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LA THÈSE A ÉTÉ MICROFILMÉE TELLE QUE NOUS L’AVONS RECEUE
NOVA SCOTIAN FOREST HISTORY—
EVIDENCE FROM STATISTICAL ANALYSIS
OF POLLEN DATA

DAVID GEOFFREY GREEN

Submitted in partial fulfilment of the requirements for the degree of Doctor of Philosophy at Dalhousie University, Halifax, Nova Scotia, October 1976.

APPROVED BY:

DAVID GEOFFREY GREEN 1978
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ABSTRACT

The history of Nova Scotia's forests since retreat of the last ice sheet is investigated using statistical analysis of pollen data. Time series analysis is introduced into pollen analysis and its use examined thoroughly.

Postglacial changes in makeup of the province's forests are traced. It is concluded that the earliest forests were composed of trees which migrated into Nova Scotia from New Brunswick and that local environmental conditions and competition from other trees were the chief factors delaying the first appearance times of tree species, rather than slow migration rates.

The impact of fire is assessed in detail. It is shown that fire plays a key role in competition between species and that the whole series of postglacial forest composition changes may be viewed as a community response to changing fire regimes triggered by shifts in climate.
### Abbreviation

B.P. — Before present

Standard physical abbreviations are also used.

### Scientific and Common Names Referred to in Text

<table>
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<th>Common Name</th>
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<tbody>
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<td>Acer</td>
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CHAPTER I

INTRODUCTION

1.1 AIMS

This project will investigate the origins and history of Nova Scotian forests. Its aims are: 1) to determine the sources of the tree species and their migration routes into the province after retreat of the last ice sheet; 2) to trace subsequent patterns of forest change; and 3) to identify important environmental forces at work in these processes.

Pollen records provide the most complete and detailed history of forest changes. Work by Livingstone (1968), Ogden (1960), Railton (1972), and others has contributed to the understanding of Nova Scotia's forest history. However, no records have been examined from southwest Nova Scotia or from northeastern New Brunswick, so the question of species sources has remained largely unresolved.

Emphasis has been given to statistical analysis of pollen data. In particular, a method of identifying pollen zones objectively has been explored in depth, and time-series analysis has been introduced into the study of pollen data. In Chapter 6, both methods are used to explore the role of fire and competition in community change.
1.2. PRESENT-DAY FORESTS

Nova Scotian forests display amazing variety and contrast in their composition. While some areas are dominated solely by boreal or deciduous species, the forests are most often composed of vast mosaics of many different tree types. It is not uncommon to find plants characteristic of arctic regions growing alongside plants typical of the warm areas of southeastern North America.

Nova Scotian forests form part of the transition from Boreal to Deciduous forest and are closely related to forests of the Great Lakes - St. Lawrence Region. Nichols (1935) classified Nova Scotia in the Hemlock-White-Pine-Northern Hardwoods Region. This is too general to adequately describe the complex vegetation patterns though, and Rowe (1972) classes Nova Scotia, along with P.E.I. and New Brunswick, as a distinct forest region - the Acadian Forest Region - containing 14 sections. The Nova Scotian sections are marked in on Figure 1.1. They are: (1) Eastern Lowlands, (2) Eastern Atlantic Shore, (3) Cape Breton Plateau, (4) Fundy Coast, (5) South Atlantic Shore, (6) Cape Breton Lowlands, (7) Central Lowlands, (8) Atlantic Uplands, and (9) Cobequid Mountains.
Figure 1.1: Forest regions (numbered—see text) and existing pollen records from Nova Scotia and southern New Brunswick.
Lakes: (A) Little, (B) Basswood Road, (C) COLLINS (D) Folly Bog (E) Caribou Bog, (F) EVERITT, (G) CURRY POND and DUCK, (H) Minard, (I) Oak Hill, (J) Canoran, (K) Bluff and Silver, (L) Gillis, (M) Wreck Cove, (N) Hillsborough.
Red Spruce (*Picea rubens*) is common throughout and is commonly associated with balsam fir (*Abies balsamea*), yellow birch (*Betula lutea*), and sugar maple (*Acer saccharum*). Beech (*Fagus grandifolia*), hemlock (*Tsuga canadensis*), and white pine (*Pinus strobus*) were all formerly more common than they are today. Black spruce (*Picea mariana*) predominates on the widespread boggy areas. Red oak (*Quercus borealis*), white elm (*Ulmus americana*), red maple (*Acer rubrum*), white birch (*Betula alba*), grey birch (*Betula populifolia*), trembling aspen (*Populus tremuloides*), and balsam poplar (*Populus balsamifera*) are all common on disturbed areas. Alders (*Alnus* spp) and dwarf willows (*Salix* spp) are common along the borders of lakes and streams. The spruces and fir predominate in sections (1) to (4) above; sections (5) to (8) have largely mixed composition; and the northern hardwoods (beech, maple, yellow birch) along with hemlock and white pine predominate in section (9) and the southern portion of section (8).

1.3. **CONSEQUENCES OF GLACIATION**

As the Wisconsin ice sheet retreated from Nova Scotia,

---

* Species names follow Roland and Smith (1969).*
herb and tree species gradually returned to the province from New England, both by systematic migration up the coast around the head of the Bay of Fundy and by aerial transport of seeds across it. Refuges on exposed portions of the coastal shelf (and possibly even Cape Breton Island) also appear to have been sources of species. The forest origins are examined in detail in Chapter 5.

The province has no land elevations of more than 600 metres. The three areas of highest elevation are the Cape Breton Highlands, Cobéquid Mountains, and South Mountain complex (Annapolis County). Prest and Grant (1969) believe that remnant ice caps were associated with all three areas. The retreating ice left behind many topographical features (moraines, eskers, drumlins etc.) and the thousands of lakes which now abound throughout the province.

Coastal rebound, due to loss of the ice load, led to an initial lowering of sea levels between 14,000 and 12,000 years B.P. followed by steady eustatic rise from about 8,000 years B.P. to the present (Grant, 1975). This means that many now submerged areas must have been exposed for a time and the Chignecto Peninsula must have penetrated much deeper into the Bay of Fundy.
The soils are almost exclusively podzols derived from glacial tills. Virtually all are acidic, usually very strongly so, with pH < 5 in the top metre (MacDougall and Nowland, 1972). Cameron (1961) concludes that most of the soils were formed from the bedrock with very little transport. The underlying rock types are mostly Ordovician slates and Devonian granites in southern and central Nova Scotia and a complex mosaic of limestones, shales, sandstones, and granite in the north and Cape Breton. Soils in most areas are thin and stony, hindering cultivation, and exposures of bare rock are common on elevated surfaces. Low-lying surfaces are often poorly drained; sphagnum and spruce bogs are very common.

1.4 STUDY AREAS

The following lakes were studied. Locations are given in Figure 1.1, bathymetry in Appendix 1.

(1) Everitt Lake (Latitude 44° 27' N, Longitude 65° 52' W) is located in Digby County, Nova Scotia, 12 km east of the town of Weymouth. It is a headwater lake, 9 metres maximum depth and surface area 40 hectares. Its watershed area is approximately 200 hectares and its flushing time (time needed for water inflow to equal the lake's total volume, assuming 50% runoff from the drainage basin) is about 18 months. The surrounding terrain is well-drained and strongly undulating, with a maximum relief of 80 m; the region
was formerly glaciated and many lakes and streams now break up the landscape.

Climate in the area is related to the coastal situation of Everitt Lake. The average July temperature is 18°C, which is average for most of the province, while the January average is -4°C, 3° warmer than areas in central Nova Scotia (Gates, 1973). Annual precipitation totals about 1200 mm, 200-300 mm less than in the centre of the province.

The forest around Everitt Lake falls within the Atlantic Uplands section. Red spruce predominates, along with sugar maple and beech. Black spruce and tamarack (Larix laricina) are prominent in damp, low-lying areas. The lake's immediate surroundings have been much disturbed by clearing. Red maple, trembling aspen, and white birch are very abundant. Eastern white pine and hemlock are common near the lake's southwest shore. Balsam fir is present but only as young trees. Red oak and black ash (Fraxinus nigra) are scattered throughout the area. Alders and dwarf willows are common on the shoreline, especially on the flat, boggy areas at the lake's north end.

(2) Collins Lake (Latitude 46°6'N, Longitude 64°6'W) is located 8 km northwest of the town of Port Elgin, New Brunswick. It is a headwater lake, 6.5 metres maximum depth
and surface area 75 hectares. Its watershed area is approximately 225 hectares and its flushing time is about 12 months. The surrounding terrain is level or gently rolling with a maximum relief of 25 m. There are few lakes in the area than almost anywhere in Nova Scotia.

The average temperatures for January and July are -6°C and 15°C respectively. Annual precipitation totals 1000 mm (Gates, 1973).

The forest around Collins Lake lies within the Eastern Lowlands Section (see section 1.2). The lake's vicinity is dominated by conifers, notably red and black spruce, balsam fir, and white pine. Red pine and jack pine (Pinus banksiana) were formerly also common. Most of the lake's southern shore has been cleared for farming and reeds are thick along the bank. Access to the lake is via a narrow channel cut from the road through an extensive area of alder swamp.

(3) Curry Pond (Latitude 43°53'N, Longitude 65°51'W) is located in Yarmouth County, 10 km northeast of the town of Tusket. It is a headwater lake, 9 metres maximum depth and surface area 22 hectares. Its watershed area is about 120 hectares and it has a flushing time of approximately seven months. The surrounding area is very hilly (maximum
relief 50 m) and abounds in lakes and streams.

The average January and July temperatures are -4°C and 20°C respectively. Total annual precipitation is about 1300 mm.

The forests surrounding Curry Pond fall on the border of the South Atlantic Shore and Atlantic Uplands sections (see 1.2). Hardwoods are dominant, especially on the hill-sides and ridges. Common species are sugar and red maple, beech, yellow birch, elm, red oak, and black ash. Part of the hillside next to the lake has been cleared and was formerly farmland. There are substantial stands of red and white spruce and tamarack near the southern end of the lake and these are more common forest components, along with white pine, to the south. Blackberry and blueberry are common on cleared areas.

(4) Duck Lake (Latitude 43°51'N, Longitude 65°55'W) is located 8 km southwest of Curry Pond and 5 km east of the town of Tusket. It is a headwater lake, 6 m maximum depth and surface area 30 hectares. Its watershed area is approximately 100 hectares and it has a flushing time of about 13 months. Maximum relief in the immediate vicinity is 30 m.

The spruces and balsam fir are more prominent in the
area than at Curry Pond.

Bathymetric maps of the lakes studied are given in appendix 1.
CHAPTER 2

PALYNOLOGICAL INVESTIGATION

2.1. SAMPLING PLAN

Lakes for coring were chosen in areas not previously investigated. In particular, four lakes in southwest Nova Scotia were cored, since records from this area were crucial to identifying species sources and migration routes. Duck lake, only five miles from Curry Pond, was included in the hope of gaining some idea of local variability in the pollen record. Since no pollen records were found in the literature from northeast New Brunswick, a core was taken from Collins Lake near the Nova Scotia border. An attempt to obtain a core from northern mainland Nova Scotia failed because the chosen lake was found to have a very short and disturbed record. This was also the case for one lake from the southwest.

All lakes cored were headwater lakes at least 6 m deep. The locations of lakes investigated and of sites for which published records were available are shown in Figure 1.1. The longest core (5.73 m, from Everitt Lake) was selected for intensive statistical analysis.
2.2 METHODS

(1) Field work was carried out during the summer of 1974. Because winter ice cover on Nova Scotian lakes is unreliable, coring had to be performed from a boat. Bathymetry of each lake was determined using an echosounder. Cores were obtained by hand from the deepest part of each lake's basin using a Livingstone piston sampler (Wright, 1967; Deevey, 1965). During coring, the boat was held in place by anchors tied to each corner. Metallic casing was used in the coring operation to help locate the core hole precisely and to ensure that the extension rods did not bend. Only cores obtained in calm conditions were analysed in detail.

Cores were stored at 1°C in aluminium tubes (3.5 cm inner diameter, length 1 m). Section lengths in the middle of each core varied from 92 to 95 cm and matched the drive distances during coring (the variations are caused by the design of the core tube and piston attachments). A continuous record was essential to time series analysis of the data from Everitt Lake. To ensure that the separate sections were continuous with no part of the column either missing or duplicated, pairs of samples that were expected to match were taken from the neighbouring ends of adjacent core sections. That they did match was confirmed by comparing
the pollen counts of each member of the pair. The pairs of pollen counts were homogeneous in each case.

(2) Samples for pollen and sediment analysis were extracted from each core using a 1 cc stainless-steel piston sampler. Sampling intervals were determined by the information sought from the cores. The Everitt Lake core was sampled at 3 cm intervals to provide enough data points for time series analysis. Both the Collins Lake and first Curry Pond (CT-1) cores were sampled at 10 cm intervals, with extra samples extracted at 5 cm intervals from the base of CT-1 in an effort to obtain detailed evidence of forest origins. The Duck Lake and CT-2 cores, to be used only for comparison with CT-1, were sampled at 20 cm intervals.

(3) Samples for pollen analysis were processed by the reduction of components method as outlined by Ogden (1969) and Faegri and Iversen (1964). The processing sequence was as follows.

1. Filtering through 150μ copper mesh.
2. Boiling in 10% KOH (1 minute).
3. Centrifuge/water rinse/centrifuge (cwc) -- repeated until all humic material removed.
4. Boiling in 10% HCl (1 1/3 minutes).
5. CWC
6. Heating in 48% HF (24 hours) -- if required.
7. CWC
8. Acetic acid rinse.
10. Acetic acid rinse.
11. CWC
12. 95% ethanol rinse.
13. Pure ethanol rinse.
15. Transfer to storage tubes using benzene, store in silicone oil (1000 cs).

In processing the Everitt Lake core, Lycopodium spores were added after acetolysis because it was feared that destruction of the spores in processing could be a serious source of variation. Experience showed the spores to be very resistant to destruction, so for other cores they were added at step 4 (the spores were suspended in HCl for storage). Samples were left unstained to prevent confusion between added and natural Lycopodium spores.

(4) Samples for sediment analysis were dried overnight in crucibles at 105°C, weighed, ashed at 550°C for two hours, and reweighed. The initial weighing determined
sample dry weight. The final weight of ash was taken as a measure of inorganic content. The ratio (dry weight - ash weight)/ash weight determined sample loss on ignition.

