abundances (Davis, 1963) and climatic conditions (Webb and Bryson, 1972). Methods for the calculation of pollen concentrations and accumulations were introduced (Davis and Deevey, 1964; Maher, 1972) and are now widely applied.

Historical Development in Canada
Auer (1927a,b, 1930) provided the first Quaternary pollen diagrams and systematic analysis of fossil pollen records in Canada through the examination of peat deposits, in Ontario, Quebec, New Brunswick and Nova Scotia. A pollen percentage diagram from peat sections along the north shore of the Saint Lawrence was published by Bowman (1931). The first pollen diagrams from Labrador were constructed from peat deposits by Wenner (1947). The initial palynological research in much of British Columbia, the Yukon and Alberta was conducted by

Hansen (1940, 1949, 1953). The first radiocarbon-dated pollen diagrams from Canada were reported from Quebec by Potzger and Courtemanche (1954). Quaternary palynological research in arctic Canada began with the work of Terasmae (1956) on Banks Island. Kupsch (1960) published the first pollen diagram from Saskatchewan while Ritchie (1964) published the first diagram from Manitoba. Early paleoecological work on the fossil pollen record of Quaternary marine sediment was conducted by Piper et al. (1978) on material from the Grand Banks.

The tempo of Quaternary palynological research in Canada has continued to increase into the 1980s. Much of the current research is conducted using lake sediment cores and almost all published diagrams include radiocarbon dates or other forms of absolute chronological control. Palynological laboratories have been established by Archaeology, Biology, Geography, and Geology departments in universities and museums. Several laboratories are operated by the federal and provincial governments. Despite the continuing research in Quaternary palynology, pollen records remain sparse from large sections of Canada (Hills and Sangster, 1980; Bryant and Holloway, 1985). Most Quaternary palynological records reported from Canada are Holocene in age. However, notable Pleistocene records have been recovered from sites in British Columbia (summarized by Clague and MacDonald, in press), the western interior and arctic (summarized by Ritchie, 1985), southern Ontario (Terasmae, 1960; Berti, 1975; Karrow and Warner, 1984), and eastern Canada (summarized by T.W. Anderson, 1985). Most Pleistocene assemblages are from earlier non-glacial intervals. Pollen records from the height of the late Wisconsinan glaciation are available from unglaciated portions of the Queen Charlotte Islands (Warner et al., 1982) and the Yukon (Rampton, 1971; Cwynar, 1982). Additional palynological data on conditions during the last glacial maximum have been obtained from marine sediments off the east and west coasts (summarized by Heusser, 1985) and from the Devon Island Ice Cap (McAndrews, 1984).

Production, Deposition, and Preservation
Pollen grains are the male gametophytes of seed plants. The spores examined by Quaternary palynologists are the immature gametophytic generation of mosses, ferns and fern allies. The pollen and spores are produced in tetrads in the anthers of angiosperms, the male cones of gymnosperms, or the sporangia of lower plants. The grains consist of a living cytoplasm which is surrounded by intine composed of cellulose, pectins, callose, proteins, polysaccharides and antigens, and a resistant exine composed of complex polymers known as sporopollenin (Heslop-Harrison, 1968). The

polymers of sporopollenin have a basic formula $(C_{90}H_{142}O_{36})^n$ and the substance is largely inert. The size of pollen grains and spores ranges from less than 10 μm to over 200 μm.

In Canada, pollen and spores are generally released by plants in the spring and summer (Bassett et al., 1978). Production of spores and pollen varies for different species. Anemophilous (wind pollinated) plants depend on wind to disperse pollen and produce large numbers of grains. A lodgepole pine (Pinus contorta) tree may release as many as 21 billion grains in one season (Critchfield, 1985). In contrast, cleistogamous (closed flowering) and entomophilous (insect pollinated) species may produce only a few hundred thousand pollen grains. The amount of pollen produced by an individual plant often varies significantly from year to year (S.T. Andersen, 1974).

The majority of grains, particularly for anemophilous species, never fulfill their reproductive function and are deposited on the ground or in water. The cytoplasm of the grains dies shortly after release. The intine and exine decay rapidly through oxidation and biological activity. However, when deposited in anoxic environments, or where the accumulation of enclosing sediment is rapid, the exine is extremely resistant to decay and palynomorphs may be preserved indefinitely. Pollen and spores have been recovered from marine and lacustrine sediments, peats, soil horizons, tufas, cave deposits, and glacial ice. The degree of resistance to decay varies from species to species and appears to be correlated with the amount of sporopollenin in the exine (Sangster and Dale, 1964; Havinga, 1967, 1984).

The pollen and spore catchment area (Figure 1) of a deposit depends on a number of factors (Jacobson and Bradshaw, 1981). Pollen may be transported and deposited either through aerial fallout, surface wash, or stream and river flow. Recent mathematical modelling and empirical studies of airborne pollen deposition (Bradshaw and Webb, 1985; Prentice, 1985) suggest that the source area for lakes increases with lake size and is inversely related to pollen grain mass. Rivers and streams may transport significant amounts of pollen long distances into lakes and the ocean (McAndrews and Power, 1973; Bonny, 1976; Heusser, 1978). The pollen deposited in peat includes both regional fallout and pollen deposited directly from plants growing on the bog surface (Janssen, 1984).

Figure 1 (upper right) Hypothetical relationship between pollen source area and lake size for lake basins that lack inflowing streams. (After Jacobson and Bradshaw, 1981).

Figure 2 (lower right) Selected examples of shapes and aperture arrangements of pollen and spores.
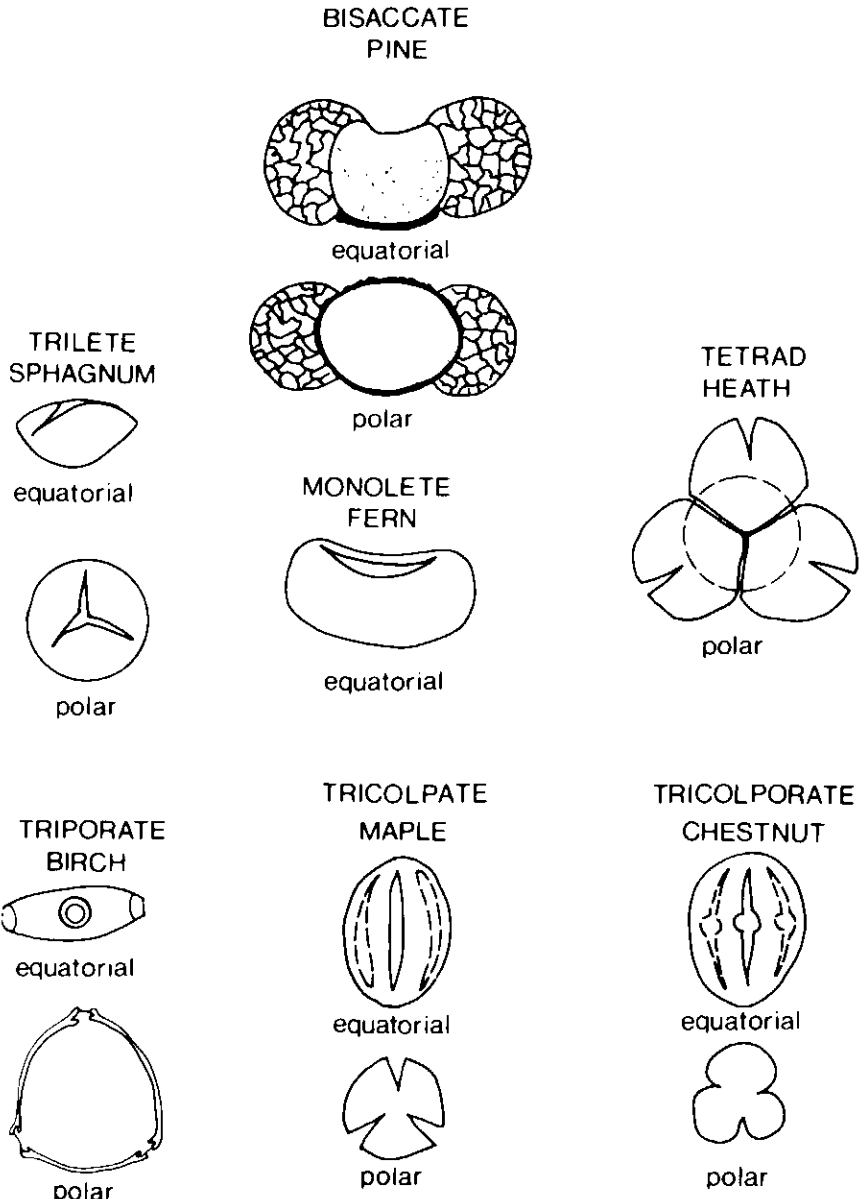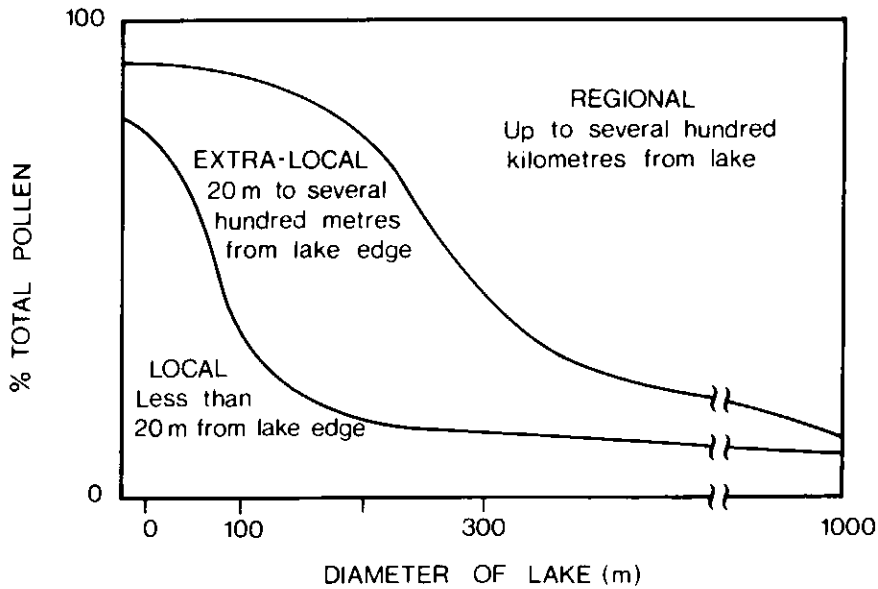
Pollen and spores have a specific gravity of 1.4 to 1.5 (Flenley, 1971) and in suspension behave like silt-size particles. Generally, the grains are deposited in low-energy environments within a matrix of fine sediments. However, due to differences in size, shape and density of grains, there appear to be differences in the hydrodynamic efficiency of pollen and spores from different species (Hopkins, 1950). Significant variation in the deposition and redeposition of pollen and spores in oceans, lakes, and bogs has been documented. Pine pollen becomes increasingly dominant seaward in marine deposits off the west coast of North America (Heusser, 1978). The increase in the dominance of *Pinus* may be a result of superior hydrodynamic efficiency (Heusser, 1978). Davis *et al.* (1971) and Davis and Brubaker (1973) showed that in thermally stratified lakes, heavy spheroidal grains such as oak *(Quercus)* were evenly distributed in the sediments. Pollen grains of pine and herbs

