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in Northern Ontario**

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HOLOCENE PALEOECOLOGY OF THE BOREAL FOREST AND GREAT LAKES–ST. LAWRENCE FOREST IN NORTHERN ONTARIO¹

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Abstract. This paper presents pollen and macrofossil stratigraphies derived from sediment cores taken near the deepest parts of Nina Lake (46°36' N, 81°30' W), Jack Lake (47°19' N, 81°46' W), and Lake Six (48°24' N, 81°19' W), which are situated along a transect across the ecotone between the boreal forest and the Great Lakes–St. Lawrence forest in northern Ontario. Paleocological data from this region of steep climatic gradient and varied landforms provide sensitive records of postglacial vegetational and climatic changes. These data are used to evaluate questions concerning the occurrence of late-glacial vegetation communities without modern analog, Hypsithermal ecotonal movements, and individualistic species response to climatic change and soil development.

The early postglacial boreal forest that colonized the Canadian Shield upland after ca. 10 000 BP was dominated by white spruce with little or no black spruce, and probably contained more oak, elm, poplar, and heliophytic herbs and shrubs than its modern counterpart. Its lack of modern analog is probably due to the widespread occurrence of fresh, unleached soil in a newly deglaciated landscape. Spruce declined and was replaced by jack pine after ca. 9000 BP as the climate continued to warm. The boreal forest was enriched floristically by the successive immigration of species such as *Myrica*, *Alnus crispa*, and *A. rugosa*.

Boreal forest was transformed into Great Lakes–St. Lawrence forest ca. 7400 yr ago when white pine, beech, and hemlock immigrated to Nina Lake. Species of the Great Lakes–St. Lawrence forest responded individualistically to Hypsithermal climatic changes. White pine populations continued to spread northward during ca. 7000–3000 BP, causing the boreal forest/Great Lakes–St. Lawrence forest ecotone to advance ca. 140 km north of its present position, only constrained by the physiographic boundary between the Clay Belt and the Canadian Shield upland.

During 6000–4500 BP northern white cedar proliferated in the Clay Belt lowlands due to a warmer and drier climate. The regional water table was lowered, permitting *Thuja* populations that were otherwise restricted to the margins of swamps and open peatlands to spread to the center. This vegetation response was landform selective, being more pronounced in the Clay Belt than on the Canadian Shield upland. The predominance of calcareous substrates and wetland habitats in the Clay Belt was favorable to the expansion of *Thuja* under a suitable climate.

Neoglacial cooling decimated the populations of northern white cedar in the Clay Belt and those of white pine in the whole region. Spruce, jack pine, and balsam fir increased over the last 4000 yr. The ecotone retreated from near Lake Six after 3000 BP, reaching Jack Lake at ca. 2600 BP, and was stabilized in its modern position during the last millennium.

Key words: boreal forest; Clay Belt; discriminant analysis; ecotone; forest succession; Great Lakes–St. Lawrence forest; Holocene paleoecology; Hypsithermal; modern analog; Ontario; palynology; post-glacial plant migration; *Thuja* expansion.

INTRODUCTION

Three decades of palynological research in Canada have greatly advanced our knowledge of the paleoecology and environmental history of the boreal forest and Great Lakes–St. Lawrence forest (Ritchie 1987). However, major gaps still exist in the data network, and several important paleoecological questions re-

main inadequately explored. One persistent question concerns the structure and composition of the late-glacial boreal forest, particularly with reference to the occurrence and interpretation of pollen assemblages without modern analog. While no-analog assemblages have been detected intuitively and by various numerical techniques from late-glacial pollen records across the boreal and temperate forest regions (Ritchie and Yarranton 1978, Amundson and Wright 1979, Liu and Lam 1985, Overpeck et al. 1985, MacDonald 1987), Ritchie (1987) has argued recently that their occurrence