(5) To measure pollen concentration, stained *Lycopodium clavatum* spores were added to the pollen samples using tablets provided by J. Stockmarr (see Stockmarr 1971, 1972). Stockmarr (1972) reports a coefficient of variation of 4% in numbers of spores per tablet (mean = 12,500 spores). To reduce this source of variation and to minimize the impact of occasional chipped tablets, the following method was used to add spores to samples:

Tablets were dissolved in KOH and the resulting suspension diluted with HCl until a concentration of $10^5$ spores/ml was obtained. Spores were removed and added to samples using a 5 ml broad-mouthed pipette with vacuum bulb attachment. The suspension was stirred at a constant rate during the operation by a magnetic stirrer.

To check the variations resulting from this procedure, a similar suspension of fresh *Lycopodium* was made up to about the same concentration.

Eight samples were made up by mixing together equal volumes of fresh and stained *Lycopodium* suspensions in the way described above. Four slides were made from each sample
and counted (to 100 stained spores). In counts to 400 stained spores per sample, an average of 287 fresh spores were counted. The coefficient of variation of these counts was only 2%. This value is an upper limit for the variation in amounts of lycopodium added to samples by the method described above and represents an improvement over the 4% variation that is found when the original tablets are used.

(6) Pollen counts for the Everitt Lake core were made to a fixed sum of 100 stained Lycopodium spores. The amounts of stained Lycopodium added were adjusted so that an average of 500 (and minimum of 100 at the base) arboreal pollen grains (AP) were counted per sample. This made calculations of pollen influx rates easier. Since only percentages were to be calculated for other cores, counts of samples from them were made to a fixed total of 250 arboreal pollen. Total arboreal pollen concentrations for these samples were calculated from the count for stained Lycopodium spores.

Pollen was identified by reference to the following sources: J. G. Ogden (1968, and reference collection), J. H. MacAndrews et al. (1973, and Royal Ontario Museum collection), P. Richard (1970), and my own slides of local pollen. Apart from attempts to count white pine in the
latter stages of the work, no taxa were identified down to species.

(7) Charcoal fragments were counted along with the pollen. A reference slide was made from ashed pieces of a variety of wood types. Particles were counted in three size classes: 225–900μ², 900–3600μ², and greater than 3600μ². Particles smaller than 225μ² were ignored. An index for charcoal influx was calculated by summing the numbers of particles in each class multiplied by the (geometric) midpoint of the size range of the class.

(8) Series of samples for radio-carbon dating were removed from the Everitt Lake, Collins Lake and Curry Pond cores and were processed by the Dalhousie Radio-Carbon Dating Laboratory. Age versus depth curves were constructed by least-squares curve fitting.

2.3. SOURCES OF VARIATION

In section 2.2(5) it was shown that variations in the amount of Lycopodium added to pollen samples were less than 1% of the mean amount. Other factors cause much larger variations in the final pollen counts. Sample size variation can be estimated using dry weight measurements of 60
samples from the top two metres of the Everitt Lake core (see section 3.2). Although the dry weights in this part of the core show no systematic changes, their coefficient of variation is 6%, which therefore represents an upper limit for the random variations caused by changes in sample size.

Precautions were taken to minimize processing losses. Actual losses of grains during processing are difficult to estimate but an effort was made to minimize the variations arising from this source by treating all samples, as far as possible, in identical fashion.

Mosimann (1970) gives theoretical expressions for the standard deviations arising in several counting procedures. The predicted coefficient of variation for counts of taxon i is (Mosimann, 1970)

\[ \sqrt{\frac{1 - \frac{p_i}{n}}{\frac{p_i}{n}}} \] \hspace{1cm} (2.1)

where n is the total count and \( p_i \) is the mean proportion of taxon i (i.e. i's count is np_i). Counts made to a fixed sum of Lycopodium have a coefficient of variation (Mosimann, 1970)

\[ \sqrt{\frac{1 + \frac{p_i}{n}}{\frac{p_i}{n}}} \] \hspace{1cm} (2.2)

where n is the spore count and np_i is species i's count.

It was feared that mistakes in identifying pollen types...
Figure 2.1: In making pollen counts, the uncertainty in the number of grains counted is smaller for the more abundant pollen types. The figure compares the variations expected in repeated counts for taxa of varying abundance (the line - computed from equation 2.2) with the coefficients of variation actually found in a counting experiment. The taxa named all varied more than expected and were all difficult to distinguish from birch pollen.
and within-sample inhomogeneity might lead to great increases in count variations. An experiment to test this was performed in which eight slides, made from a single pollen sample, were each counted to a fixed sum of 100 Lycopodium spores. Figure 2.1 compares the actual coefficients of variation found (crosses) with those predicted (line). As can be seen, most values lie on or very near the line. Among the taxa showing higher variations than expected are Alnus, Corylus, and Ostrya—all members of the Corylaceae family and easy to confuse with birch and with each other. Possible within-slide variations were allowed for by making half of each count near the slide's edge and the other half in traverses across its centre. In the few cases where counts at the centre and edges differed markedly, new slides were made up and counted.

Calculating from equations 2.1 and 2.2, and assuming that no losses occur during processing, the coefficient of variation in the abundance estimate of a pollen type accounting for, say, 20% of total arboreal pollen would be 11½%. The coefficient of variation in estimating its concentration, assuming that its concentration equals that of the Lycopodium spores, is around 14%. The uncertainties are much higher for less common taxa. Thus an abrupt abundance change registered at a single level is
highly suspect. On the other hand, important abundance trends indicated by values at several levels are almost certainly genuine.

Another major source of uncertainty is the radio-carbon dating. The greatest uncertainty in the dates from the Everitt Lake core was 12\% (65\% confidence limit). It is therefore possible that the uncertainties in species deposition rates could be substantially more than those due to counting and sample size alone. The added uncertainties are, fortunately, not random, since the date curve constructed from radio-carbon dates applies to the whole sequence of samples. Hence, in comparing adjacent samples, the effects of dating errors are trivial. Also, use of dates read off a curve of best fit to the radio-carbon dates should involve less uncertainty than that associated with any one date alone.

The sample from which the count variations shown in figure 1.1 were obtained came from the first metre of the Everitt Lake core. Charcoal was also counted in the experiment and its values were found to have a coefficient of variation of 18\%. The total uncertainty in estimating charcoal concentration is therefore 25\% (65\% confidence level) when errors from Lycopodium concentration and sample size are allowed for.
2.4 STATISTICAL ANALYSIS

Pearson product-moment correlations have been used throughout. In Chapter III, correlations of spectra with surface sample data are used as an aid in deducing the types of forests represented by the pollen records. Surface pollen spectra indicative of eastern North American forest regions were obtained from Davis and Webb (1975). Surface spectra characteristic of modern Nova Scotian forests were obtained from Railton, 1972. In Chapter IV, between-level correlations have been used to delimit assemblage zones—the method is explained in section 4.2. Between-level correlations are also used to help assess similarities and differences between separate pollen records. In Chapter VI, serial and cross-correlations are used to deduce succession patterns and the effects of fire. Spectral estimates are also used in the analysis in Chapter VI.
CHAPTER III

RESULTS

3.1 POLLEN Profiles

An absolute pollen diagram is presented for Everitt Lake only. Percentage diagrams (based on sum of all terrestrial pollen types) are given for all of the cores. The assemblage zones shown and used in describing the diagrams were obtained by the method discussed in section 4.2. Counts of minor pollen types are tabulated in Appendix 2. The basal sediments of both the Everitt Lake and Curry Pond (CT-1) cores contain evidence of "G-zones". This will be discussed separately at the end of the section. Vegetational interpretations are based on surface sample data given by Davis and Webb (1975) and by Railton (1972)—the method used is explained in Chapter II.

(1) EVERITT LAKE

Both absolute and percentage diagrams were obtained and are given in Figures 3.1 and 3.2. All major contributing taxa are shown. Ages based on radio-carbon dates are shown. Charcoal influx rates are given in Figure 3.1. Gaps between zones denote transition periods; these are discussed in section 4.2.
Figure 3.1. Everitt Lake Influx Pollen Diagram
The Everitt Lake diagrams consist of eleven assemblage zones (excluding the G-zone, see end of section). Because of the close sampling interval, transition periods were detected between most pairs of zones. The features described below were common to both diagrams, except where "percentage" or "influx" are specified.

ZONE 1 (11050-10700 yrs BP). No taxa have large influx rates. *Picea*, *Pinus*, and *Betula* have the highest percentages.

ZONE 2 (10700-10360 yrs BP): The herbs (sedge, grass, ferns, heath, Compositae, notably *Artemisia*) contribute 50% of total pollen. Tundra conditions are indicated. Of the shrubs, *Salix* and *Myrica* have the highest percentages. Increases in *Picea* and *Betula* influxes suggest that elements of closed forest are established by the end of the period.

ZONE 3 (10240-9670 yrs BP). *Picea*, *Betula*, herbs, and *Salix* continue to dominate the percentages. *Pinus* begins to increase on percent. The rise of *Picea* to its maximum influx and correlations with surface data suggest that the vegetation resembles spruce parkland.

ZONE 4 (9670-9090 yrs BP). *Pinus* and *Alnus* pollen have peak percentage values. *Abies*, *Ulmus*, *Fraxinus*, and *Quercus* pollen influxes are significant for the first time. Traces of *Acer* and *Tsuga* pollen also appear. *Populus* pollen is briefly abundant early in the zone, and *Larix* becomes prominent near its end. Boreal forest is indicated by correlations with surface data.
ZONE 5 (9080-8520 yrs BP). Picea pollen percentage decreases while Abies, Pinus, and Quercus pollen percentages increase throughout the period, reaching their greatest values at the zone's end. Acer, Betula, Fraxinus, and Ulmus pollen influxes increase sharply at the start of the zone. After reaching their greatest values, both Fraxinus and Ulmus influxes decrease again from about the middle of the zone. Transition to mixed conifer-hardwood forest occurs.

ZONE 6 (8520-7710 yrs BP). Pinus, Quercus, Abies, and Picea influxes all decrease. Tsuga pollen influx increases sharply at the start of the period and Fagus pollen appears for the first time.

ZONE 7 (7480-6560 yrs BP). There is a long period of disturbance between zones 6 and 7 during which Tsuga influx increases abruptly and Picea pollen influx is briefly higher. In zone 7, Tsuga pollen is at its greatest prominence in terms of both influx and percentage and both Fagus and Betula influx increase; Pinus pollen abundance is lower throughout the zone.

ZONE 8 (6560-4610 yrs BP). Tsuga pollen influx decreases while Pinus pollen influx increases again. Betula pollen is at its greatest abundance. Abies begins to increase in the latter part of the period. For the first time forest composition begins to resemble that of modern Nova Scotian forests, especially sugar maple-hemlock-pine associations.
ZONE 9 (4610-2080 yrs BP). The influxes of Pinus and Betula and the percentage of Quercus all decrease. Abies, Picea, and Tsuga percentages all increase. Fagus pollen becomes prominent for the first time. The influx of Ostrya-Carpinus pollen reaches its greatest value.

ZONE 10 (1850-1040 yrs BP). From the values of their pollen influxes, Picea, Tsuga, and Fagus appear to predominate. Betula increases slightly. Correlations with surface data indicate a sugar maple-hemlock-pine association.

ZONE 11 (930 yrs BP - Recent). Fagus and Tsuga pollen are less abundant. After decreasing during the transition period between zones 10 and 11, Picea pollen influx increases once more. Cultural effects (rise in percentage of herbs, especially Ambrosia) are evident in the top 15 cm.

(2) COLLINS LAKE

The percentage diagram for Collins Lake is given in Figure 3.3. Counts of taxa not shown are tabulated in appendix 2. Pollen zones, sediment type and total pollen
Figure 3.3. Collins Lake Percentage Pollen Diagram.
concentrations are also given. The ages given are inferred from radio-carbon dates. The record at Collins Lake is very similar to the one from Folly Bog, Colchester County, Nova Scotia (Livingstone, 1968). The main zone characteristics are as follows:

ZONE 1 (8000-7700 yrs B.P.). Herbs, especially sedge, predominate. The low pollen concentration and correlations with surface data point strongly to a tundra environment.

ZONE 2 (7700-7400 yrs B.P.). There is a greater mixture of herbs common in this zone—including heath, grass, Artemisia, ferns, Lycopodium, and composite species. Alders and willows are also common. Spruce is the most abundant tree type. Surface correlations indicate persistence of tundra, though the rising pollen concentrations suggest that forest elements may be present. Like the Folly Bog record, the bottom of the core has no extensive period of herbal dominance.

ZONE 3 (7400-7200 yrs B.P.). High pollen concentrations indicate the formation of closed forest, dominated by spruce. Surface data strongly indicate spruce parkland or boreal forest.

ZONE 4 (7200-6800 yrs B.P.). Birch dominates. Oak, pine, fir, elm, and larch all increase. Maple appears for the
first time. Surface data indicate a transition to a conifer-hardwood forest strongly resembling modern communities dominated by sugar maple, yellow birch, fir, and white pine.

ZONE 5 (6800–5900 yrs B.P.). Pine dominates. Birch, oak, and tamarack decrease. Spruce has a brief increase at the start but steadily declines. Poplar and ash are common towards the end of the period.

ZONE 6 (5900–5200 yrs B.P.). Beech and hemlock first appear, hemlock becoming very prominent but declining at the top of the zone. Ash reaches its greatest prominence. Birch, spruce and tamarack are all less abundant than in Zone 5. Oak is briefly prominent at the bottom of the zone.

ZONE 7 (5200–4400 yrs B.P.). This is really a long transition period between zones 6 and 8, with increasing birch and declining hemlock abundance the most prominent features.

ZONE 8 (4400 – 900 yrs B.P.). This is an extremely long period of stable forest structure. Beech, hemlock, birch, and maple abundances are all relatively high, while pine and oak are low. Fir increases slowly throughout the period. Surface data reveal strong similarities to present forests dominated by sugar maple, hemlock, white pine, yellow birch, and fir.
ZONE 9 (900 - 300 yrs B.P.). Spruce and fir rise to dominance while beech, hemlock and maple all decline. The forest becomes strongly boreal in character.

ZONE 10 (300 - 0 yrs B.P.). Birch increases while spruce declines slightly. Increased amounts of grass, ragweed and other herbs reveal cultural effects. Correlations with surface data indicate a strong resemblance to modern forests dominated by red spruce, hemlock, and pine.