were deposited in greater numbers at the lake edges. In addition, the pollen of plants which grew along the edges of the lakes was most abundant in sediments along the periphery. Davis and Brubaker (1973) suggested that relatively small differences in density and settling velocity determined whether the grains would sink through the thermocline and be deposited or would remain suspended and moved to the periphery of the lakes. Lake bathymetry can exert control on the overall depositional pattern of pollen sized particles (Davis *et al.*, 1971; Lehman, 1975). Changes in lake bathymetry can lead to significant variation in the accumulation rates of pollen and spores at specific sites on the lake bottom. This effect is referred to as sediment focussing and can lead to difficulties in interpreting pollen accumulation data (Davis *et al.*, 1984). Following deposition, bioturbation can redistribute pollen vertically by as much as 15 cm in small lakes (Davis, 1974). Rowley

and Rowley (1956) demonstrated that small spheroidal pollen grains could percolate downward in peat deposits while the movement of larger grains was more restricted.

Field and Laboratory Techniques
Many of the fondest reminiscences of Quaternary palynologists revolve around sampling expeditions. Although Quaternary palynomorphs have been recovered from a number of sediment types, the principal source remains lake and bog deposits. Samples from sediment exposures may be taken at selected intervals during the logging of the sections. Sampling ice-caps and the deep sea sediments requires relatively specialized and sophisticated equipment. Platforms for sampling sediment from extant lakes have included water-craft, float planes, and winter ice. Samples of the surface sediments of lakes may be obtained using a variety of cup samplers and gravity corers (Aaby and Digerfeldt, 1986). The most widely used device for obtaining cores of lake sediments is the modified Livingstone piston sampler (Wright *et al.*, 1984). The piston action preserves the finest laminations and sedimentary structures. The Livingstone sampler is driven into the sediment and recovered using a series of metal core-rods, making it difficult to use in deep lakes (>50 m). Corers driven by compressed air (Mackereth, 1958) or cables and weights (Aaby and Digerfeldt, 1986) have been devised for use in deep water. Peats are often sampled using chamber corers which are driven into the sediment and then rotated to fill a sample chamber. The two most common peat corers are the Hiller and modified versions of Russian samplers (Jowsey, 1966). The Russian sampler has the advantage of preserving stratigraphy. In addition, a new version of the Livingstone corer has been developed to sample peats (Wright *et al.*, 1984).

The concentrations of pollen and spores in sediment samples may range from <1 grain per mL in loess, cave and marine sediments to >100,000 grains per mL in lake sediments from the temperate forest region. However, the grains must be concentrated from the sediment before analysis. The resistant nature of the exine allows palynologists to use chemical reagents to remove most other mineral and organic matter from the samples. A standard processing sequence is as follows:

(1) Sub-sampling of a standard volume of sediment. Often 1 mL of material is used.
(2) Addition of a known quantity of exotic palynomorphs (Stockmarr, 1971). The exotic palynomorphs are used to calculate the volumetric concentrations of pollen and spores in the sediment samples.
(3) Removal of carbonates using 10% HCl.
(4) Removal of humic acids using 10% KOH in a hot water bath.
(5) Removal of pyrite using concentrated HNO_3.

WALL STRUCTURE

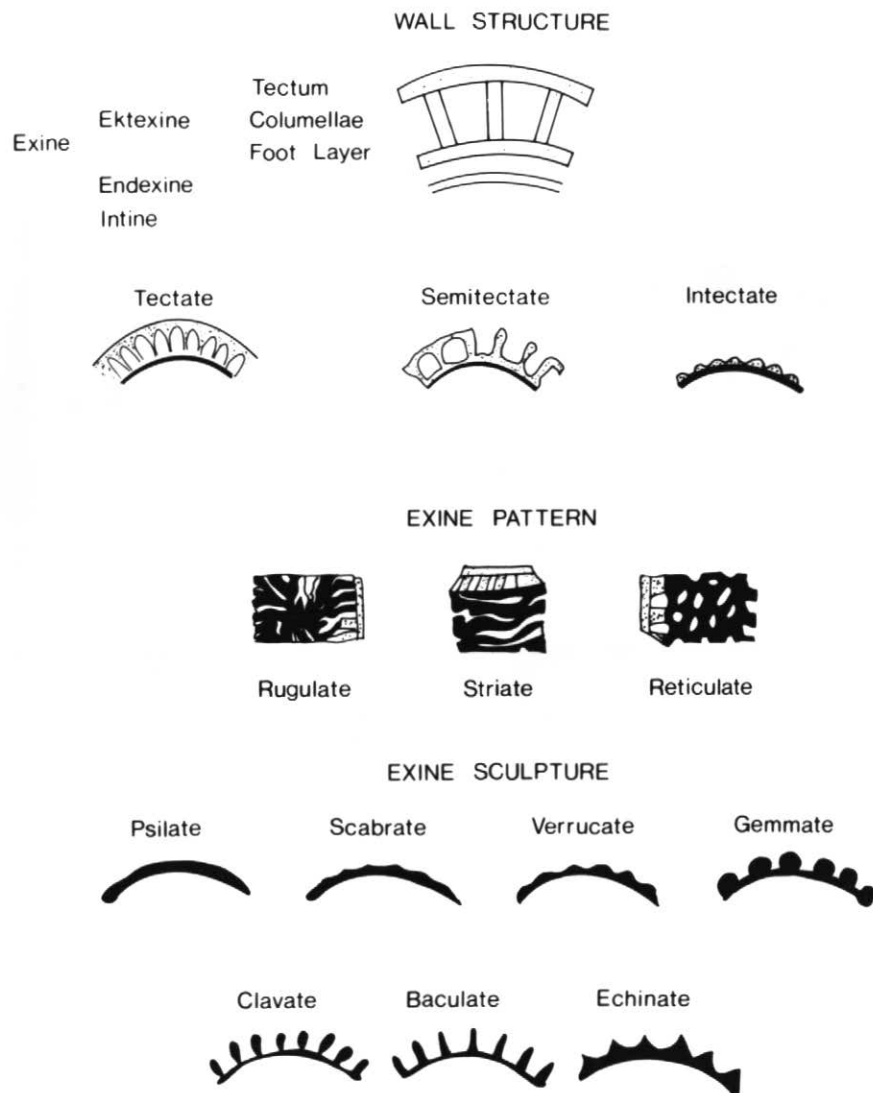EXINE PATTERN

EXINE SCULPTURE

Figure 3 *Pollen wall structure and sculptural elements.*

(6) Removal of silica using 50% HF in a hot water bath.

(7) Removal of cellulose using an "acetolysis" treatment (9 parts $(CH_3CO)_2O$ to 1 part H_2SO_4 preceeded and followed by washes in CH_3COOH).