(3) CURRY POND

Percentage diagrams for cores CT-1 and CT-2 are given in Figures 3.4 and 3.5 respectively. Counts of additional taxa for CT-1 are given in appendix 2. Surface correlations are given in appendix 3. Age estimates for zones are not given because dates are lacking. The CT-1 zones are as follows:

ZONE 1 (320-300 cm). These samples were taken from blue clay underlying gyttja. Spruce, birch, and pine are the main tree pollen types. Though surface data indicate forest tundra, the low pollen concentrations point to an absence of trees. Herbs contribute much of the pollen and Artemisia is common.
ZONE 2 (290 cm). Spruce and pine appear to dominate. The higher pollen concentrations together with the appearance of elm, a poor pollen producer, point to the formation of patches of closed forest.

ZONE 3 (280-275 cm). Ash, hop-hornbeam, and (probably) fir appear in the forest for the first time. Surface data indicate boreal forest. Spruce is probably at its greatest dominance.

ZONE 4 (270-260 cm). Pine, tamarack, and spruce decline. Oak is abundant early in the period, then declines, while poplar, ash, elm, and alder all increase. The community best resembles mixed conifer-hardwood forest.

ZONE 5 (250-229 cm). Hemlock and maple appear. Spruce, pine, and tamarack are common once more; alder and Corylus reach their greatest abundance. Hop-hornbeam, oak, fir, and elm all decrease. The increases in spruce, alder and sedge all suggest a damper climate.

ZONE 6 (229-200 cm). Pine, oak, maple, birch, fir, and elm all increase. Tamarack is very abundant early, then declines. There is a sudden drop in the abundance of virtually all herbs and shrubs. This corresponds with a major increase in pollen concentrations and high correlations with surface data from mixed hardwood-conifer forests.
ZONE 7 (190-185 cm). Spruce and birch abundances decrease while pine, hemlock, and oak abundances increase. Surface correlations indicate very warm conditions.

ZONE 8 (165-140 cm). Beech appears suddenly and becomes common immediately. Pine, elm, and oak decrease, while birch, spruce, tamarack, maple, and ash are all more common. Oak and hemlock both increase sharply at the end of the zone. Surface spectra indicate conifer-hardwood forest once more.

ZONE 9 (130-50 cm). Beech and hemlock attain their highest abundances. Oak abundance is considerably lower than before. Both maple and birch have low abundance early but increase steadily throughout.

ZONE 10 (40-0 cm). Pine and fir abruptly increase at the start of the period while hemlock drops sharply. Birch and maple are both at their maximum abundance.

The cultural horizon appears to be missing from the CT-1 core while it is present in CT-2. Also, while spectra from CT-1 nowhere match well with surface spectra from Nova Scotia, those from CT-2 do. This will be discussed further in Chapter IV.

The bottom sediments are missing from the CT-2 core
Figure 3.5: Curry Pond Percentage Pollen Diagram (core CT-2)
because a wind that sprang up during the coring operation displaced the boat enough to force the coring apparatus askew and make it impossible to penetrate the sediments any deeper. The sections recovered contain seven zones:

ZONE 1 (320 cm). Tamarack, birch, and herbs are all high. The best correlations are with arctic surface samples, the high pollen concentrations show that closed forest is already established. Ash, elm, maple, hop-hornbeam, and fir are all already present.

ZONE 2 (300 cm). Pine and fir increase. Oak appears. Conifer-hardwood forest is indicated.

ZONE 3 (280-260 cm). Hemlock appears and increases. Pine and oak are very abundant. Spruce, birch, tamarack, and herbs are all less common. Maple is very common at first but declines. Beech first appears. The best surface correlations indicate warm climatic conditions.

ZONE 4 (260-200 cm). Hemlock and beech become more abundant. Oak, fir, ash, and pine are much decreased, although pine increases throughout the period. Birch and tamarack are briefly more common at the start of the zone but decline throughout.
ZONE 5 (180-200 cm). This is a long period of slow change, in which the community reverts to conifer-hardwood forest in form. Hemlock and ash achieve their greatest abundance. Fir, maple, birch, and beech are all more common than in zone 4.

ZONE 6 (60-80 cm). Fir and spruce are more common, while pine reaches its lowest percentage abundance. Birch, maple, and beech are very common. Strongest surface correlations are with communities dominated by sugar maple, yellow birch, hemlock, pine and fir.

ZONE 7 (20-0 cm). Spruce, ash, and alder increase while hemlock, maple, and beech all decrease, suggesting a cooler, moister climate. Surface data indicate boreal forest. The major increase in herbs, especially ragweed, indicate cultural effects.

(4) DUCK LAKE

The percentage diagram for Duck Lake is given in Figure 3.6. As with core CT-2, it was not possible to obtain the basal sediments.

ZONE 1 (440-400 cm). Spruce, pine, birch, maple, and oak all appear to be common. Surface data suggest mixed forest.
Figure 3.6 Duck Lake Percentage Pollen Diagram.
ZONE 2 (360-280 cm). This is really a long period of disturbance with poor correspondence between levels. Hemlock and hop-hornbeam first appear. Fir is more common, and pine increases greatly throughout while both spruce and oak decline.

ZONE 3 (260-260 cm). This is a long period of slow change during which the community closely resembles many of Nova Scotia's modern forests, especially sugar maple-hemlock-pine, fir-pine-birch, and coastal spruce-fir associations. Pine and spruce are greatly reduced. Beech appears and, along with hemlock, birch, and elm, is very abundant. Tamarack is more common than previously; Corylus, willow, and herbs all increase towards the top of the zone.

ZONE 4 (40 cm). This is a short period of disturbance during which fir is more abundant than in either of zones 3 and 5, and pine, birch, beech, and herbs are temporarily greatly reduced.

ZONE 5 (20-0 cm). Spruce, fir, oak, maple, and alder are more common. Hemlock abundance is much lower. Surface spectra suggest the association of sugar maple, yellow birch, spruce, pine and fir which dominates the modern forest around the lake.
"G-ZONES"

"G-zones" (Livingstone, 1968; Railton, 1972) are sections of a pollen record characterized by: 1) presence of warmth-adapted species; 2) similarity to spectra higher in the record; 3) a substantial gap separating the G-zone spectra with those similar to it above; and 4) occurrence of the spectra in late-glacial sediments at the bottom of the record. G-zones are common in Maritime pollen records. Livingstone (1968) suggested that G-zones derived from tills or preglacial deposits. An alternative explanation (Railton, 1972; Ogden, 1976) is that they arise by slippage of whole slabs of sediment into holes left by melted ice-blocks. This view is supported by the results of this study since the two lakes showing G-zones (Everitt and Curry) both appear to be kettle lakes, having well-defined basins with steep sides, while Collins Lake, with a broad flat basin, has no G-zone.
3.2 SEDIMENTARY DATA

Lake sediments in the cores examined were classified subjectively, based on West (1968) and Faegri and Iversen (1964). No attempt at detailed classification was made. Sediment stratigraphy is shown on pollen diagrams for each of the lakes studied and in each of the diagrams in this section.

Figures 3.7 to 3.10 summarize the following data for cores from each of the lakes studied: (1) sediment type, (2) pollen assemblage zones, (3) pollen concentrations, (4) sample dry weights, (5) percentage losses on ignition and (6) charcoal/pollen ratios. Pollen concentrations were not determined for the Duck Lake record. For the Everitt Lake core, influx rates of pollen, inorganic matter, and charcoal are given instead of the variables listed in (3), (4), and (6). Percentage losses on ignition were taken to represent the amounts of organic matter in samples and the inorganic content was taken to be the amount of a sample left after ashing. Inorganic influx is used in Chapter VI as a measure of erosion.

The lack of either a decrease in percent loss on ignition or increase in sample dry weights at the bottom of the Duck Lake record indicates that the bottom sediments are missing from the core.
Charcoal/pollen ratios are given for all the cores except Everitt Lake. Swain (1973) has used these as an indicator of fire occurrence. The relationship of charcoal abundances to pollen abundances and to fires is discussed in section 6.4.
Figure 3.7 Sediment data for Evenitt Lake.
Figure 3.8: Sediment data for Collins Lake.
Figure 3.9. Sediment data for Curry Pond, core CT-1.
Figure 3.10. Sediment data for Duck Lake.
3.3 CHRONOLOGY

Table 3.1 gives the new radio-carbon dates obtained in the course of this study. Most sediments were poor in organic matter and only half of the samples extracted for radio-carbon dating finally provided dates.

The date curves for Everitt and Collins Lakes were obtained by least-squares curve-fitting. The curve of best fit to the Everitt Lake data was the straight line \( T = 76 \pm 19.25 \) D, where \( T \) is the age in years and \( D \) is depth in centimetres (see Figure 3.11A). Extrapolation using the date curve gives a basal date for Everitt Lake of 11,050 years B.P.

The curve of best fit to the data for Collins Lake was the straight line \( T = 88 \pm 18.49 \) D, where \( T \) is age in years and \( D \) is depth in centimetres (see Figure 3.11B). Extrapolation using the date curve gives an age estimate of 7,500 years B.P. for the beginning of the pollen record.

Only one radio-carbon sample from Curry Pond finally yielded a date (see Table 3.1). It was noted in section 3.1 that the top of the core CT-1 may be missing; in section 4.3 the loss will be shown to be about 20 cm. Taking these two facts into account and assuming a constant deposition rate throughout the core, gives an age estimate for the first forest appearance of 12,000 years B.P.
<table>
<thead>
<tr>
<th>Lake and Depth (cm)</th>
<th>Date (C$^{14}$ years)</th>
<th>Laboratory Code</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Everitt Lake</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>50-60</td>
<td>1070 ± 200</td>
<td>DAL-208</td>
</tr>
<tr>
<td>150-60</td>
<td>1940 ± 180</td>
<td>DAL-209</td>
</tr>
<tr>
<td>250-60</td>
<td>7030 ± 340</td>
<td>DAL-210</td>
</tr>
<tr>
<td>450-60</td>
<td>8080 ± 410</td>
<td>DAL-212</td>
</tr>
<tr>
<td><strong>Collins Lake</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>33-45</td>
<td>910 ± 90</td>
<td>DAL-234</td>
</tr>
<tr>
<td>122-133</td>
<td>2175 ± 200</td>
<td>DAL-236</td>
</tr>
<tr>
<td>242-56</td>
<td>5500 ± 170</td>
<td>DAL-238</td>
</tr>
<tr>
<td>306-32</td>
<td>5450 ± 200</td>
<td>DAL-239</td>
</tr>
<tr>
<td><strong>Curry Pond</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>180-190</td>
<td>8130 ± 400</td>
<td>DAL-232</td>
</tr>
</tbody>
</table>
Figure 3.11. Date curves for Everitt and Collins Lakes. The bars shown indicate confidence intervals for the radio-carbon dates obtained. The straight lines are the curves of best fit to the data and were used to calculate all ages referred to in the text.
Further samples have been extracted from the core in the hope of eventually basing conclusions on more than one sample.

No radio-carbon samples were extracted from the other cores considered in this study.
CHAPTER IV

PATTERNS OF POST-GLACIAL FOREST CHANGE

There are two fundamental ways of identifying past forest changes from pollen diagrams. First, important abundance changes, here called horizons, may be seen in the profiles of individual taxa. The second is to look for major changes in the composition, or assemblage, of the spectra. Each method depends, ultimately, on the assumption that changes in amounts of preserved pollen reflect changes in tree abundances within the community represented by the pollen data.

4.1 TAXON HORIZONS

Each pollen profile contains features important for assessing and comparing tree abundance changes. These features will be called horizons and include first appearances of pollen types, maxima and minima, and abrupt shifts in taxon abundance. They will be used to trace migrations and to compare species histories at different localities.

Certain horizons appear in almost all pollen diagrams from north-eastern North America. Referring to Figures 3.1 and 3.2, the most prominent of these and their times of
occurrence at Everitt Lake are listed in Table 4.1. The first appearances referred to occur at the lowest levels above which the pollen types appear consistently. Where maximum or minimum values occur repeatedly over a period, the time when the value is first reached is listed. All horizons listed in the table are visible in records from the other lakes studied and in most records available for Nova Scotia, New Brunswick and northern New England, and therefore must represent major vegetational events. In this chapter they will be used to help construct a picture of post-glacial forest patterns in the province. Chapter V will employ them in discussing species sources and migration routes. An attempt to explain why they occur so consistently over large regions is made in the conclusion to Chapter VI.

Horizons other than those tabulated occur in each record and many are common to several or even most sites. The Collins Lake and Curry Pond records, for example, show a distinct birch minimum just after the initial rise in hemlock abundance, though this minimum is not so clearly defined at Everitt Lake. The Everitt Lake record, on the other hand, contains some horizons—such as the prominent ash peak at 8300 years BP—that do not occur at all in the other records.
<table>
<thead>
<tr>
<th>TAXON</th>
<th>TIME (yrs BP)</th>
<th>TYPE OF HORIZON</th>
</tr>
</thead>
<tbody>
<tr>
<td>Herbs</td>
<td>~ 9100</td>
<td>Maximum</td>
</tr>
<tr>
<td></td>
<td>~ 500</td>
<td>Start of rise (&quot;Cultural horizon&quot;)</td>
</tr>
<tr>
<td>Picea</td>
<td>9000</td>
<td>Maximum</td>
</tr>
<tr>
<td></td>
<td>6100</td>
<td>Start of minimum</td>
</tr>
<tr>
<td></td>
<td>2200</td>
<td>Start of rise</td>
</tr>
<tr>
<td>Pinus</td>
<td>8100</td>
<td>Abrupt increase</td>
</tr>
<tr>
<td>Tsuga</td>
<td>8400</td>
<td>First appearance</td>
</tr>
<tr>
<td></td>
<td>7600</td>
<td>Abrupt increase</td>
</tr>
<tr>
<td></td>
<td>7000</td>
<td>Maximum starts</td>
</tr>
<tr>
<td></td>
<td>4800</td>
<td>Minimum starts</td>
</tr>
<tr>
<td>Abies</td>
<td>7900</td>
<td>Maximum</td>
</tr>
<tr>
<td></td>
<td>4900</td>
<td>Start of rise</td>
</tr>
<tr>
<td>Acer</td>
<td>84.00</td>
<td>First appearance</td>
</tr>
<tr>
<td>Fagus</td>
<td>7600</td>
<td>First appearance</td>
</tr>
<tr>
<td></td>
<td>4400</td>
<td>Start of rise</td>
</tr>
<tr>
<td></td>
<td>1200</td>
<td>Decline starts</td>
</tr>
<tr>
<td>Quercus</td>
<td>8800</td>
<td>First appearance</td>
</tr>
<tr>
<td></td>
<td>7600</td>
<td>Maximum</td>
</tr>
</tbody>
</table>
Taxon horizons have been used in many studies as the basis for delimiting assemblage zones. In particular, many of the horizons listed in Table 4.1 were used by Deevey (1951), Livingstone (1968), and others to help classify the successive communities that occurred in Nova Scotia and New England. Their classification can be summarized as follows (the numbers given are the times referred to in Table 4.1):

ZONE L — Herb maximum (9100), low pollen concentrations

ZONE A — Spruce maximum (9000), birch rises.

ZONE — Pine increase (8100)

ZONE C1 — Hemlock increase (7600), Oak maximum (7600)

ZONE C2 — Hemlock minimum (4800)

ZONE C3 — Spruce rise (2200)
4.2 ASSEMBLAGE ZONES

Yarranton and Ritchie (1972) found that product-moment correlations between adjacent spectra of a pollen record (calculated as shown in equation 4.1) were usually high when the two spectra fell within a single zone (identified subjectively) but were considerably lower when they lay within different zones. Their method can be modified to give a detailed picture of community change through time.

Let $p_{ij}$ denote the abundance (however expressed) of taxon $i$ (of $n$ taxa) at level $j$ (of $\ell$ levels) in a pollen record. The product-moment correlation between any two levels $j$ and $k$ is $\rho_{jk}$, where

$$\rho_{jk} = \frac{\sum_{i=1}^{n} (p_{ij} - \bar{p}_{j})(p_{ik} - \bar{p}_{k})}{\sqrt{\sum_{i=1}^{n} (p_{ij} - \bar{p}_{j})^2 \sum_{i=1}^{n} (p_{ik} - \bar{p}_{k})^2}}$$  (4.1)

with $\bar{p}_{j}$, $\bar{p}_{k}$ the average abundances on levels $j$ and $k$ respectively.

It follows from equation 4.1 that the contribution of any taxon $i$ to the value of $\rho_{jk}$ depends on the moment $(p_{ij} - \bar{p}_{j})$ of its abundance about the mean abundance for level $j$. Since the abundances of most pollen taxa are small (about 5% of total arboreal pollen, on average), very abundant taxa
must have high moments about \( \bar{P} \) and thus exert great influence on the values of \( \rho \). The most abundant taxa (birch, pine for example) are also among those whose pollen drifts furthest, so their abundances are the least sensitive to variations produced by local changes. Major shifts in their abundances, and hence lower between-level correlations, therefore reflect genuine community changes on a regional scale.

The between-level correlation table for Everitt Lake is plotted in figure 4.1. Deposition rates for all the taxa shown in figure 3.1 were used in the calculations. Off-diagonal blocks of values above .95 are not distinguished from the areas above .85. The patterns of change are much more complicated than would be suggested by correlations between adjacent spectra alone. Blocks of high values about the diagonal represent periods of relatively constant forest composition—for instance the period between 0 and 30 cm. Sections within which blocks of values above .95 appear to overlap—between 30 and 95 cm for instance—represent times of gradual drift in forest composition. Sharp breaks between blocks of high values, such as at 500 cm, represent abrupt changes in the forest structure. Near the core base, there is a sudden jump at the boundaries of the blocks of high values from above .95 to below .85, whereas in the upper parts of the core the blocks of values above .95 are normally
Figure 4.1 Between-level correlations for Everitt Lake.
surrounded by large regions of values above .85. This happens because fewer species are abundant early in the record, so that changes in any one species' abundance has a greater impact on between-level correlations.

To try to summarize the complex changes indicated by the correlations, the column has been divided into zones within which the community composition appears to remain stable or changes slowly in a systematic way. Thus zone boundaries occur wherever a rapid composition change leads to a stable community different from the previous community. At the bottom of the core, sharp breaks occur and clear boundaries can be drawn. In the rest of the column, though, the numbers of species determining the correlations are greater and large scale community changes are not so abrupt, making it necessary to identify short periods of rapid change (transition periods) between zones. Spectra within these transition periods correlate well with spectra in both of the zones they link, while spectra from the two zones themselves do not match well at all. The section between 105 and 339 cm (zones 8 and 9) is unique, representing a long period of similar forest composition. In the first half (zone 8) the composition changes steadily (shown by the overlapping blocks of values above .95) and by the end of zone 8 the composition is different from earlier in the zone.
A short period of rapid change leads to zone 9 which begins with a long period of virtually constant composition, followed by increasingly rapid change which leads eventually to a major shift in forest composition. The increasing pace of this change could represent a community response to climatic change and that spruce abundance increases throughout the zone suggests that the climate may be becoming cooler.

Zones for the other lakes studied were derived in the same way as described for Everitt Lake, except that percentages were used in the calculations of correlations. This makes no difference to the computations, however, since dividing both numerator and denominator of equation 4.1 by the total pollen influx turns taxon influx rates into proportions but makes no difference to the resulting correlation. In general, boundaries between zones were much sharper in the other cores examined because the wider sampling intervals did not provide such a detailed picture of the way the forest composition alters.

Because zones represent patterns of change for the whole community, it is possible for individual taxa to have abrupt abundance changes within a zone. For example, hemlock decreases sharply midway through zone 8 while pine increases. Rapid abundance shifts within zones are common for the less
abundant pollen types which do not influence correlations so strongly. In most cases though, taxon horizons correspond with zone boundaries. An approximate correspondence between the zones at Everitt Lake and the sequence described by Livingstone (1968) for Nova Scotia is: zones 1 and 2 - L, zone 3 - A; zones 4 and 5 - B; zones 6 and 7 - C1; zones 8 and 9 - C2; zones 10 and 11 - C3. However, since zones are here determined by different methods, it is not meaningful to apply Livingstone's names to them.

Davis et al. (1975) used a combination of clustering and sequential correlations to arrive at their assemblage zones for Moulton Pond in Maine. A rough correspondence with their assemblages is: zones 1 to 4 - I(a) to I(d), zones 5 and 6 - II(a), zones 7 and 8 - II(b), zones 9 and 10 - III, and zone 11 - IV. Comparisons of various numerical zoning methods may be found in Gordon and Birks (1972).

4.3 LOCAL VARIATION

The methods of sections 4.1 and 4.2 provide a means of comparing separate pollen records. Before attempting to compare records from different regions, it is helpful to have some idea of how much pollen records may vary within a single area, or even within a single lake.
Since both Curry Pond records represent exactly the same community, major features of the two records—taxon horizons, zone boundaries, charcoal peaks, sediment and concentration changes—should coincide in time precisely.

Absence of important taxon horizons and high basal pollen concentrations confirm that the bottom of the CT-2 record is missing, as noted in Chapter III. The bottom sediments of CT-2 correspond in time with CT-1 sediments somewhere between the initial rises of maple and hemlock. High *Larix* and herb abundances at the bottom of CT-2 suggest that the correspondence is with a depth of about 220 cm in the CT-1 record.

The top of the CT-1 record seems to be missing also. This is indicated, at the top of the CT-1 record, by lack of major increases in spruce, alder, and herb abundances and by lack of major decreases in pine abundance and total pollen concentration. Care was taken when obtaining both Curry Pond cores to include the mud-water interface and that it was obtained was confirmed by presence of water at the top of each column when the cores were extruded. Curry Pond is a kettle lake whose basin has very steep sides. It seems likely that the loss from CT-1 is a result of mud slumping down the outer rim of the basin.
Figure 4.2. Comparison of the two Curry Pond records. Dots represent corresponding horizons. Shading is based on the average values of between-level correlations within pairs of zones from the two cores. The rectangle encloses pairs of levels from the peat layers in the two cores. The straight lines (ABCD) give a rough correspondence between levels in the two cores.
Coincident events in the two records are shown in figure 4.2. Correlations between assemblages at different levels in the two columns were obtained using equation 4.1. Shaded blocks in the figure indicate zones in the two records that match well. The correlations indicate that zones 1-4 in CT-1 have no equivalent in CT-2, zone CT-1/5 corresponds with CT-2/1, CT-1/6 with CT-2/2, etc.; and that CT-2/7 has no equivalent in CT-1. The peat layer present in both profiles is shown as a block also. The lines fitted to the data give a rough (subjective) approximation to the relation between coincident levels in the two records and show that about 20 cm of sediment is missing from the top of CT-1. A similar use of the matching of simultaneous events in pollen records can be found in Thompson (1972).

Many of the differences between the matching sections of the two Curry Pond records can be attributed to a combination of intermittent sampling and random variation. Since the sampling interval was about 200-300 years in CT-1 and about 500 years in CT-2, it is easy for the relative times of major events to appear different in the two cores. Thus for example beech's first appearance seems to follow the pine maximum at 190 cm in CT-1, while these two events appear to coincide in CT-2. Since slow composition changes occur within zones, the placement of zone boundaries is
slightly different in the two records. Thus the boundaries of matching zones do not always correspond in time, as shown by the fact that a tamarack peak occurs in CT-2 zone 1 (which matches CT-1 zone 5) but occurs in zone 6 of the CT-1 record.

Some substantial differences occur within individual taxon records, showing the danger of inferences based on single values in a spectrum. In the CT-1 record, beech's initial appearance occurs as an abrupt increase to its maximum abundance followed by a decrease. The CT-2 record, however, shows a much less explosive increase at the beginning of beech's record. Since samples in both cores are taken so far apart, it is possible in such cases as this that both records give true abundances of the taxon concerned, but that large short-term abundance fluctuations occur.

Generally, correspondence between the two records is good and most taxon records match very well, even in fine details. The only really puzzling difference occurs between the tops of the two profiles for pine. In zone 10 of CT-1, pine increases substantially while in the corresponding zone 6 of CT-2, pine decreases.

Both the CT-1 and CT-2 cores were taken from the deepest part of Curry Pond's basin, no more than 15 metres apart. A study of the variations occurring in pollen spectra from
different parts of lakes may be found in Davis et al. (1969).

Important physiographic differences exist between Curry Pond and Duck Lake. Duck Lake lies at a lower elevation than Curry Pond, 15 m versus 20 m, and is closer to the ocean—only 600 m separates Duck Lake from Eel Lake, which connects with a complex series of channels, bays, and tidal flats leading to the open sea. The effects of these differences on local vegetation are evident both in the modern forests surrounding the two lakes (see Chapter I) and in the pollen records (figures 3.4, 3.5 and 3.6). In section 1.4, it was noted that spruce and fir were more prominent in the area around Duck Lake. These differences can be seen in the pollen records too. While spruce abundances in the Duck Lake record are only marginally higher than in the Curry Pond records, the fir abundances at Duck Lake are about twice as high at most levels. Similar differences can be seen in other taxon abundances as well, especially in samples from levels higher than 3 metres in the Duck Lake core: oak, elm, birch, alder, and herbs all have visibly higher abundances throughout the upper parts of the Duck Lake core than they do in either Curry Pond core, and maple and hemlock abundances are lower. All of these differences are consistent with the idea of a more rigorous coastal climate at Duck Lake restricting the growth of some species while favouring
others. The biggest differences occur near the tops of the records (remembering that the top 20 cm of CT-1 are missing). This is consistent with the fact that rising sea-levels in the past few thousand years must have made environmental differences between the two sites greater as the sea encroached onto dry land closer and closer to Duck Lake. Correlations between spectra of the three cores (see appendix 3) indicate that the Duck Lake assemblage zones (D1-D5) match best with Curry Pond assemblages as follows:

D1  CT-1 zones 7 and 8; CT-2 zones 3 to 5.
D2  CT-1 zones 8 and 9; CT-2 zones 5 and 6.
D3  CT-1 zone 10; CT-2 zone 6.
D4  No match.
D5  No match in CT-1; CT-2 zone 7.

The lack of a match for zone D4 suggests that D4 represents a period of disturbance (or may simply result from an abnormally high fire-count).

Most major horizons in the two lakes' records appear to correspond though there is not the same matching of fine details that the two Curry Pond records possess. In general, the matching of taxon horizons agrees with the zone matches and only a few major differences are to be seen: Duck Lake's
tamarack curve has no significant peaks in it at all, although the zone matching indicates that one should occur in zone D2; the major rise in oak abundance in zone D5 does not occur in the corresponding zone 7 of the CT-2 record. These and other similar differences may simply result from random count variations or could represent different community responses to changing environmental conditions.

Since major widespread community changes at lakes so close together should occur almost simultaneously, it is reasonable to suppose that the longest zones in each record (zones D3, CT-1/9, and CT-2/5) should correspond with each other. That this is so for D3 and CT-1/5 is confirmed both by taxon horizons and by correlations between spectra. However, the correlations are much lower than might be expected and correlations between spectra in D3 and CT-2/5 are not high at all. This major difference between communities so close together over a long period of stable climate further shows just how much difference the local conditions can have on forest structure. This point has great importance in the discussion in Chapter V concerning forest origins.

4.4 SUMMARY OF NOVA SCOTIA'S FOREST HISTORY

The ideas of sections 4.1 and 4.2 can be used to help trace the forest changes that have occurred throughout
Nova Scotia since the end of the last glaciation. By comparing the relative times at which major composition changes occur and by matching communities with similar compositions at given times, it is possible to construct a picture of the way the province's forests have developed.

On a much larger scale, methods like these have been used by Davis (1967) to examine late-glacial climates and forest changes over the whole of north-eastern North America and by Bernabo and Webb (1976) to trace changing species distribution patterns over the same area. Accounts of the province's forest history have been given by Livingstone (1968), Railton (1975), and Ogden (1976a).

Data from all the sites shown in figure 1.1 were used in the reconstruction. The forest origins will be discussed in detail in Chapter V and community processes in Chapter VI.

14,000-12,000 years B.P. Ice retreated from most of central Nova Scotia. Raised sea-levels at first led to flooding of now coastal areas (see section 5.1). By 12,000 years B.P. the sea had fallen to its present level and, after that time, increasing amounts of land on the coastal shelf became exposed. Residual ice caps persisted on South Mountain, on the Cape Breton Highlands, and (probably) on the Cobequid Mountains. Tundra prevailed on all ice-free areas. Boreal parkland existed in New Brunswick by the end of the period.
12,000-10,000 years B.P. Trees began to invade the province successfully during this time and it is probable that boreal parkland existed at Curry Pond and at Folly Bog and Silver La (Livingstone 1968, see figure 1.1) by 11,000 years B.P. The residual ice caps continued to shrink—those on Cape Breton and on the Cobequids may already have disappeared at the beginning of the period. By 10,000 years ago much of the province's south-west was also ice-free, with tundra predominating. Isostatic crustal rebound exposed large areas of the coastal shelf and a broad neck existed between Nova Scotia and New Brunswick. Byers (1975) places the first human occupation at Debert (near Folly Bog) at around 11,000 years B.P. However, as Livingstone (1968) notes, human occupation of the province had no visible effects on the forest composition until recent times and the introduction of agriculture.