(8) Dehydration using $(CH_3)_3COH$.

(9) Staining with safranin or basic fuchsin.

(10) Storage of prepared material and mounting on microscopic slides with 2000 cs silicone oil or glycerine (refractive index 1.55).

Sieving may be used to remove large particles of peat or coarse clastic sediments. Micro-sieving techniques have been developed to remove small ($< 7 \mu m$) mineral and organic particles (Cwynar et al., 1979). Flotation methods may be used also to remove heavy minerals. The exact sequence of chemical treatment varies for different labs and different samples. Full details are available from Faegri and Iversen (1975) and Berglund and Ralska-Jasiewiczowa (1986).

Taxonomic keys for the identification of modern pollen and spores from Canada are available from Kapp (1969), McAndrews et al. (1973), and Bassett et al. (1978). Most palynological identification and counting is done using transmitted light microscopy. Typically, a magnification of 400 × is used to identify and count samples, while 1000 × magnification is used for critical determinations. Pollen and spores may be differentiated by a suite of morphological characteristics (Figures 2 to 4). The most important characteristics are shape, size, aperture arrangement, exine structure, and surface ornamentation.

Most palynomorphs are spheroidal, but may be significantly compressed or extended along the polar axis. Pollen from many gymnosperms is bisaccate in form, consisting of a central body (colpus) with two wing-like bladders (sacci). Some plants, including cattails (Typha) and heaths (Ericales), release pollen in which the tetrad form is retained.

Apertures are apparent on most grains. On spores, the aperture often takes the form of a monolete or trilete scar on the proximal face of the grain. Angiosperms possess apertures which are pores (pori), furrows (colpi), or a combination of both (colporate grains).

Three important structural subdivisions are recognized for the exine (Figure 3). These are the tectum, the columellae, and the foot layer. The three structures are often referred to collectively as the ektexine (Faegri and Iversen, 1975). The tectum may be complete, perforated, or absent. Surface ornamentation may be present on the tectum or it may be featureless. The columellae may form surface ornamentation on the foot layer.

Many pollen taxa cannot be satisfactorily differentiated to the specific or generic level using transmitted light microscopy. Electron scanning microscopy (Figure 4) may be useful for some determinations (Bassett et al., 1978). This technique is not practical for the large counts (~ 300 to 1000 grains per sample) required for quantitative palynology. Numerical taxonomic techniques based upon precise measurements of one or more grain dimensions have proven useful in separating morphologically similar species such as Picea glauca and P. mariana (white and black spruce) (Birks and Peglar, 1980). However, natural variation commonly occurs in the size of pollen grains from the same species (Ives, 1977; Birks, 1978). In addition, the size of palynomorphs can be affected by chemical preparation techniques and slide mounting mediums (Andersen, 1960, 1978).

Palynological data from sediment sequences are most often presented as percentages, volumetric concentrations, or accumulation rate diagrams (Figure 5). The concentrations of palynomorphs are usually calculated using the exotic pollen method (Stockmarr, 1971). Volumetric concentrations may be converted to pollen accumulation rates when a reliable estimate of sediment deposition rates is available (Maher, 1972). The advantage of pollen accumulation rates is that the record of a plant taxon is not influenced by variations in the abundance of other taxa, but accumulation rates are prone to variation and anomalies caused by variations in sedimentation (Davis et al., 1984). Independent chronological control for pollen records is often provided by radiocarbon dating. Chronological control may also be provided by short-lived isotopes such as ^{210}Pb (Oldfield and Appleby, 1984), paleomagnetism (Thompson, 1986), tephrochronology (Einarsson, 1986), and varve counts of annually laminated sediments (Saarnisto, 1986).

Pollen diagrams are often divided into zones that contain stratigraphically conterminous samples with pollen assemblages that are internally similar and dissimilar from the assemblages of adjacent zones (Figure 5). The zones are generally based upon percentage data and correspond most closely to the assemblage biozone defined by the International Stratigraphic Code (Hedberg, 1976). The local assemblage zones described from individual sections

30 μm

10 μm

10 μm

10 μm
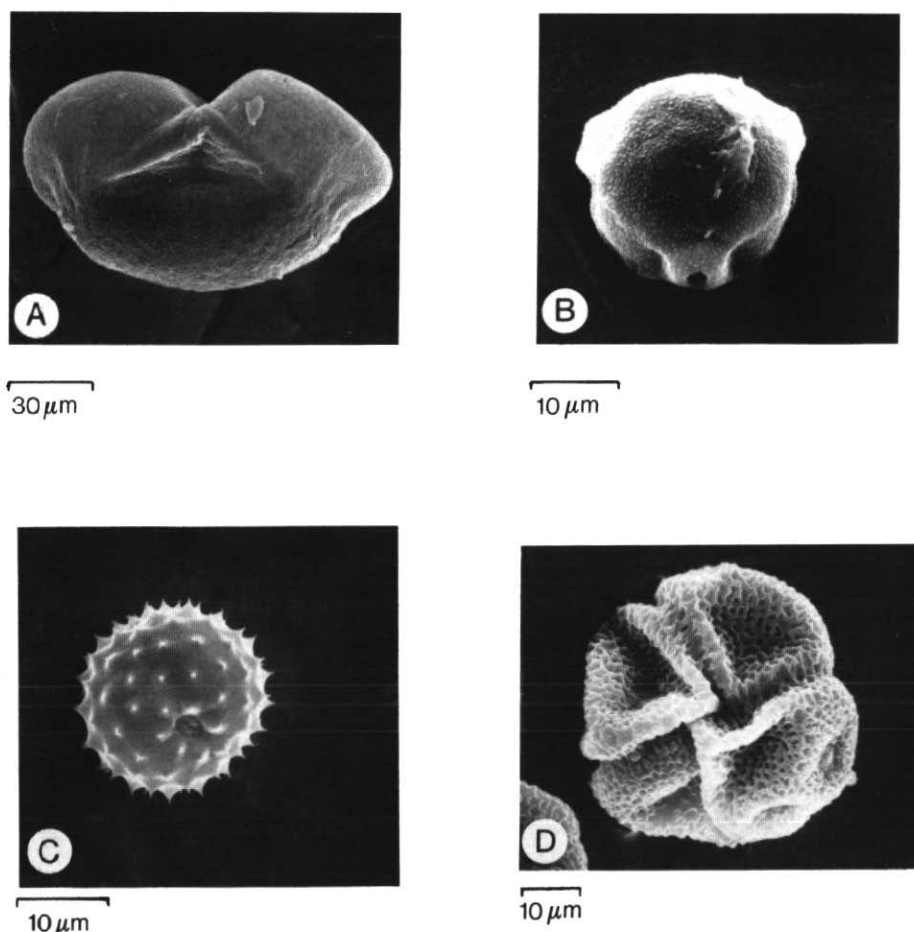
Figure 4 Scanning electron micrographs of selected pollen types:

(a) White spruce (Picea glauca), a bisaccate grain.

(b) Dwarf birch (Betula glandulosa), a triporate grain with microscabrate sculpturing.

(c) Giant ragweed (Ambrosia trifida), a tricolporate grain with echinate sculpturing.

(d) Cattail (Typha latifolia), a tetrad with reticulate sculpturing.

Scanning electron micrographs reproduced from Bassett et al. (1978) by permission of the Biosystematics Research Centre.
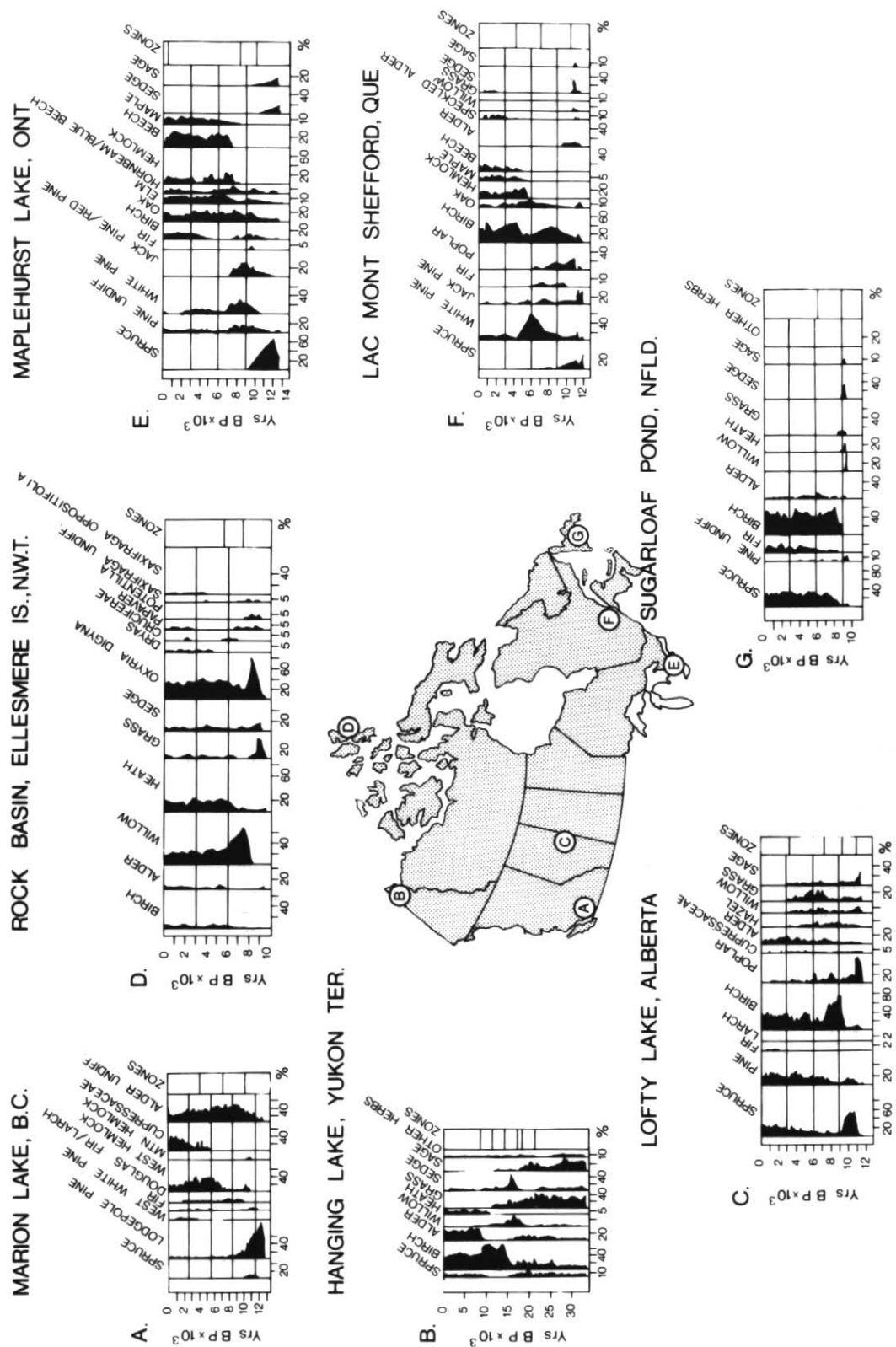
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Figure 5 *Representative pollen percentage diagrams from Canada. Sources are:* **(a)** *Mathewes (1973),* **(b)** *Cwynar (1982),* **(c)** *Lichti-Federovich (1970),* **(d)** *Hyvärinen (1985),* **(e)** *Mott and Farley-Gill (1978),* **(f)** *Richard (1978), and* **(g)** *Macpherson (1982).*

may be combined to form composite regional zones. A variety of numerical techniques are available for the zonation and comparison of pollen diagrams (Birks and Gordon, 1985). Some workers question the usefulness of zones and suggest that they are often artificial constructs which serve to obscure the importance of transition periods in pollen records (Walker, 1982). Others suggest that zones are useful for ease of discussion and formal stratigraphic description (Birks and Gordon, 1985).

Non-stratigraphic pollen data are often presented in tabular form. The spatial distribution of pollen taxa from surface samples or from temporally synchronous levels in chronologically correlated cores may also be presented as isopollen maps (Figure 6) and their variants (MacDonald and Waters, 1987).

Selected Applications of Quaternary Palynology

Palynology is an invaluable research tool for a wide variety of Quaternary studies. Chronostratigraphic correlation, paleoecology, paleoclimatology and archaeology are arguably the four sub-disciplines of Quaternary research where palynology is of the greatest importance.

Chronostratigraphic correlation. Pollen and spores from Quaternary deposits have long been used as chronostratigraphic tools. The use of fossil pollen for chronostratigraphy requires a regional master stratigraphy.

If absolute dates are to be assigned on the basis of pollen assemblages, then the regional stratigraphy must be reliably dated by independent means. In southwestern Ontario, deposits that contain pollen assemblages dominated by *Picea* can be assigned an age of approximately 13,000 to 10,000 BP (^{14}C years Before Present) on the basis of the regional pollen stratigraphy (McAndrews, 1981). Chronostratigraphic applications of pollen spectra are based upon the assumption that vegetation changes are regionally synchronous. Figure 7 illustrates the asynchronous nature of the pine *(Pinus)* pollen record in western Canada (MacDonald and Cwynar, 1985). Pine pollen is an important component of
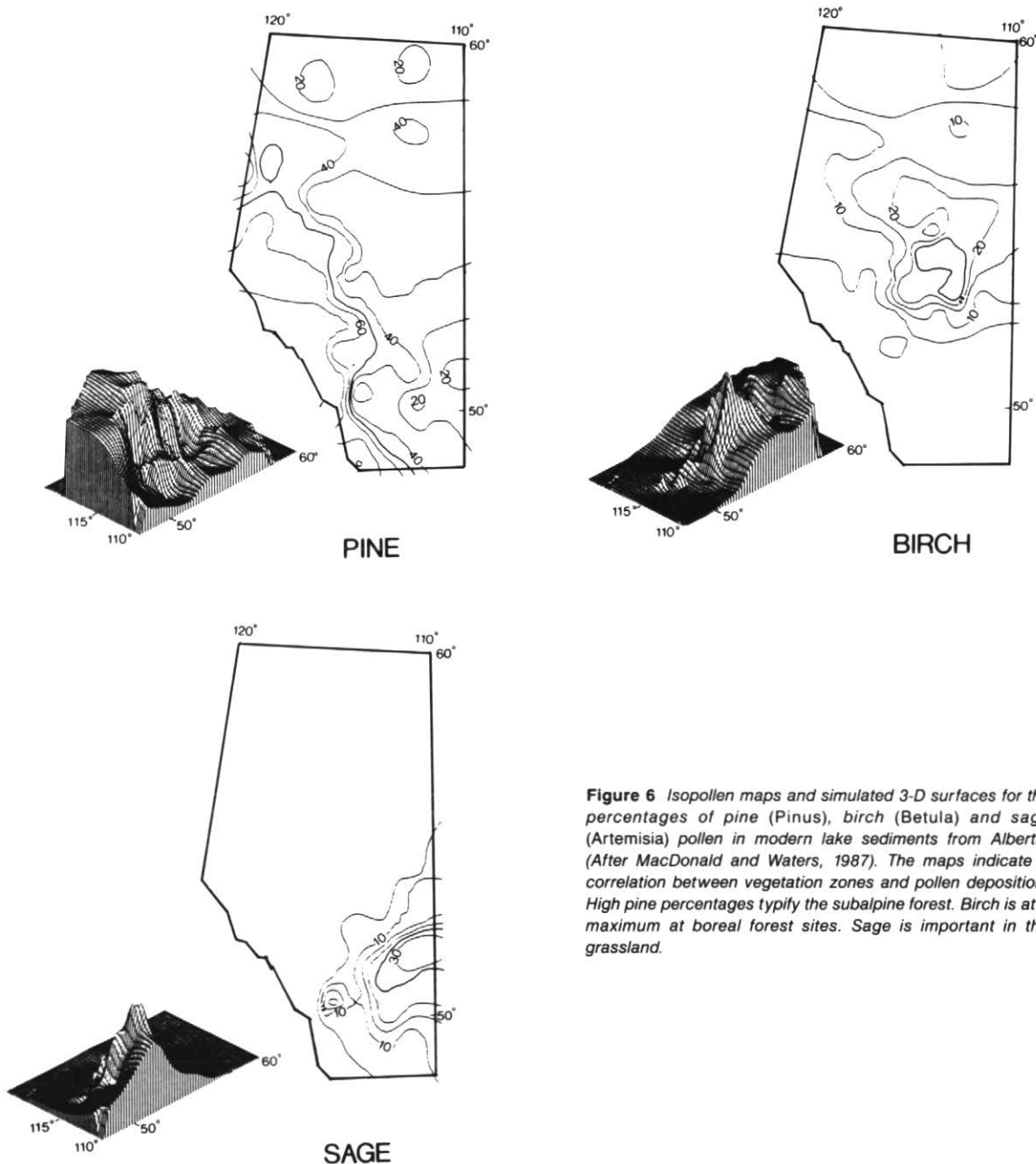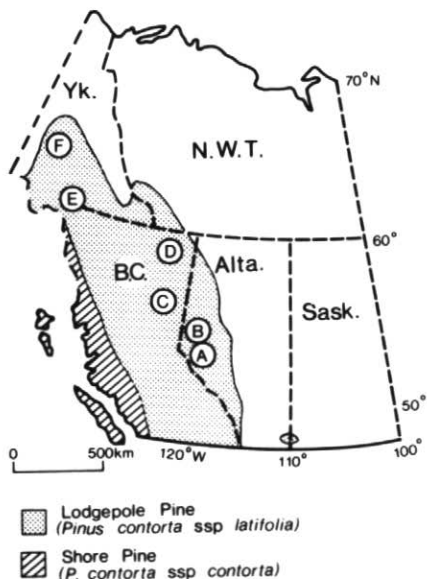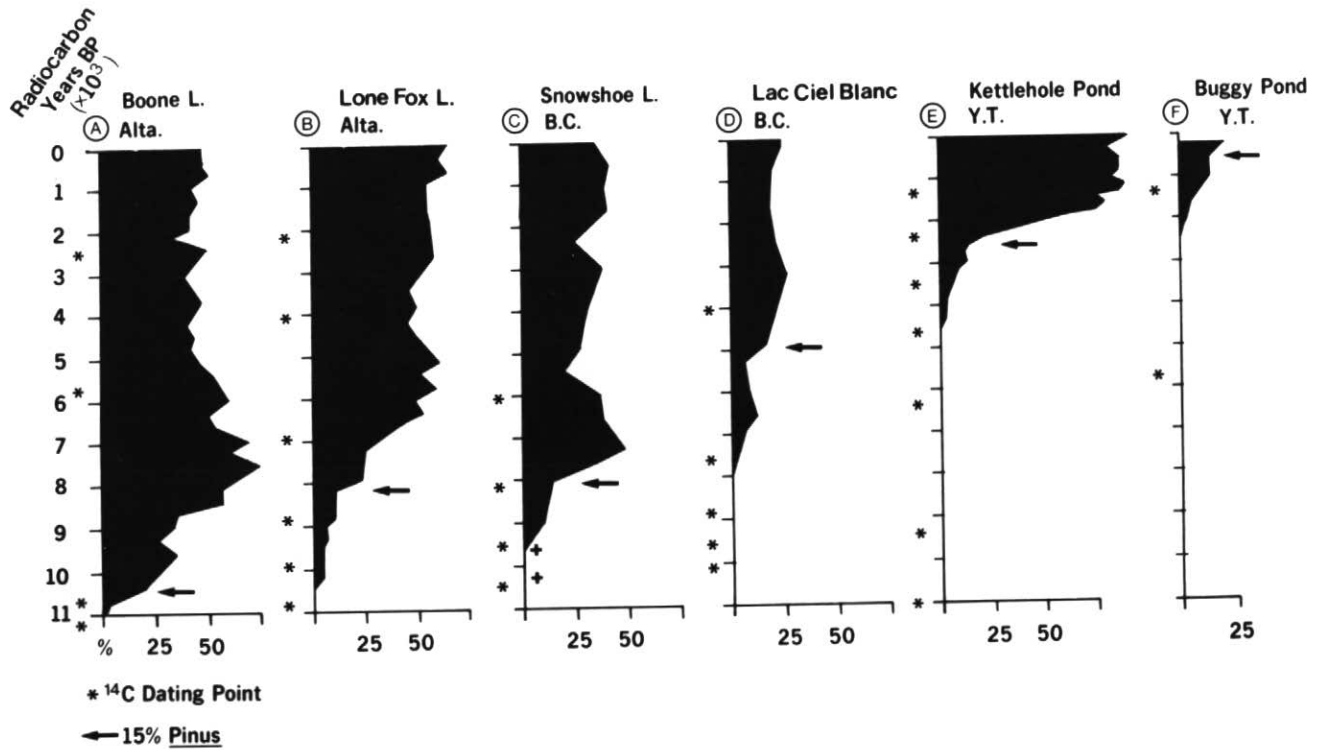