10,000-8,000 years B.P. A rapid climatic warming about 10,000 years ago led to the formation of closed boreal forest almost everywhere in the province by about 9,000 year B.P. Only near South Mountain (Railton, 1972) and near Collins Lake was no organic sediment accumulating. Forests everywhere were boreal in nature, dominated by spruce and fir. Soon after 9,000 years B.P. the transition to mixed conifer-hardwood forest began at Silver Lake near Halifax.
(Livingstone, 1968) and by 8,000 years B.P. occurred also at Everitt Lake, Folly Bog, and at Gillis and Wreck Cove Lakes on Cape Breton Island. It is clear from the detailed record available at Everitt Lake that this transition involved increases in tamarack, fir, pine, birch, ash, oak, and elm, a gradual decrease in spruce abundance, and the first appearances in the pollen record of hemlock and maple. According to Ogden (1965), this transition marks the start of the hypsithermal interval, a period of warmer, drier climate than at present.

3,000–6,000 years B.P.  The transition from boreal to mixed conifer-hardwood forest occurs at the beginning of the period at Collins Lake. In most other areas, hemlock, oak, and maple all become dominant and beech appears. For the first time communities begin to resemble the province's modern forests. At Everitt Lake and Curry Pond the forest composition most resembles deciduous forest, suggesting very warm conditions. After reaching its lowest level, the sea begins to rise again and differences become apparent between the Duck Lake and Curry Pond records.
6,000-4,000 years B.P. On the mainland throughout this period climatic conditions appear to be very warm everywhere; although tundra seems to persist at Minards Lake (Railton, 1972) until about 5,000 years B.P. In Cape Breton, the effects of a probably cooler climate than on the mainland become evident: at both Gillis Lake (Livingstone and Livingstone, 1958) and Wreck Cove Lake (Livingstone and Estes, 1967) beech does not appear in significant quantities, maple is much reduced in abundance, the hemlock maximum is very short, and birch contributes up to 80% of all pollen.

4,000-2,000 years B.P. The slow rise of fir and spruce and decline of pine and birch at Everitt Lake from about 5,000 years B.P. suggest that the climate begins to become cooler and moister. Similar trends are evident in most other pollen records in the province. These conditions apparently favour beach which reaches maximum abundance almost everywhere and appears for the first time in the pollen records from Cape Breton.

2,000 year B.P.-Present. The cooling trend apparently continues, as indicated by major increases in spruce abundance at most sites. Cultural effects become apparent after about 400 years B.P. in most records, with increases in non-arboreal pollen, especially ragweed (Ambrosia).
CHAPTER V

FOREST ORIGINS

5.1 GLACIAL RETREAT

At its maximum extent the last ice sheet, formed by coalesced Laurentide and Maritime ice, covered all of Nova Scotia, New Brunswick (Prest and Grant, 1969) and coastal New England as far south as New York. Off-shore erratics indicate that the last ice sheet extended at least 65 km offshore on the Scotian Shelf, though it probably never reached as far as Sable Island (King, 1969). About 16,000 – 14,000 years ago the ice began to recede (Prest and Grant, 1969). The general pattern of its retreat from Nova Scotia is shown in figure 5.1.

The sea, flooding in behind the retreating ice, covered many newly exposed coastal areas. It is thought to have invaded the Bay of Fundy at about this time (Prest and Grant, 1969) and must have bordered the ice in places. The coastal shelf was considerably warped because of the ice load so that, while sea-levels 13,500 years ago were up to 120m above their present levels in the centre of the Gulf of Maine (Schnitker, 1974; see figure 5.2), they were never more than 40m higher than at present at Digby and never higher than the modern
Figure 5.1: Hypothetical ice marginal positions during retreat of last ice sheet (After Prest and Grant, 1969).
Figure 5.2: Sea-level variations for the Gulf of Maine in the last 14,000 years (After Schnitker, 1974). (A) Maximum sea-level, (B) Sea at same level as at present, (C) Maximum exposure of banks begins. The difference (eustatic sea-level - crustal rebound) gives the actual height of the sea relative to today's level. The maximum exposure at A was nowhere as great on the Nova Scotia coast or on Georges and Brown Banks.
level at Yarmouth (Ogden, 1976b; see figure 5.3).

By 12,800 years B.P. the sea had dropped to its modern level in the Gulf of Maine and by 11,000 years B.P. had fallen a further 59 m, exposing much of the coastal shelf. After reaching a minimum about 8,000 years B.P., sea-levels everywhere on the coast began to rise once more as eustatic rise gradually overtook crustal rebound (see figure 5.2). Grant (1975) points out that tilting of the coastal shelf occurred in this process, with the axis of tilt running through eastern New Brunswick. The result is that parts of Nova Scotia have been sinking faster than New Brunswick, with the most rapid sinking near Truro at the head of the Bay of Fundy.

5.2 FOREST REFUGES

There are three possible sources for the plant species that invaded Nova Scotia as the glacial ice retreated: areas of New England beyond the limits of glaciation, refuges on exposed areas of the continental shelf, and localized ice-free sanctuaries (nunataks) within Nova Scotia itself.

It is unlikely that any ice-free areas within the province (if they existed) were important sources of tree species. In fact, no clear evidence exists for areas free of ice throughout the whole Wisconsin period and the whole province seems to have been glaciated for most of that time.
Figure 5.3. Banks in the Gulf of Maine (shaded areas), locations of pollen records (black squares), and range in Nova Scotia of Thuja occidentalis (shaded area within Nova Scotia). Lakes (study sites shown by capitals): (A) Little, (B) Basswood Road, (C) Collins, (D) Polly Bog, (E) Caribou Bog, (F) Everitt, (G) Curry Pond and Duck, (H) Minard, (I) Oak Hill, (J) Canoran, (K) Bluff and Silver, (L) Gillis, (Wreck Cove), (N) Hillsborough.
Drury (1969), discussing the question of plant persistence in the Gulf of St Lawrence region, concludes that discontinuous ranges of plants are more likely a result of post-glacial changes in vegetation patterns than a result of plants sheltering in ice-free sanctuaries. While in some areas of the province, notably the Cape Breton Highlands, glacial striæ are lacking or few in number, Prest and Grant (1969) conclude that the areas involved were probably centres for local icecaps which expanded to merge with the advancing Wisconsin ice sheet. No organic deposits have been found anywhere in the province that contain a continuous record covering the full Wisconsin period. Buried organic deposits on Cape Breton Island (Mott and Prest, 1967) seem to belong to an early interstadial period and the youngest date obtained from them is 38,000 years B.P. A pollen record from southern Cape Breton (Livingstone and Livingstone, 1958) has a date of 10,340 years B.P. at a depth of 42m and a further 22m of organic deposits below that, indicating that the area must have been ice-free very early. However, the presence of tundra-like pollen assemblages and low pollen concentrations (mostly herbs, birch, and pine) in the lower sediments make it unlikely that any trees were present earlier than 11,000 years B.P.

The coastal shelf of Nova Scotia and northern New England features a number of banks which must have been exposed for much of the period of glacial retreat (see
figure 5.3). In fact, if Grant (1975) is right about warping of the shelf, the banks may have been exposed for much or all of the Wisconsin period. From off-shore moraine patterns, King (1969) concludes that the last ice sheet, even at its maximum extent, probably did not cover the entire Scotian Shelf. Georges and Brown Banks, therefore, could conceivably have acted as plant refuges during part or all of the last glaciation. Submerged peat deposits on Georges Bank indicate that the sea there was about 60m below its present level 11,000 years B.P. (Emery, Wigley, and Ruben, 1965). Spruce cones, pine, fir, and arctic willow found with a number of such deposits, indicate that tree communities probably existed on the continental shelf before significant numbers of trees grew in southern Nova Scotia (see chapters III and IV).

Modern surface samples from Sable Island contain large amounts of exotic pollen, including most of the common tree taxa of Nova Scotia and New England, but no evidence exists that trees ever grew on the island, which must formerly have been considerably larger because of lower sea-levels. The tiny amount of exotic pollen found in peat samples dated at the retreat of glacial ice (10,900 years B.P.) -- Tarasmae and Mott (1971) -- implies that trees could not have invaded the province from the northern part of the Scotian Shelf.
5.3 PLANT MIGRATION ROUTES

One of the oldest pollen records available from northern New England and the Maritimes comes from Moulton Pond in Maine (Davis et al., 1975), which seems to have started about 13,500 years B.P. The influx diagram suggests that spruce trees may have been present there before 13,000 years B.P. By 12,300 years B.P., when the sea had fallen to its present level, much of the New Brunswick coast was free of ice. Pollen records from Basswood Road and Little Lakes appear to commence at about this time (Mott, 1975). The record for Curry Pond, near Yarmouth, starts at about the same time too (see chapter IV).

Between 12,000 and 8,000 years B.P., the land available for tree growth increased considerably and was determined by the combined effects of falling sea-levels and local ice-caps. Between about 13,000 and 10,000 years B.P. minor ice readvances apparently occurred in several places. Lee (1959) describes one in northern New Brunswick and Maine. Davis et al. (1975) give increased climatic severity caused by glacial readvance as one possible reason for their assemblage fluctuations and spruce decline between 13,000 and 10,000 years B.P. Prior to 12,300 years B.P. water may have been continuous between Fundy and the Gulf of St. Lawrence. Lowered sea-levels after 12,300 years B.P. mean that the Bay of Fundy must have been much smaller in size, with a very broad neck joining Nova Scotia to New Brunswick, thus
opening a wide bridge for plant migrations into the province.

The Curry Pond record begins about 12,000 years BP. and the first tree community appears soon after. The Everitt Lake record begins about 11,000 years B.P. and the influx diagram indicates that trees were present by 10,700 years B.P. No records anywhere in the province show tree communities present earlier than at these two sites. Thus the early vegetation of southern Nova Scotia almost certainly migrated into the area from refuges on the coastal shelf.

From the assemblages and concentrations of pollen in the early sediments at Silver Lake (near Halifax) and Folly Bog (near Truro), it appears that tree communities were present at both sites before 10,000 years B.P. Glacial retreat in southwest Nova Scotia took the form of an ice cap on South Mountain (Railton, 1972). Though this ice cap had disappeared by 10,000 years B.P. (Ogden, 1976b), pollen records at none of the sites investigated by Railton start prior to that time. It is therefore unclear how great an effect the ice cap had in halting plant migrations from coastal refuges. However, the very early date for first tree appearances at Curry Pond and the fact that large areas on Brown Bank and on the southwest coast of Nova Scotia must have provided an ice-free corridor for migrations, makes it likely that many of the early invading tree species came into the province from the southwest.
The records at Basswood Road and Little Lakes have high pollen influxes in all sediments younger than 12,000 years (Mott, 1974). It therefore appears that prior to 10,000 years ago there were tree communities on what is now the coastal shelf (Georges and Brown Banks), throughout southern New Brunswick, and in southern and central Nova Scotia.

Local environmental conditions appear to have played a dominant role in the early forest history throughout the Maritimes and northern New England. The first appearance of forests in any area appears to be not so much a matter of how long trees took to migrate in, but of how soon the local environment permitted them to be established. This hypothesis is supported by a variety of evidence:

1. Prior to 10,000 years B.P. several localities (Moulton Pond, Little Lake, Basswood Road Lake, Folly Bog, Silver Lake, Curry Pond, Everitt Lake, and Gillis Lake) were free of ice, but not all had trees present. While it may be claimed that ice could have blocked tree migration to Gillis Lake in Cape Breton Island, the same argument cannot apply to Moulton Pond in Maine, where there would have been a clear access to areas exposed on the coastal shelf and where spruce does seem to have been present for a time very early in the record.

2. While the majority of localities shown in figure 5.3 had forest communities present soon after 10,000 years ago, some did not until much later. At Collins Lake, extrapolating from
the dates obtained, the first trees appeared no earlier than about 8,000 years ago, and at Oak Hill and Minards Lakes (Railton, 1972, 1975), the two Lakes nearest the South Mountain ice cap, the first forests appear about 7,000 and 5,000 years ago respectively.

5.4 SPECIES SOURCES

Roland and Smith (1969) divide the plants of Nova Scotia into six elements based on their distributions in other areas:

(1) The arctic-alpine element consists of species most prominent in tundra and other extreme environments and contains probably all of the plants that first appeared at most sites and includes Artemisia, and several species of sedge, grass, and willow.

(2) The boreal element consists of the plants common in the boreal forest, notably black and white spruce, balsam fir, tamarack, trembling aspen, balsam poplar, and white and grey birch.
(3) The **Canadian** element consists of plants common in north-eastern North America today, which make the forests of this region so distinctive. It includes white pine, hemlock, beech, and yellow birch.

(4) The **Alleghanian** element consists of plants with a more southern distribution today and most are rare in our forests. Sugar maple is included in this element though many trees, such as hickory and chestnut, seem never to have made their way as far north as Nova Scotia.

(5) The **coastal-plain** element consists of plants that grow only on coastal areas.

(6) The **weed** element consists of all the plants introduced by man.

Apart from coastal-plain species, plants of the elements listed above seem, from the pollen record, to have appeared in about the same order as they are listed.

As remarked in section 5.2, very little can be deduced from the present distributions within Nova Scotia of species of the various elements. Roland and Smith (1969) list a number of species' ranges that are suggestive of past migration patterns, but most of the implied migrations are not supported by the pollen record. For example species of
Panicum show a series of sharp range limits along a line from southwest Nova Scotia to Cape Breton Island, suggesting that the plants had migrated into the province from the southwest and, in spreading northeastward, each species was halted in turn by a combination of hostile environment and competition. But the pollen record shows that climates everywhere in Nova Scotia were warmer 8-2,000 years ago, suggesting that even Panicum species now restricted to the province's extreme southwest had much wider distributions (Note: Panicum pollen cannot be distinguished from that of other grasses).

Two cases where the pollen record does support implied migration patterns are the present distributions of eastern white cedar (Thuja occidentalis) and of some coastal element species. White cedar occurs naturally in the area about Wolfville and the Annapolis Valley (see figure 5.3) and its pollen is present in small quantities in the Everitt Lake core (see Appendix 2). However, it is absent virtually everywhere else in the province and is extremely rare in the pollen records. Though Thuja pollen is difficult to identify, its extreme rarity suggests that the species migrated into the province across an enlarged neck between Nova Scotia and New Brunswick. The second case is the distribution of Ilex glabra which grows all along the eastern shore of North America, as far north as Massachusetts, is virtually absent along northern New England and New Brunswick shores, but is found all around Nova
Scotia's southern and Atlantic shores. This gap in the range of such a widespread species suggests that it migrated into Nova Scotia via the exposed coastal shelf. This conclusion is supported by the fact that while Livingstone (1968) found traces of Ilex in cores from Bluff Lake near Halifax, Davis et al. (1975) found none at all in the core from Moulton Pond in Maine.