PINE

BIRCH

SAGE

Figure 6 *Isopollen maps and simulated 3-D surfaces for the percentages of pine* (Pinus), *birch* (Betula) *and sage* (Artemisia) *pollen in modern lake sediments from Alberta. (After MacDonald and Waters, 1987). The maps indicate a correlation between vegetation zones and pollen deposition. High pine percentages typify the subalpine forest. Birch is at a maximum at boreal forest sites. Sage is important in the grassland.*

pollen assemblages throughout the Holocene in central Alberta. Pine does not appear in pollen records of northwestern Alberta until 5500 BP. In central Yukon, pine does not appear until ~500 BP. Clearly, the asynchronous nature of the pine record precludes the use of pine pollen as a reliable indicator fossil for broad-scale chronostratigraphic correlation in the western interior of Canada. Fossil pollen mapping for eastern North America indicates that most taxa have asynchronous records (Davis, 1981b). However, the distances at which the asynchronous nature of the record becomes significant may vary from a few hundred to

several thousand kilometres. As reliable absolute dating techniques have developed, less emphasis has been placed on the chronostratigraphic use of the Holocene pollen record. Indeed, much research has centered on documenting and attempting to explain the asynchronous nature of vegetation change reflected in the pollen stratigraphy. Pollen-based chronostratigraphic correlations remain important for Pleistocene deposits that are often impossible to date using the radiocarbon technique.

Paleoecology. Fossil pollen and spores provide long-term records of vegetation that are unavailable from any other source.

Perhaps the most powerful technique for reconstructing vegetation history from pollen records is the comparative approach (Birks and Birks, 1980). Fossil assemblages are compared with modern samples from known vegetation types in order to aid in the interpretation of the fossils by discovering if past vegetation has a modern counterpart. In many cases, the comparison of the fossil and modern spectra is done using numerical ordination procedures (*e.g.*, Ritchie and Yarranton, 1978; Liu and Lam, 1985; MacDonald and Ritchie, 1986) or direct mathematical distance measures (Overpeck *et al.*, 1985). Examples of the numerical comparison of


Figure 7 *Pine (Pinus) pollen percentages for sites from the western interior of Canada. (After MacDonald and Cwynar, 1985). The diagrams demonstrate asynchroneity in the stratigraphic record of pine. The asynchroneity reflects the slow northward spread of pine from a southern refugium following the close of the last glaciation.*
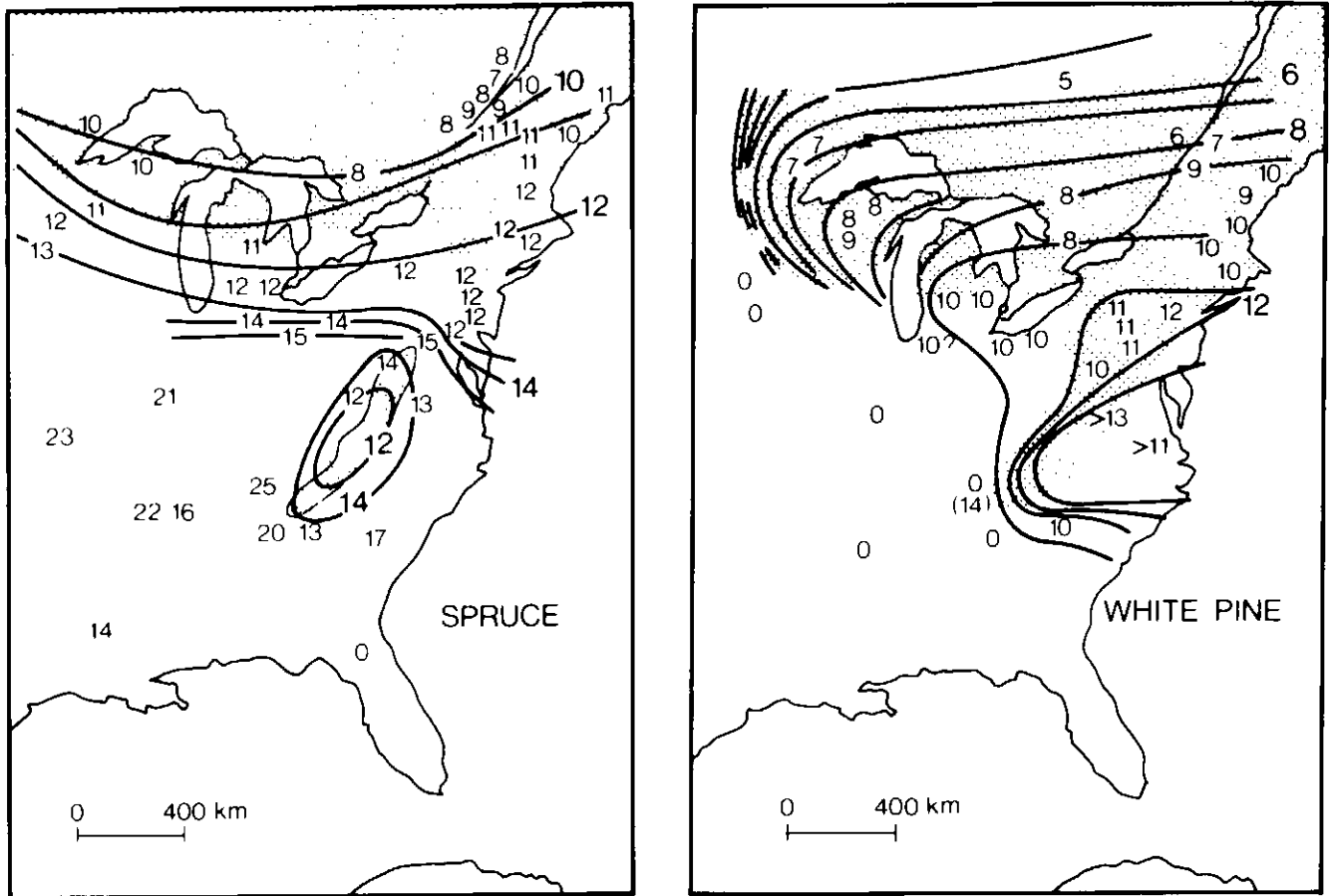
Figure 8 *Isochrone maps depicting the northward spread of spruce* (Picea *spp.) and white pine* (Pinus strobus) *during late Quaternary time. Each isochrone line depicts the range limits of the taxa at thousand year intervals. (After Davis, 1981b).*
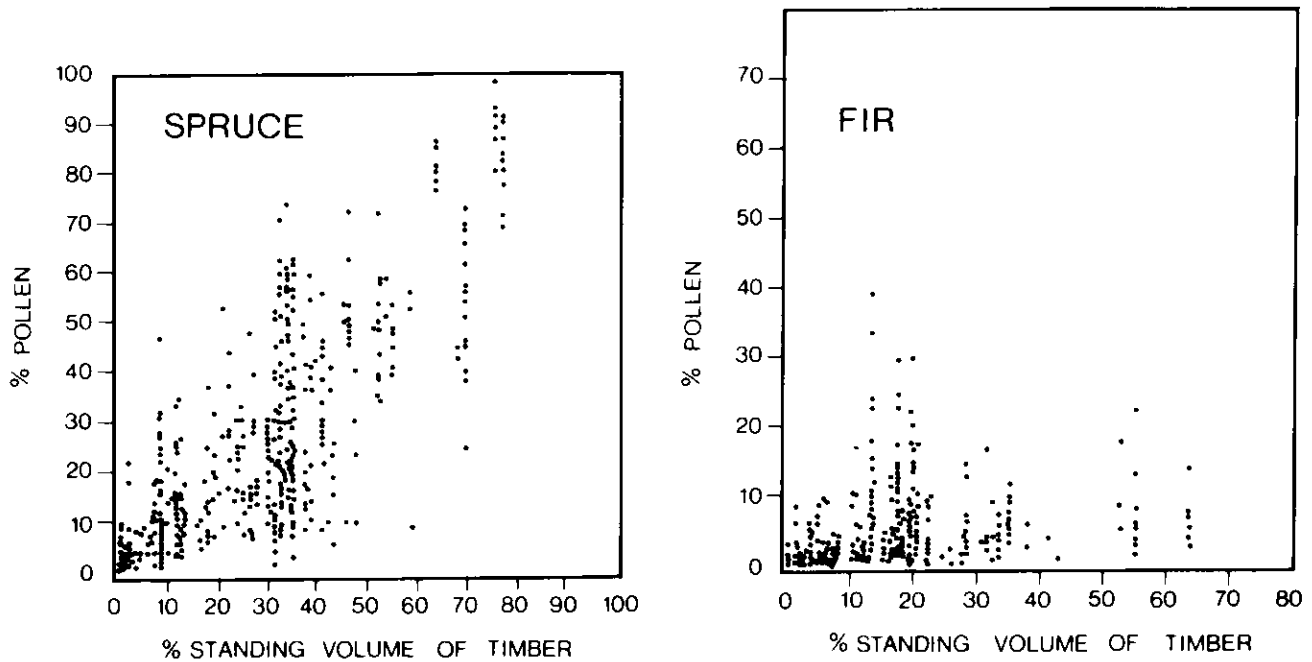
Figure 9 *The relationship between the percentages of spruce* (Picea) *and fir* (Abies) *pollen in modern sediments and the percentage of the spruce and fir trees in adjacent forests. (After Delcourt et al., 1984). A good relationship is suggested for spruce. However, the relationship between fir pollen percentages and abundance in the vegetation is less clear.*

fossil and modern spectra are available from a number of sites in the western interior of Canada (Ritchie and Yarranton, 1978; Ritchie, 1977; MacDonald, 1983; MacDonald and Ritchie, 1986; MacDonald, 1987). These studies suggest that early Holocene vegetation of the western interior of Canada lacks a modern counterpart in the region. During the mid-Holocene, the grassland boundary and the northern limits of boreal forest were both located significantly north of their modern positions, presumably due to climatic change. Between approximately 5000 BP and 3500 BP the modern vegetation was established. Deducing the factors that produced early Holocene vegetation which lacks modern regional counterparts remains an important and sometimes contentious field of research for Quaternary palynologists (Prentice, 1983).

Fossil pollen can be used to provide records of vegetation disturbance and response which span millenia. Particular interest has focussed on the use of fossil pollen and charcoal to examine the role of fire in forested ecosystems. Charcoal particles are retained during the chemical processing of sediments for fossil pollen and spores. The abundance of charcoal may be estimated using transmitted light microscopy (Tolonen, 1986; Patterson et al., 1987). Cwynar (1978) examined the charcoal, pollen and geochemistry of a five hundred year long section of laminated sediment from a small lake in Algonquin Park, Ontario. He deduced that fires had occurred approximately every 80 years in the lake drainage basin. Greene (1982) used time series analysis to statistically examine Holocene fire record preserved in the fossil pollen and charcoal from a small lake in southwest Nova Scotia. He suggested that fire was a much more important agent of vegetation disturbance prior to 6000 BP than it is in the modern forests of the region.

Table 1   R-values for important pollen taxa from the Inuvik area, N.W.T. (Ritchie, 1984). In this region, alder is greatly over-represented in the pollen record, the heaths are greatly under-represented, and juniper is equally-represented.

Pollen Taxon	R-value
Spruce	0.5
Larch	0.2
Poplar	0.6
Birch	3.0
Alder	11.8
Willow	0.6
Juniper	1.0
Heath	0.1
Sage	5.0
Grass	3.4
Sedge	2.2

The epidemiology of plant pathogens is an intriguing application of palynology. The North American chestnut (Castanea dentata) was decimated by the accidental introduction of the fungal pathogen at the turn of this century. The decline of chestnut trees is clearly reflected in the declines in chestnut pollen in recent deposits (T.W. Anderson, 1974). Fossil pollen records from eastern North America provide evidence that hemlock trees (Tsuga canadensis) underwent a similar decline at approximately 4850 BP (Davis, 1981a; Allison et al., 1986). Davis (1981a) interpreted this decline as the impact of a virulent pathogen. The pollen record indicates that hemlock populations recovered approximately 1900 years after the decline, possibly due to the development of an immunity to the pathogen (Davis, 1981a; Allison et al., 1986). It is impossible, however, to determine what pathologic agent affected the hemlock populations.

Fossil pollen can also be used as a long-term record of individual plant species and genera. Maps depicting the northward movement of plant populations into Canada following the end of the last glacial period have been produced from pollen accumulation and percentage data (e.g., Davis, 1981b; Webb et al., 1983; MacDonald and Cwynar, 1985; Ritchie and MacDonald, 1986)(Figure 8). These maps indicate that many plant species found in association today had very different migrational histories during the late Pleistocene and Holocene. Study of the migrational patterns provides important insights into the long-term patterns of community development and the response of individual plant species to environmental change (Davis, 1981b).

Interest has focussed on the use of the fossil pollen record to test hypotheses developed by population ecologists and geneticists. Studies in Japan, the United States and England have used pollen accumulation data to estimate the doubling time of local tree populations as they increased following the end of the Pleistocene (Tsukada, 1982; Tsukada and Sugita, 1982; Bennett, 1983). The estimates of doubling times for tree species range from 31 to 462 years and appear to correspond well with the available observational data on tree population doubling times (Bennett, 1986). A recent study in western Canada used the fossil pollen record of lodgepole pine (Pinus contorta ssp. latifolia) to test hypotheses about the relations between plant population history and genetic variation (Cwynar and MacDonald, 1987). This study concluded that population residence time as determined from the pollen record was positively correlated with the genetic diversity of pine populations.

Both migration maps and tree species population estimates made from fossil pollen data are prone to significant uncertainties. It is often unclear from most pollen records if

low amounts of pollen from a particular species indicate that the species is present near the site in low numbers, or if the species is present some distance from the site and the pollen is derived from long distance transport (Bennett, 1985). The sampling area represented by the pollen record may vary from several hectares to > 1000 km² depending on the size of the lake and the pollen production and dispersal capabilities of the species under study. It is unknown whether the relation between plant population size and representation in the pollen record is linear. A non-linear relation between plant population and pollen accumulation rates could confound estimates of doubling time. Sediment focussing leads to increases and decreases in pollen accumulation rates which may invalidate the population doubling rates calculated from the pollen record.

Due to inter-specific variation in pollen production and preservation, the abundance of a plant species in the fossil record may not be directly proportional to the abundance of the species in the vegetation (Fagerlind, 1952). The relationship between modern pollen deposition and the abundances of contributing trees (Figure 9) has been examined to provide correction factors or "R-values" (Davis, 1963) which allow fossil pollen data to be used to estimate the past abundance of plants. R-values are calculated as:

R-value for species a   =

$$\frac{\text{% of species a in pollen spectra}}{\text{% of species a in vegetation}}$$

Taxa that are over-represented in the pollen record have high values while under-represented taxa have low R-values (Table 1). Both linear and non-linear relations between pollen abundances and tree abundances have been used to approximate R-values (Webb et al., 1981; Prentice and Webb, 1986). Past vegetation abundance can be estimated:

% of species a in past vegetation   =

$$\frac{\text{% of species a in pollen spectra}}{\text{R-value}}$$

The use of R-values to calculate past plant species abundances is based upon the assumption that the R-value for the species has not changed through time. This assumption is uncertain when past vegetation lacks a modern counterpart.