As noted in section 5.3, dispersal rates do not seem to have been the major factor delaying the establishment of plant species in Nova Scotia after the last ice sheet withdrew. This is well illustrated in the Everitt Lake and Curry Pond records by comparing relative first appearance times of hemlock, maple, beech, and oak. Hemlock and maple both produce seeds that may easily be dispersed by wind whereas beech and oak do not. While hemlock and maple pollen first appear simultaneously at both lakes, hemlock does not increase significantly for about a thousand years (slightly more at Curry Pond), suggesting that it was excluded by competition. As soon as hemlock did increase, though, beech pollen appeared for the first time. Beech's consistent presence from then on indicates that some beech trees were probably present but severely limited in numbers by competition. Exclusion of tree species by competition will be dealt with in more detail in Chapter VI. The sudden abundance rise of beech when it first appears in the Curry Pond record (though the rise is
not as abrupt as the CT-1 record suggests—see section 4.3)—implies a sudden invasion of beech into an area where conditions already favoured it. That beech's first appearance at Curry Pond follows the hemlock rise, rather than coinciding with it as at Everitt Lake, supports the idea that beech had to migrate into the province from New Brunswick but had its progress to Curry Pond delayed by unfavourable environment and by competition. Oak first appears in appreciable quantities at (or near) the beginning of the Curry Pond record, roughly coinciding with or preceding its first appearance at Everitt Lake. It is unlikely that oak would have migrated into southern Nova Scotia directly from Maine, since the opening to the Bay of Fundy, though much smaller than now, would still have posed an impassable barrier to trees having such large, heavy seeds. Small numbers of oak trees must therefore have established themselves over the areas free of ice prior to 10,000 years ago and increased when the climate became warmer. Oak's early record at Little, Silver, and Gillis Lakes and at Folly Bog supports this idea.

The early records of other tree types suggest processes at work similar to those described above. Prior to 10,000 years ago (or whenever particular sites became suitable for colonization) plant species, especially those producing wind-blown seeds, continually seeded exposed areas until
conditions finally became mild enough to permit seedling growth and the survival of some tree species to maturity.

Most of the tree types that first appear at each site produce seeds that can be transported considerable distances by strong winds. Van der Pijl (1972) notes that while verified distances for seeds transported by storms are not great (from \( \frac{1}{2} \) km for Ash to 30 km for Poplar), the facts that worms, stones, and fish can be transported by cyclones and that planes pick up large seeds at high altitudes suggest just how great the extreme distances may be. Thus hurricanes at the right time in the growing season could transport large quantities of seeds of many species considerable distances. In any 50-year period (the sampling interval at Everitt Lake) probably several such storms occur. These storms most likely accounted for the bulk of seeds deposited on any given area and must have given trees with the lightest seeds a great competitive advantage, as shown by poplar's early increase at Everitt Lake.

An ability to grow well in cold, wet, exposed conditions and to produce large amounts of wind-blown pollen, that is to survive and to reproduce easily, are the other two factors that helped determine the composition of the early forests. This is why spruce and birch are the greatest early contributions of arboreal pollen to the Everitt Lake record.
CHAPTER 6

COMMUNITY CHANGE AND FIRE

6.1 INTRODUCTION

Fire is a powerful ecological force, producing regular disturbances of both vegetation and environment. Van Wagner (1973) computes that 0.3% of Canadian forests are burned each year, that is, each individual forest stand is burned about once every 300 years on average; the rate is much higher in many communities. The selective pressures imposed by fire are so great that the majority of widespread and abundant tree species are adapted to cope with it in some way or other.

Heinselman (1973) has described in detail the cyclic processes ("fire cycles") consisting of fire, regeneration, succession, fuel accumulation, and (eventually) fire again that are typical of forest stands. Fire cycles affect forest communities profoundly. Climate and topography (besides floral composition) determine the severity of fire cycles within an ecosystem and together they control regional vegetation. Komarek (1968) has presented a biogeographic zonation of North America with each region characterized by distinctive climate, vegetation, and fire patterns.
This chapter will consider the effects of fire at Everitt Lake during the post-glacial period. Three questions will be considered: (1) how do fire and climate combine to determine forest composition? (2) what are the immediate and long-term effects of fires on the abundances of individual tree species? and (3) can post-fire successional trends be inferred from the pollen record?

Various analytic techniques have been used with the aim of revealing ecological patterns directly from the pollen record. In particular, time series methods have been introduced to help identify tree species' responses to fire.

6.2 EFFECTS OF FIRE ON COMMUNITY COMPOSITION

It was shown in Chapter 4 that between-level correlations indicate similarities in the regional forest community at different times. Abrupt zone transitions (shown by low correlations between adjacent spectra) imply rapid replacement of one community type by another. Since the sampling interval at Everitt Lake is nowhere more than 50 years, most zone changes must have occurred within single tree generations, suggesting that pronounced disturbances
Figure 6.1. Postglacial forest changes at Everitt Lake compared with charcoal abundances. Note that charcoal peaks correspond in time with zone boundaries.
trigger the rapid changeovers. The series of changes between 4400–4200 years BP, for example, shows a period of disturbance, after which the forest returns to nearly its original form and changes only slowly thereafter.

Figure 6.1 summarizes the post-glacial forest history at Everitt Lake, using the zonation inferred in Chapter 4. Charcoal influx values are plotted alongside.

Note that each major zone boundary corresponds with a peak in the charcoal influx. The forest community apparently responds slowly to climatic changes. Established species prevent the invasion of new colonists; that is, they exclude potential successors, as suggested by Drury and Nisbett (1973). Major fires, however, destroy the existing community. It is then prevented from regenerating with its pre-fire composition by unfavourable environmental conditions.

Fire was undoubtedly a key factor in the successful establishment of invading tree species at Everitt Lake. As is clear from the pollen abundance curves, as shown in Figure 3.1, and from the rates of charcoal influx, as shown in Figures 3.1 and 6.1, invasions of new tree types follow major fires in every case. As can be seen, this is true of fir, tamarack, hemlock, maple, beech, ash, oak, elm, and
alder. Moreover, as is apparent from Figure 6.1, each abrupt change in forest composition is immediately preceded by a major fire. The pine abundance curve provides a good illustration of this, having many sharp abundance changes coinciding with times of major fires.

6.3 TIME SERIES

Discussion in all the remaining sections will be based on the results of time series analysis of the pollen data. The aim in applying these methods is to reveal species trends and relationships not immediately evident from inspection of the pollen diagram. Time series analysis makes two major assumptions: (1) time intervals between adjacent samples are all equal; (2) the series considered is stationary in time, that is, there are no systematic changes in either mean or variance. Since sedimentation rates vary throughout a core and since long-term abundance changes occur in every species record, it is necessary to restrict analysis to short sections of the record, within which departures from the above assumptions are negligible. Each species record within a single zone can thus be considered as a distinct time series. Finally, absolute pollen influx rates have been used in the analysis because percentages introduce prior relationships between different series.
The cross-correlation, at a lag of $k$ sample intervals, between the abundances of taxa $x$ and $y$ is $\rho_{xy}(k)$, where

$$\rho_{xy}(k) = \frac{\sum_{j=1}^{l-k} (x_j - \bar{x})(y_{j+k} - \bar{y})}{\sqrt{\left\{ \sum_{j=1}^{l} (x_j - \bar{x})^2 \sum_{j=1}^{l} (y_j - \bar{y})^2 \right\}^{1/2}}} \quad (6.1)$$

Here $x_j$ denotes the abundance of $x$ at level $j$, $l$ is the total number of samples in the series, and $\bar{x}$ is the mean value of $x$. In the special case where $x$ and $y$ are the same taxon, $\rho_{xx}(k)$ is the serial or auto-correlation at lag $k$. Serial correlations were first used in palynology by Martin and Mosimann (1966) in an attempt to classify forests on the basis of typical species responses.

The power spectrum $S_X(f)$ of a time series $X$ gives the relative contributions to the variance of $X$ from cycles of each frequency $f$. In this study, the estimate $\bar{S}_X(f)$ of the power spectrum was used, where

$$\bar{S}_X(f) = 2\delta \rho_X(0) + 2\sum_{k=1}^{l-1} \rho_{xx}(k) w(k) \cos (\pi k f \delta), \quad (7.2)$$

Here $\delta$ is the sampling interval in years and $\frac{1}{2\delta} < f < \frac{1}{2\delta}$; the smoothing function $w(k)$ is described and explained in appendix 4.
Spectral analysis has not previously been applied to pollen data, although there have been several recent applications to related areas of ecology. The uses of spectral analysis in ecology have been reviewed by Platt & Denman (1975). Detailed accounts of time series methods are given by Jenkins and Watts (1968) and by Box and Jenkins (1970).

To aid in the interpreting of correlograms, it is helpful to construct models of the series being tested and to compare the correlograms of actual series with the correlograms of the models. Figure 6.2 presents models for both the charcoal curve associated with a single fire and the pollen curve for an ideal tree species which steadily reinvades the area denuded by the fire. The cross-correlogram between these two abundance curves considered as time series was then obtained and is also shown. Since the charcoal abundance is zero almost everywhere, the mean must be small; so the value at the peak differs from the mean much more than other parts of the curve. The cross-correlogram therefore indicates the abundance of pollen relative to this peak: positive correlations imply above-average pollen abundance, negative correlations imply below-average pollen abundance, and the positive time lag at which correlation reach a maximum equals the time required for the tree species to regain its maximum abundance after the fire. If several fires were to occur in the series, a
Figure 6.2. Theoretical responses of charcoal and tree pollen abundances to fire. The cross-correlogram between the two curves considered as time series is also shown. The finite length of the two series results in steadily decreasing correlations at large lags. Further explanation is in text.
similar pattern would emerge but repeated each side of zero at intervals corresponding to the average interval between fires. The pattern in the correlogram between charcoal and tree pollen abundance thus reveals the typical fire response of the species concerned.

Two complications should be noted:

(1) in a series of charcoal peaks, the largest will have the greatest effect on correlograms. In the extreme case of only one major peak in the series, the resulting correlograms will show the post-fire response to that particular fire only.

(2) correlograms for series having long-term trends emphasize the parts of the series that deviate most from the mean and, if the trend is strong enough, may mask all short-term behaviour completely. In such a case it is necessary to detrend the data before proceeding further. An example is given in appendix 5. The subject is discussed in depth by Box and Jenkins (1970).

6.4 FIRE OCCURRENCE

The first point to clarify is the relation between
charcoal peaks and actual fires. There seems little doubt that the major peaks (for example, the one at 8800 years BP) represent severe fires. It is not clear, however, whether single fires are responsible in all cases, since most peaks show considerable spreading. Major peaks may be the results of many fires in a short period, fires being made more likely through the accumulation of fuel from trees dying in unfavourable environmental conditions.

Since the discussion in following sections will hinge on the occurrence of fires in zone 9 (4200-2200 years BP), which contains no major charcoal peaks, it is important to know whether any of the fluctuations visible in the charcoal curve during this period do represent fires. In section 2.3 it was noted that the uncertainty in charcoal counts (of about the mean size in zone 9) was 18% (65% confidence level). Thus any charcoal peak exceeding the surrounding low influx values by anything more than about 50% of the mean influx value is almost certainly genuine. This means that all of the peaks visible in the charcoal influx curve for zone 9 represent actual increases in charcoal influx.

In comparing preserved charcoal with historical fire records, Swain (1973) found that: (1) heights of peaks in charcoal curves bore little relation to fire intensity; (2) some charcoal peaks resulted simply from changes in erosion
or deposition rates; (3) some fires were unrepresented in the data. Figure 3.7 compares charcoal deposition rates at Everitt with two other key variables: influx of inorganic matter (indicating erosion) and total influx of arboreal pollen. As can be seen from figure 3.7, the rates of inorganic influx are fairly stable throughout zone 9, having a coefficient of variation of 8% and a maximum variation (between greatest and least values) of only 20%. Charcoal influx values, on the other hand, have a coefficient of variation of 67% and a maximum variation of 120% of the mean value. It seems unlikely, therefore, that changes in inorganic influx can be responsible for any but minor fluctuations in charcoal influx. Thus most of the peaks visible probably represent genuine fires. Swain (1978) points out that the physical disruption caused by fire and the loss of binding materials from soils leads to increased erosion for many years afterwards. Inspection of the inorganic influx curve reveals only one major increase in erosion related to a charcoal peak—at 8800 years BP. Apart from this one peak, short-term fluctuations in the inorganic influx are small and are difficult to detect without reference to the raw data.

Figure 6.3 presents correlograms for the three variables under discussion. The dramatic decrease in pollen
FIGURE 6.3. Correlograms for charcoal, pollen and inorganic influx at Everitt lake. (a) Charcoal/pollen cross-correlogram, (b) Charcoal autocorrelogram, (c) Inorganic influx autocorrelogram, (d) Charcoal/inorganic influx cross-correlogram. In (b)-(d) the vertical scale is marked off in units of 0.5; the horizontal scale in lag periods of 500 years. The vertical dashed lines mark off periods of one fire interval. Changes after fire are indicated by the correlations between zero lag and the dashed line. Further explanation is in the text.
influx following charcoal peaks is shown by figure 6.3a. This gives the charcoal/pollen correlogram for the period 6000 - 4000 years BP (chosen because the pollen influx curve is most nearly stationary there). As the correlogram shows, pollen influx drops sharply after a charcoal peak, then recovers slowly. This is more evidence that most charcoal peaks represent actual fires. The further drop in correlations at a positive lag of 250 years is probably the result of a further fire.

The remaining correlograms were calculated for the period 4200-2200 years BP. Serial correlations for charcoal and inorganics are shown in figures 6.3b and 6.3c. From the correlogram it can be seen that charcoal influx reaches its lowest value about 250 years after a burn. This time indicates the maximum spreading of charcoal peaks produced by sediment recycling and erosion. The rise in correlations at a lag of 350 years indicates the mean time between charcoal peaks and represents the average fire interval for zone 9. This interval has been marked in on all the remaining correlograms.

As figure 6.3c shows, erosion has distinct increases each 350 years also. The long period required before correlations reach a minimum results from long-term trends in the inorganic influx series. The cross-correlogram between
charcoal and inorganic influx (figure 6.3d) shows that the periodic increases in erosion immediately follow burns and confirms Swain's observation that erosion remains high for many years after a fire.