Paleoclimatology. Two approaches are used to estimate past climatic conditions from pollen data. The indicator species approach requires knowledge of the climatic limits of one or more plant species. The presence or absence of the species in the fossil record is used to infer past climatic conditions. In northwestern Canada, poplar and aspen (Populus), cattail (Typha latifolia), and bog myrtle (Myrica gale) do not occur north of the present treeline. Ritchie et al. (1983) found evidence in the pollen record that all three of these species were present at sites

beyond the modern treeline during the period 11,000 to 6,000 BP (Figure 10). This was interpreted as evidence for warmer summer conditions during the early Holocene in northwestern Canada.

The assemblage approach (Birks and Birks, 1980) assumes that climate serves to control the proportions of plant species in vegetation assemblages. Multivariate numerical analysis is used to determine the modern relationship between pollen proportions and climatic variables (Figure 11). A mathematical transfer function is derived from the modern pollen-climate relationships and used to estimate past climatic conditions from fossil pollen spectra:

Climate Estimate =

Transfer Function × Pollen Proportions.

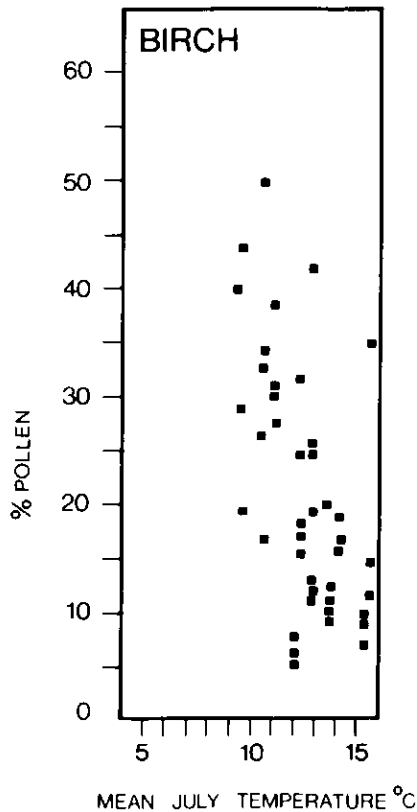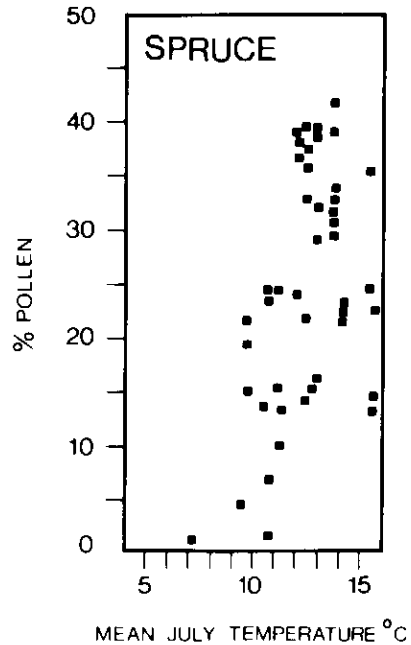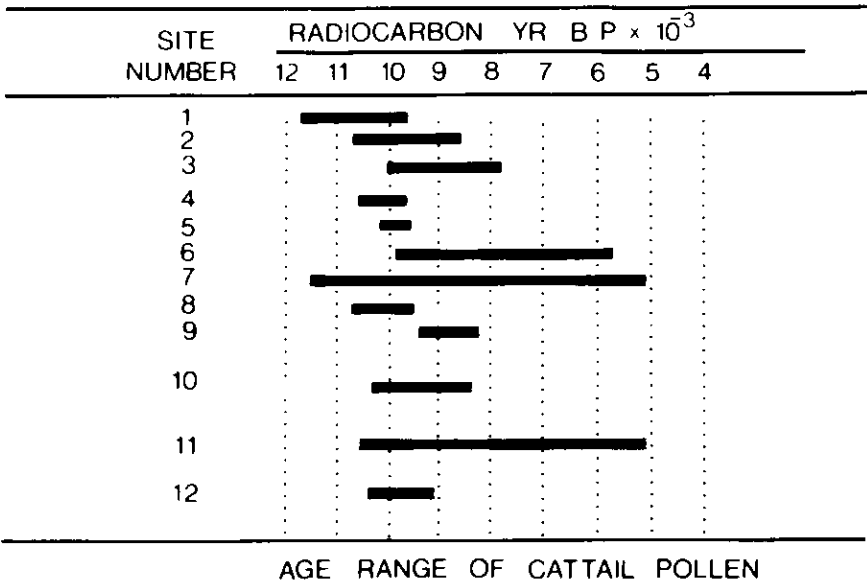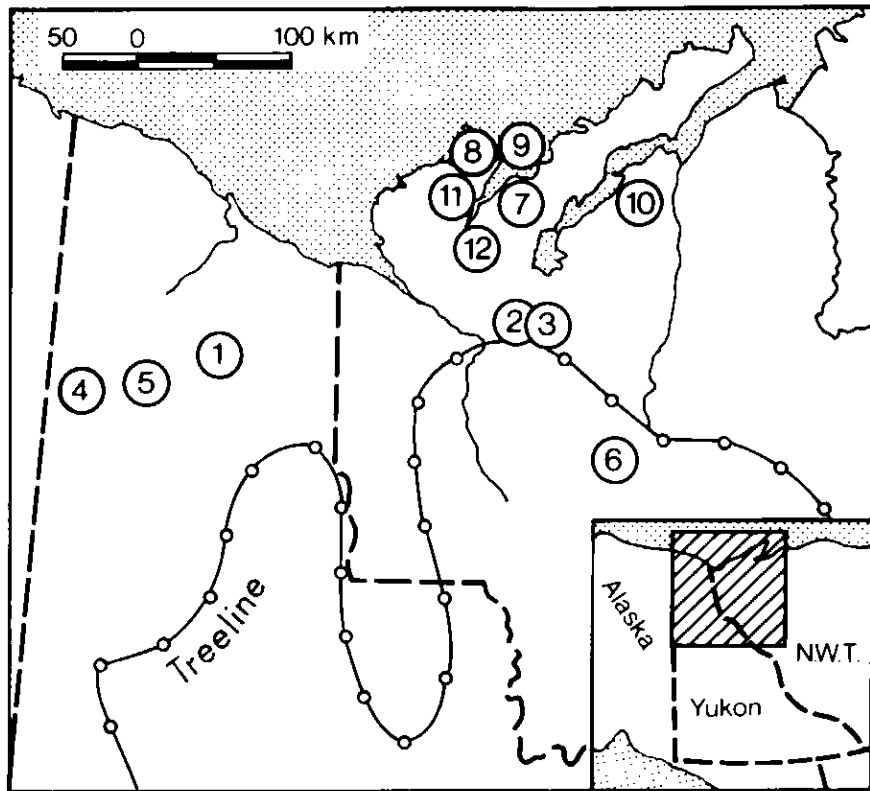Detailed discussion of transfer function methodology is presented by Howe and Webb (1983).

Figure 10 Evidence from northwestern Canada for the northward extension of cattail (Typha latifolia) during the early to mid Holocene. (After Ritchie, 1984).

Figure 11 The relationship between the percentages of spruce (Picea) and birch (Betula) pollen in modern lakes sediments and mean July temperature. (After Kay and Andrews, 1983).

Mathewes and Heusser (1981) con-structed mathematical transfer functions from modern pollen and climate data from the Pacific Northwest. They applied transfer functions to the fossil pollen record from Marion Lake, British Columbia (Figure 5)

and produced estimates of mean July tem-perature and mean annual precipitation. The results suggest that the early Holocene cli-mate was significantly warmer during July and drier than present (Figure 12).

A number of factors may give rise to unreli-

able estimates of past climate from transfer functions. The two most troubling assump-tions of the transfer function approach are: (1) past and present vegetation conditions reflect states of equilibrium between climate and vegetation; and (2) the past vegetation-
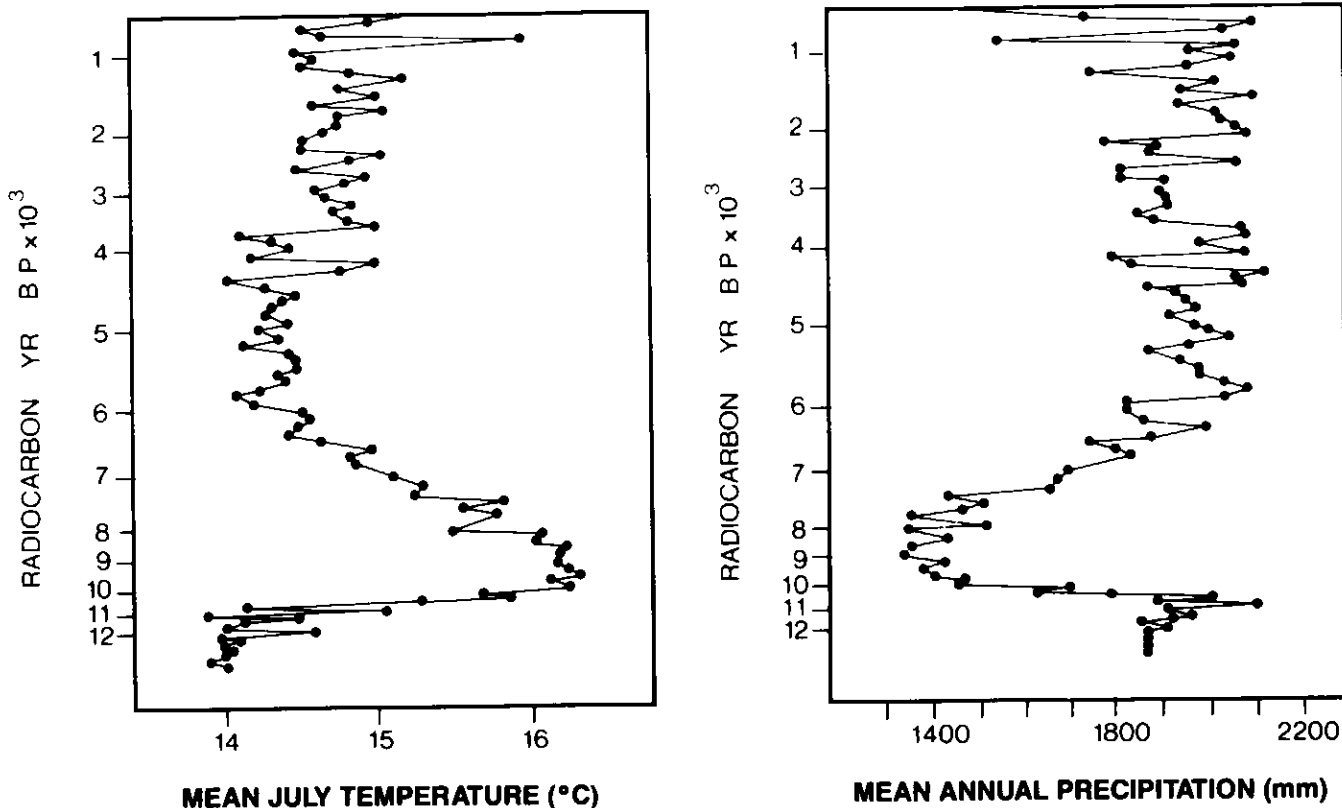

Figure 12 *A reconstruction of post-glacial temperature and precipitation based on pollen-climate transfer functions from the Pacific Northwest applied to the fossil pollen record from Marion Lake, B.C. (After Mathewes and Heusser, 1981).*
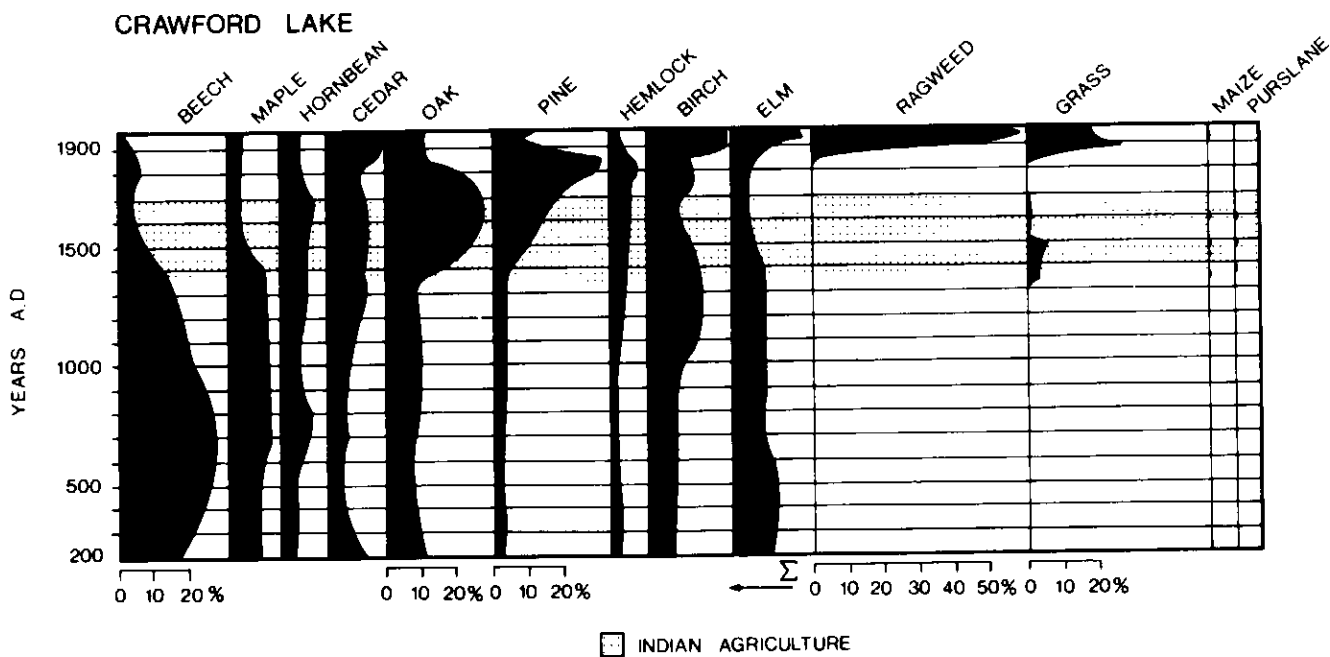

Figure 13 *The fossil pollen record from Crawford Lake, Ontario, highlighting the period of Indian agriculture. (After McAndrews, 1976).*

climate relationships have analogues in the present relationships between climate and vegetation. A number of factors including climatic conditions which were unique to the past, lags between climatic change and vegetation response, and the effect of progressive soil development on vegetation may produce spurious estimates of past climate using the transfer functions. However, the disequilibrium conditions caused by the above factors will only produce significant distortion of climatic estimates if the lag time between vegetation change and climate are large compared with the rate of climatic change (Prentice, 1986; Webb, 1986). In addition, climatic change involves simultaneous variation in a number of variables, and the simplifying assumptions made during the estimation of mean summer temperatures or annual precipitation may be unreasonable given the complex nature of the climate and vegetation-climate relationships (Bryson, 1985). Comparison of climatic estimates from the pollen record with estimates from independant sources such as other fossil groups or paleoclimatic models provides a potential test of pollen-climate transfer functions.

Archaeology. Pollen analysis has been widely used in archaeology to provide chronological control and paleoenvironmental information. In a classic study, Byrne and McAndrews (1975) recovered purslane *(Portulaca oleracea)* pollen from the annually laminated sediments of Crawford Lake. They were able to demonstrate that purslane was native to North America and was likely an important Indian pot-herb (Figure 13). Detailed pollen analysis indicated that relatively large amounts of maize *(Zea mais)* pollen were deposited in Crawford Lake between 1400 AD and 1700 AD (McAndrews, 1976). This suggested that an Indian settlement had been located near the lake. Archaeological investigations have uncovered an Iroquois village of approximately 500 people which was inhabited during the period of maize and purslane pollen deposition (Finlayson et al., 1973).

Recently, Hebda and Mathewes (1984) compared the pollen record of cedar *(Thuja)* pollen and the age range of native artifacts used for massive woodworking at a number of sites in coastal British Columbia and Washington. They found that cedar migrated northward along the coast, spreading from central Washington to northern British Columbia between 9000 and 2500 BP. A clear relationship was revealed between the appearance of cedar and the first occurrence in the archaeological record of massive woodworking tools. Hebda and Mathewes suggested that the development of massive woodworking technology was environmentally constrained until large cedar trees became available.

Future Directions

A number of research directions will continue to entice Quaternary palynologists in Canada. Large areas of the country, particularly in the arctic, are unknown in terms of Quaternary pollen stratigraphy and vegetation history. Important data on both Pleistocene and Holocene palynology remains to be collected. The usefulness of fossil pollen for plant population studies will serve to provide exciting research avenues for palynologists and to attract a new audience of population ecologists and population geneticists. Palynology has the potential to provide empirical tests of plant population and genetic hypotheses and perhaps contribute new theory (Edwards, 1983; Birks, 1985). Quaternary palynology will continue to play a key role in paleoclimatology. In particular, the fossil pollen record provides one of the best sources of data to test the large-scale paleoclimatic models which are now being developed (Bartlein et al., 1986). Archaeological studies will long benefit from the paleoecological insights which the fossil pollen record can contribute to the understanding of cultural traditions and development. It is safe to say that palynology will continue to play a fundamental role in Quaternary ecology.

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