The above results show that many minor charcoal peaks also represent actual fires. Why are most major peaks those connected with regional zone boundaries? Probably, major peaks represent very widespread and severe fires while minor peaks represent only light (or distant) burns. The broken landscape around the lake no doubt restricts the extent of most fires, so that existing vegetation can reinvade burnt areas even in unfavourable climatic conditions. Apparently, only widespread fires clear enough land to give climatically favoured species a real competitive advantage during reinvasion.

In section 6.2 it was noted that fires are associated with rapid shifts in community structure and with changing trends in species abundances. It is not clear, however, whether fires are the prime cause of these changes or are simply more likely to occur in unsettled conditions resulting from changing forest composition.
6.5 SPECIES RESPONSES TO FIRE

In section 6.4 it was found, from the charcoal autocorrelogram, that the fire interval in the period 4200-2200 years BP (zone 9) was 350 years. Sections 6.5 and 6.6 will analyze the behaviour of particular tree taxa during this time. This time period is considered for several reasons: (1) It is the longest single zone having no major charcoal peak; (2) most tree taxa give stationary series for this period; (3) changes similar to those elsewhere in the core occur but on a much longer time scale.

The fire responses of several taxa are shown in Figure 6.4. The 350 year fire interval has been marked in on each correlogram. The responses of taxa to fire are indicated by the correlations between charcoal and pollen within this period. In most cases, the patterns found in this part of the diagram can be seen to be repeated at 350 year intervals throughout the correlogram. In the between-species correlograms, positive lags refer to the first named species correlated with later values of the second species.

The responses to fires of poplar (Fig. 6.4a) and beech (Fig. 6.4c) are as one would expect: poplar is very abundant about the time of fire and just after, but not
Figure 6.4. Cross-correlograms of tree pollen influxes with charcoal influxes and with each other: (a) Charcoal/poplar; (b) charcoal/birch; (c) charcoal/beech; (d) beech/fir; (e) beech/maple; (f) ash/maple.

Note that fire responses are not exactly as predicted by the model in figure 6.7. For instance, high correlations at negative lag between poplar and charcoal seem to show poplar abundances anticipating fires. While sediment mixing and fire interval variations contribute to cause this anomaly, it is due chiefly to the fact that, besides high charcoal and poplar abundances being well-correlated, low values are well-correlated too. It is important to remember that the values plotted are correlations and not actual abundances.

On each correlogram the units for the lag K are hundreds of years. The vertical dashed line on each figure marks one fire interval from the origin.
otherwise (the slight rise in correlations at about 200 years after fire may result from occasional intermediate fires); beech recovers slowly and does not become common again until just before the next fire. The correlogram of charcoal with birch (Fig. 6.4b) shows a very slow recovery of birch after fire—more like beech than poplar—suggesting that yellow birch is the major contributor of birch pollen in this period. Cross-correlograms with other taxa support this conclusion.

Figures 6.4d to 6.4f show the cross-correlograms between pairs of taxa. High fir abundance (see Fig. 6.4d) seems to precede high beech abundance, as indicated by the peak in correlations at negative lag, while the correlogram peak at zero lag between beech and maple indicates their association (Fig. 6.4e). Figure 6.4f shows that maple and ash are also closely associated.

The surprisingly small correlations between beech and maple (Fig. 6.4e) and the odd shape of the charcoal/beech correlogram (Fig. 6.4c) result from a long-term increase in beech. The effect of this trend is to put extra emphasis on points at each end of the series when calculating correlograms (these points differ most from the series mean) and leads to mostly negative correlations, at near-
zero lag, with charcoal (Fig. 6.4c). The post-fire response is still clear though. Detrending procedures, required in cases where the post-fire response is not clear, are described in appendix 5.

The fact that the pattern of each taxon's post-fire response is repeated several times in its cross-correlogram with charcoal reflects the cyclic nature of the processes concerned. In every case the pattern seems to repeat itself over a period of about 350 years. A more accurate picture of cyclic changes in charcoal and pollen abundances can be found from their power spectra.

Figure 6.5 presents power spectra for the abundances of charcoal and two tree taxa in zone 9. The charcoal power spectrum (Fig. 6.5a) has a significant peak at cycle periods of 330-400 years. The average interval between fires for zone 9 was found from the serial correlogram for charcoal to be 350 years; the spread of the peak in the power spectrum shows that this period fluctuates between 270 and 500 years. The power spectrum for poplar abundances (Fig. 6.5b) also shows a peak at about the same frequency. The contribution of low frequency cycles is also high for poplar, indicating long term changes in poplar abundance. Fir's power spectrum (Fig. 6.5c) also has a peak at frequencies close to that for charcoal, though
Figure 6.5. Power spectra for influxes of a) charcoal, b) poplar, c) fir. The bars with arrows at either end give the bandwidth (horizontal) and 80% confidence interval (vertical) — further explanation is given in appendices 4-6. The horizontal scales are in units of cycles/sampling interval, associated cycling periods are shown too (in years). The vertical scales are in arbitrary units. Open arrows point out the peaks discussed in the text.
slightly lower (period 400-500 years). Fir shows a strong
cyclic trend of period 150-125 years as well. Since char-
coal abundances appear not to cycle at anywhere near these
periods, it seems unlikely that they arise from fires.
Heinselman (1973) points out that fir mortality increases
due to budworm outbreak and other causes about 100 years
after fire. Factors such as these could easily operate in
a cyclic fashion to produce the observed periodicities.

Difficulties encountered in analyzing spectra are dis-
cussed in the appendices: white noise in appendix 4, de-
trending in appendix 5, and aliasing in appendix 6.

6.6 POST-FIRE SUCCESSIONAL PATTERNS

From cross-correlograms showing the fire responses
and interrelationships of individual pollen taxa, it is
possible to deduce the course of succession after fire.
This was done for zone 9 at Everitt Lake in the following
series of steps: (1) the average fire interval was de-
termined from the serial correlations for charcoal (see
Fig. 6.3); (2) cross-correlograms between charcoal and
all major tree taxa were computed (only pine needed de-
trending); (3) from the correlations with charcoal the
times of greatest abundance during each fire interval were
determined for each taxon; (4) probable stand composition was inferred (for each 50-year period) by finding groups of taxa, all positively correlated, amongst the abundant taxa; (5) probable successional trends were inferred from the cross-correlograms between the major taxa.

The inferred successional patterns for Everitt Lake in zone 9 (4200-2200 years BP) are shown in Figure 6.6. The picture is restricted by the limitations of pollen data: because of the sampling interval, glimpses are separated by 50 years; most species take many years to mature and start producing pollen; and many species have been lumped together. Thus the appearance of white and grey birch as disturbance species is not indicated and, because spruce was uncommon, no relation was found between spruce and tamarack. The major features, however, agree with the general trends expected: taxa that grow well in disturbed conditions appear first and are slowly replaced by climax taxa.

The early rise in beech (at 100-150 years after fire) most likely represents the regeneration of beech from root suckers on areas where it was common prior to burning. Open arrows show the results of intermediate fires. These are inferred on the basis of the known behaviour of poplars, pines, and the other taxa concerned from their cross-correlograms with charcoal (see section 6.5).
Figure 6.6. Inferred successional trends at Everitt Lake 4200-2200 years B.P. See text for explanation.
Various authors (Mutch, 1970; Habeck and Mutch, 1973; Kilgore, 1973; Heinselman, 1973) have discussed the importance of fuel accumulation in regulating the natural fire rotation. Mutch (1970) claims that fire-dependent forests have non-random fire frequencies and Heinselman (1973) describes the way factors such as growth rates, wind damage, and mortality (besides climate), combine to produce these frequencies. Examination of the patterns in Figure 6.6 helps explain the way fire frequency causes long-term changes in forest composition. The charcoal autocorrelation for zone 8 (6200-4400 years BP) gives a fire interval of 250 years. During that period, pine rises and hemlock declines in abundance and beech abundance remains low. In zone 9, both hemlock and beech become more common while pine declines. The reason is obvious from the successional trends: except for beech's quick resurgence on areas where formerly abundant, neither beech nor hemlock become prominent for at least 250 years following major fires. Thus the higher fire frequency in zone 8 leads to their exclusion. On the other hand, pine is most prominent early in succession and after 250 years is largely replaced by oak or fir.

Oak and birch are also much more abundant in zone 8 than in zone 9. Birch shows much quicker recovery after fire too. The difference is most likely due to greater
quantities of white and grey birch in zone 8. The change in oak agrees with Little's (1974) observation that fire suppression programs in New England have prevented the light fires which formerly removed the seedlings of oak's competitors.

6.7. STAND COMPOSITION AND FIRE FREQUENCY

Mutch (1970) claims that fires occur with non-random frequency in fire-dependent forests. Here "fire-dependent" is understood to mean "requiring frequent fires to persist". The implication of the foregoing discussion, however, is that all forests are fire-dependent in the sense that particular sorts of fire regime are necessary for their existence. Komarek's zonation (Komarek, 1967) of North America is based on this and accounts exist describing the way fires help maintain numerous sorts of forests (e.g. Kilgore, 1973; Little, 1974; Swan, 1970).

It was concluded in section 6.4 that most fires represented in the record were of small extent. Broken and varied landscapes restrict the areas burnt by most fires and lead to complex stand mosaics like those found in the area around Everitt Lake today. Pure stands of (say) a flammable and fast-growing species ought to burn at a
higher and more regular frequency than stands in which it is mixed with slower-growing, fire resistant species. Furthermore, pure stands of any tree species or, at least, stands in which it predominates, are most likely to occur on a large scale when the species is very common. Thus the more abundant a tree type is, the more regular ought to be the frequency at which it burns.

Table 6.1. Cycling periods (in years)*

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Zone 8</th>
<th>Zone 9</th>
<th>Zones 10 &amp; 11</th>
</tr>
</thead>
<tbody>
<tr>
<td>Abies</td>
<td>120-400</td>
<td>100-130/300-600</td>
<td>200-250</td>
</tr>
<tr>
<td>Picea</td>
<td>100-125/500-600</td>
<td>120-400</td>
<td>100-125</td>
</tr>
<tr>
<td>Pinus</td>
<td>150-225</td>
<td>200-500</td>
<td>400-600</td>
</tr>
<tr>
<td>Tsuga</td>
<td>150-600</td>
<td>125-600</td>
<td>330-400</td>
</tr>
<tr>
<td>Betula</td>
<td>220-400</td>
<td>150-600</td>
<td>140-60/250</td>
</tr>
<tr>
<td>Fagus</td>
<td>150-400</td>
<td>180-300</td>
<td>160-300</td>
</tr>
<tr>
<td>Quercus</td>
<td>330-400</td>
<td>160-250/400-500</td>
<td>125-600</td>
</tr>
<tr>
<td>Charcoal</td>
<td>100-120/250-300</td>
<td>330-500</td>
<td>140-500</td>
</tr>
</tbody>
</table>

* All peaks tabulated are significant at the 80% level.

This hypothesis is born out by the data in Table 6.1 which shows the peak cycling intervals for the major tree taxa that have marked abundance changes in the top four zones. Cycling periods for times of greatest abundance are
underlined. In each case the range of cycling periods for an abundant taxon is very small.

Many of the cycling periods tabulated do not coincide with the cycling period for charcoal. The arguments above for fire can equally well be applied to other factors that may show up as cyclic processes—mortality, wind damage, and insect infestation, for example. Another possibility arises from the fact that local fires are much better represented in the charcoal record than distant ones. Thus fires in a large community some distance from Everitt Lake could cause cyclic abundance changes in pollen records without significantly affecting the charcoal record.

Also apparent from the table is that the shortest charcoal cycles occur in the zones where spruce, pine, and birch are abundant, while the longest occur where beech, hemlock, and fir are common. Furthermore, the greatest range of cycling periods for charcoal occurs in the top two zones, where five of the taxa reach greatest abundance; the large range of cycling periods could be due to a systematic shift in fire frequency between zones 10 and 11 but this is unlikely since hemlock and beech (the only taxa that change in abundance between the two zones) have very narrow ranges of cycling periods. The above observations further support the initial hypothesis of this section.
6.8. CONCLUSION

Time series methods have been used throughout the latter part of the analytical discussion. The value of correlograms and spectra in reconstructing ecological processes should be clear. The time series approach has drawbacks: a continuous core must be obtained, close interval sampling and accurate counting are necessary, and great care must be exercised in the interpretation of the results. The rewards, however, are great: relationships are revealed at a glance that only the most painstaking inspection of the raw data could uncover, and in sufficient volume to provide detailed pictures of past community processes. Pollen data are evidently an even richer source of ecological information than has generally been thought.

The chief conclusions drawn about fires are the following:

(1) Forest fires have occurred regularly at Everitt Lake throughout the post-glacial period.

(2) Established forest communities resist change by excluding competitors. Widespread fires in a community no longer favoured by prevailing climate can trigger shifts in the forest's species makeup.
(3) The initial rises in abundance of many tree types immediately follow major fires. The presence of a wide variety of young trees and no old ones ensures that there will be no exclusion, by long-established trees, of colonists that might thrive. Thus, environmentally favoured species are allowed to proliferate.

(4) Succession after fire leads to great changes in stand structure. Fire frequency exerts tremendous influence on forest composition simply because limits are placed on the time available for succession to proceed before a new burn occurs. Many long-term species abundance changes are a direct result of changing fire frequency.

(5) Fire frequency in forest communities is determined by the dominant tree types. Stands dominated by conifers tend to burn more frequently than those dominated by deciduous species. Intervals between fires are less variable in communities dominated by just one or two species than in those where many species are abundant.

It is difficult to confirm these results with data from the other lakes studied. The sampling interval at Everitt Lake was 50 years throughout; at Collins Lake and Curry Pond the interval ranged from 200 to 400 years. Some confirmation is visible, however: the initial
appearances of beech and maple at Curry Pond both coincide with or immediately follow fires, as does hemlock's initial rise at Collins Lake, and in both diagrams high poplar abundance accompanies times of high charcoal abundance. Most zone boundaries for Collins Lake coincide with charcoal peaks.

The results obtained in this chapter shed light on the nature of the transition from boreal to deciduous forests in Nova Scotia. Conifers possess resinous, highly inflammable sap and most are evergreen, which ensures a constant source of fuels for fires. The pines and spruces have adapted to cope with frequent, widespread fires. Communities of hardwood species such as beech and sugar maple burn much less frequently. Thus beech and sugar maple are normally excluded from spruce and pine forests, while spruce and pine are excluded from beech/maple forests because of their low shade tolerance. So, at its northernmost limit, each deciduous species ought to grow up to an abrupt boundary beyond which climatic severity and increasing fire frequency prevent it from successfully establishing itself. This phenomenon is illustrated dynamically in the pollen record by abrupt first appearances and abundance increases of deciduous taxa as their northward expansion brings them into Nova Scotia.
The sequence of composition changes leading to deciduous forest can be viewed as a community response to shifting fire regimes triggered by climatic warming. The Everitt Lake record can be interpreted as follows. Spruce dominated the forest community till about 8000 years B.P. As the climate became warmer and drier, pine competed with spruce in frequently burned stands and soon largely replaced it. At the same time pioneer hardwoods, including the birches, poplars, red oak, red maple, and elm were able to grow in the warmer conditions and continually competed with the conifers on burned areas. Hardwood and mixed stands formed this way, and because of the lower flammability of hardwoods, fires were fewer and less intense in these stands. The landscape played an important role in this process by limiting the extent of intense fires in the conifer stands, so allowing hardwood stands to survive and spread. The spread of hardwoods probably led to a decline in the numbers of severe fires generally, so that succession often proceeded much further than formerly in many conifer stands and fir, oak, and ash all became prominent for a time. That most fires were less severe meant that fire-tolerant species, notably hemlock, were often able to survive burns and formed pure stands wherever fires removed the seedlings of competitors. As the fire regime became less severe, shade-tolerant, fast-reproducing species were increasingly favoured,
leading eventually to the rise of beech, sugar maple, and yellow birch. This picture is a gross generalization, of course, but the fact that basically similar patterns of forest change occur all over northeastern North America indicates that some universal process must have been responsible for them. Two observations will demonstrate the way that topography and climate interacted with fire patterns in deciding forest composition.

The great variety of Nova Scotian forests results chiefly from the extremely broken and varied landscape left behind by the retreating ice. Complex topography limits the extent of most fires, allowing many different forest elements to exist side by side. The impact of differing landscape on floral composition can be seen by comparing the pollen records from Everitt and Collins Lakes. While both sites have similar climates, there are fewer lakes near Collins Lake, and the land surface is flatter than at Everitt Lake. This means that fires can usually burn greater areas at one time around Collins Lake, making it harder for communities of fire-intolerant species to persist there. This explains why conifers are much more dominant in the forests around Collins Lake and why beech, ash, and oak have never been as prominent there as they have been at Everitt Lake.
Davis et al. (1975) observe that although the present ranges and northern limits of beech and hemlock coincide almost exactly and although they usually now occur on the same sites, the initial rise of hemlock abundance precedes that of beech by increasing times in records from further and further northeastward. This is consistent with the idea of a large initial climatic warming (Ogden, 1967; Webb and Bryson, 1972; Terasmae, 1973; Saarnisto, 1974) with only minor fluctuations afterwards. In these circumstances, warm-adapted species would have increasing trouble surviving as climates became more severe further northward. Thus the processes described above would occur much more slowly, resulting in the increasing times observed between the rises of hemlock and beech. This applies to other major composition changes too and in comparing the Curry Pond and Collins Lake records a number of differences of this sort can be seen: for instance, the first appearance of hemlock coincides with a pine maximum at Curry Pond but follows the equivalent pine peak by almost a thousand years at Collins Lake, and while oak remains abundant until well after beech becomes common at Curry Pond, while at Collins Lake it declines long before beech abundance rises appreciably.
BIBLIOGRAPHY


___________ (1976b). Personal communication.


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APPENDIX 1

SAMPLING SITES

The following maps show the lakes studied. Marked on each map are: 1) coring sites (black squares), 2) bathymetry, 3) watershed area (inside dashed line). The following table summarizes additional information about the lakes.

<table>
<thead>
<tr>
<th>Lake</th>
<th>Elevation above sea-level (m)</th>
<th>Conductivity (μohm)</th>
<th>Secchi Disc (m)</th>
<th>O₂ (ppm)</th>
<th>CO₂ (ppm)</th>
<th>pH</th>
</tr>
</thead>
<tbody>
<tr>
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Figure A1.1: Everitt Lake, Digby County, Nova Scotia
Figure A1.2: Collins Lake, New Brunswick
Figure A1.3: Curry Pond, Yarmouth County, Nova Scotia
Figure A1.4: Duck Lake, Yarmouth County, Nova Scotia
APPENDIX 2

ADDITIONAL POLLEN COUNTS

Except where figures are given in brackets, presence or absence is noted only. Depths of occurrences are in centimetres.

(1) Everitt Lake


(2) **COLLINS LAKE**  Counts are given for *Pinus strobus*.

(a) *Juniperus-Thuja*: 210-220, 330, 370.

(b) *Carya*: 180, 240, 260, 360.

(c) *Tilia*: 0, 40, 120.

(d) *Castanea*: 110, 220, 330, 360.

(e) *Cheno-Am*: 10, 230, 310, 350, 400.

(f) *Aquatics*: 0, 50, 120, 133, 210, 280, 310, 330, 360, 370, 380, 400.

(g) *Pinus strobus*: 0(5), 10(2), 29(2), 40(2), 50(3), 70(3), 90(4),

100(1), 110(2), 133(3), 140(1), 150(4), 160(3), 200(1), 210(1),

220(1), 230(3), 260(3), 270(3), 280(3), 290(12), 300(3),

310(10), 320(6), 330(3), 340(6), 350(4), 360(3), 370(3),

380(3), 390(2), 400(6), 420(3). *Counts given in % total poll.

(h) *Ambrosia*: 0, 20, 60, 120.

(3) **CURRY POND (CT-1)**

(a) *Juniperus-Thuja*: 30, 50, 60, 90, 100, 130, 170, 218, 229, 235, 250,

255, 260, 265.

(b) *Carya*: 5, 10, 20, 40, 90, 165, 170.

(c) *Tilia*: 90, 255, 320.

(d) *Castanea*: 190, 200, 210, 235, 250.

(e) *Cheno-Am*: 30, 40, 190, 200, 210, 265, 310, 320.

(f) *Aquatics*: 0, 20, 30, 60, 90, 130, 170, 179, 190, 200, 210, 218, 240,

245, 250, 255, 260, 265, 280, 290.

(g) *Ambrosia*: 5, 10, 70, 90, 150, 165, 179, 185, 210, 240, 245, 250, 260.

(h) *Pinus strobus*: 5, 1, 1/2, 3, 1, 4 1/2, 1, 1, 5, 2, 3, 1 1/2(100 cm),

1, 1/2, 1, 3, 6, 1, 4, 3, 3, 7, 15, 5(200 cm), 3, 4, 3, 6, 3, 3, 9, 1, 6,

6, 4, 5, 8, 10, 4(300 cm), 1, 12. *Percentages are given.

(4) **CURRY POND (CT-2)**

(a) *Juniperus-Thuja*:

(b) *Carya*: 40, 200, 220.

(c) *Tilia*:

(d) *Castanea*: 55


(f) *Aquatics*: 20, 40, 160

(g) *Ambrosia*: 0, 20

(h) *Pinus strobus*: 5, 1, 5, 8, 9, 8(100 cm), 6, 7, 7(200 cm), 6,
2', 4, 13, 3 (300 cm), 4.

(5) **DUCK LAKE**

(a) *Juniperus-Thuja*: 40, 60, 80, 162, 200.
(b) *Carya*: 40, 60, 100, 140, 162, 200, 220, 240, 260, 280, 400.
(c) *Tilia*: 162, 180, 200, 440.
(d) *Castanea*: 20, 100.
APPENDIX 3

SURFACE AND BETWEEN-LAKE CORRELATIONS

The following are the types of surface spectra used:
From Davis and Webb (1975): (A) TUNDRA
  (B) FOREST TUNDRA
  (C) BOREAL FOREST
  (D) CONIFER-HARDWOOD FOREST
  (E) DECIDUOUS FOREST

From Railton (1972): (F) SUGAR MAPLE-HEMLOCK-PINE CODOMINANT
  (G) SUGAR MAPLE-YELLOW BIRCH-FIR
  (H) RED SPRUCE-HEMLOCK-PINE
  (I) SPRUCE-FIR (COASTAL)
  (J) PINE-PINE-BIRCH

(1) CORRELATIONS BETWEEN SURFACE SPECTRA

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* The taxa used in calculations are those referred to in section 4.2.
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*Mean correlations for the spectra in each zone are given.*

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APPENDIX 4

SMOOTHING, CONFIDENCE INTERVALS, AND WHITE NOISE

Raw spectral estimates, even for very long series, have a standard error of $\pm 100\%$ (Platt and Denman, 1975). This error can be reduced considerably by smoothing the spectral estimates by use of a lag window $w(k)$ which assigns weights to each lag in the computation of spectra. The price paid is that spectral peaks are spread over a greater bandwidth. In fact,

$$\text{Variance} \times \text{Bandwidth} = \text{Constant.} \quad (A4.1)$$

Bartlett's smoothing procedure was used in this study (Bartlett, 1953). The Bartlett lag window $w(k)$ is defined by:

$$w(k) = \begin{cases} 
1 - |k|/T, & |k| \leq T \\
0, & |k| > T,
\end{cases} \quad (A4.2)$$

where $T (< \ell$; the series length) is called the window width. Decreasing $T$ is called window closing. It reduces the variance and smoothes out the curve, leaving only major peaks. The bandwidth for Bartlett's window is $3/2T$ cycles per sampling interval. The 80% confidence interval is of constant width when spectral estimates are plotted on a logarithmic scale and were computed from tables given by
Jenkins and Watts (1969). Both bandwidths and confidence intervals are marked in on the spectra given in Chapter 6.

The standard deviation of a single correlation coefficient estimate is $\frac{1}{\sqrt{N}}$, where $N$ is the number of data. Thus, the correlation estimates in Chapter 6 have a standard deviation of $\pm .16$ at near-zero lag. An 80% confidence interval is therefore $\pm 1.281 \times .16$, or $\pm .2$. Changes in cross-correlation values are the essential features of interest in determining post-fire species responses, and in most cases the changes occurring are much greater than can be accounted for by random errors.

Random variation in pollen abundances shows up in power spectra as background contributions from all frequencies and is termed white noise. The less abundant a taxon is, the greater the uncertainties are, and the greater the white noise component in the power spectrum becomes. For even moderately rare taxa, white noise swamps any real trends that exist; in general, cyclic abundance changes smaller than the standard deviation of the series probably would not show up at all.

*Using the value 1.281 of the $t$-distribution with 36 degrees of freedom.
APPENDIX 5

DE Trending TIME SERIES

Figure A5(a) shows the charcoal/pine correlogram for zone 8 of the Everitt Lake core. As can be seen, the post-fire response is not clear: pine appears to increase rapidly immediately after fire, but its behaviour after that is obscured. When features of interest are obscured in this way, it is necessary to detrend the data before calculating correlations; that is, the effects of other trends or processes must be removed. This is done by performing calculations on the residuals of the data about expected values of the obscuring trend. In this case, using the deviations of pine values from a regression line drawn through the data emphasizes short-term fluctuations. Figure A5(b) shows the charcoal/pine correlogram after detrending the pine curve this way. The immediate post-fire behaviour of pine is revealed more clearly and the two peaks, as in poplar's response, suggest occasional intermediate fires.

The power spectrum for pine abundance in zone 8 is shown in Figure A5(c). Long-term abundance trends show up as cycles of very low frequency. Detrending pine abundance by the above method (figure A5(d)) reveals at least one significant peak at higher frequency (.075-.125 cycles/
Figure A5.1 Effects of détrending pine: (a) Charcoal/pine cross-correlogram, (b) Charcoal/pine cross-correlogram after detrending pine, (c) Pine power spectrum, (d) Pine power spectra after detrending by two methods. See explanation in text.
sampling interval). A more drastic way to emphasize high-frequency trends is to calculate the power spectrum from first differences between adjacent points in the original data. The result of doing this for the pine data is shown in Fig. A5(d) as a dotted line. Since deferring data this way puts enormous emphasis on short term trends, the spectrum of a detrended white-noise process (i.e. equal contribution from all frequencies) will show a major peak at the highest frequencies. Thus (in the dotted spectrum) the peak at high frequency probably results from white noise—in the original spectrum its value was not significantly greater than those of frequencies contributing least to the variance.
APPENDIX 6

ALIASING

Aliasing refers to the seeming occurrence of high frequency cyclic processes at much lower frequencies because of intermittent sampling or observation. A good example is found in the use of a stroboscope: if a spinning wheel, say, is viewed under a flashing light, its apparent motion can be slowed down and even stopped simply by increasing the rate at which the light flashes. The same thing happens to cyclic pollen abundance changes when intermittent sampling is used: high frequency (short period) cycles show up as apparent cycles of lower frequency (longer period).

The sampling interval for the Everitt Lake core was 3 cm, or about 50 years. The power spectrum of the time series for each taxon partitions the variance amongst frequencies less than 1/2 cycle/sampling interval (Nyquist frequency F), that is cycles of period greater than 100 years. Cycles of higher frequency than the Nyquist frequency are seen as apparent cycles of much lower frequency. These lower frequencies are known as aliases of the higher ones. The apparent contribution from cycles of any frequency \( f \) represented in the power spectrum is composed of contributions from cycles of each frequency \( f \pm 2nF \), where \( n \) is a natural number. Thus cycles of period 66 years (0.75 cycles/sampling interval) and 40 years (1.25 cycles/sampling interval) would
both show up as apparent cycles of period 200 years (.25 cycles/sampling interval).

This casts doubt on many of the specific cycling times quoted in section 6.7. In practice, the physical size of samples (1 cc, encompassing about 17 years of the record) together with sediment mixing probably smother periodicities of less than about 1 1/2 sampling intervals (75 years). Thus only the shorter periods (100-150 years) are really in doubt.

To test whether shorter periods do show up in pollen records, data from laminated sediments of Crawford Lake, Ontario (MacAndrews et al., 1974) were subjected to spectral analysis. Data from continuous sampling of these sediments was available at 5 year intervals covering a period of 200 years. The results showed that short period cycles do occur in pollen data and eleven of thirteen taxa tested had significant cyclic trends at periods of 20-25 years. The fact that every one of the series needed to be detrended before analysis, however, points out the importance of longer term processes on species abundances.

It is doubtful whether closer sampling would yield much new information from sediments such as those at Everitt Lake. A 2 cm sampling interval would improve frequency estimates, but is unlikely to reveal anything new. At closer intervals still, sediment mixing would probably obscure much of interest, though the inferences in section 6.6 could be made with more confidence.