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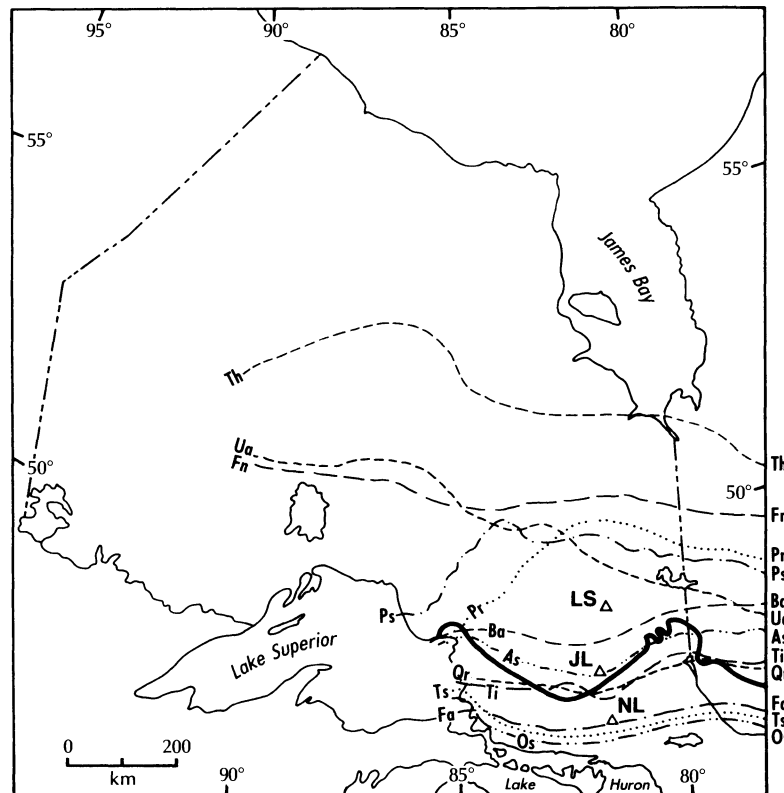


FIG. 1. Northern limits of 12 selected tree species in northern Ontario (dashed and dotted lines), after Little (1971); the modern position of the boreal forest/Great Lakes–St. Lawrence forest ecotone (—), after Rowe (1972); and the location of the three study sites (Δ): Nina Lake (NL), Jack Lake (JL), and Lake Six (LS). As = *Acer saccharum*, Ba = *Betula alleghaniensis*, Fa = *Fagus grandifolia*, Fn = *Fraxinus nigra*, Os = *Ostrya virginiana*, Pr = *Pinus resinosa*, Ps = *Pinus strobus*, Qr = *Quercus rubra*, Th = *Thuja occidentalis*, Ti = *Tilia americana*, Ts = *Tsuga canadensis*, Ua = *Ulmus americana*. - - - = provincial boundaries of Ontario.

is perhaps more apparent than real, and might have been exaggerated due to an inadequate understanding of the vegetation composition represented by the early spruce-dominated assemblage and the migration patterns of major tree taxa. In any case, the paleoecological and paleoclimatic interpretation of these no-analog assemblages—whether they are a result of dispersal lag (Davis 1976, 1981) or a function of a unique climate and soil conditions (Amundson and Wright 1979, Webb 1986)—remains a question of intense interest and controversy (see Davis 1986).

Paleobotanical records from the Arctic treeline and from the forest–grassland transition have revealed significant displacements of these ecotones during the Holocene (Ritchie 1976, Gagnon and Payette 1981, Spear 1983). Along the more diffuse transition between the boreal forest and Great Lakes–St. Lawrence forest in east-central Canada, Holocene ecotonal movements have been demonstrated in northern Ontario (Liu and Lam 1985), and, somewhat less clearly, implicated by changes in the range and relative abundance of individual tree taxa in Quebec (Terasmae and Anderson 1970, Webb et al. 1983). Nevertheless, the precise na-

ture of these ecotonal movements remains imperfectly understood. The response and sensitivity of vegetation to climatic change can also vary with variations in physiography and soil types (Brubaker 1975, Jacobson 1979, Grimm 1983, Pennington 1986). The occurrence of contrasting landforms and soils in the boreal forest, which is in turn a function of a complex glacial history, provides opportunities to examine the interactions between climate and soil and their effects on vegetation change.

This paper presents detailed pollen and macrofossil data from the transitional zone between boreal forest and Great Lakes–St. Lawrence forest in northern Ontario. The data come from three sites along a transect that straddles the modern ecotone. I focus on the following aspects of the Holocene vegetational history of northern Ontario: (1) paleoecology of the early post-glacial boreal forest; (2) Hypsithermal displacements of the boreal forest/Great Lakes–St. Lawrence forest ecotone; and (3) contrast in vegetational histories between the Clay Belt and the Canadian Shield upland as a function of complex interactions between climatic and edaphic controls.

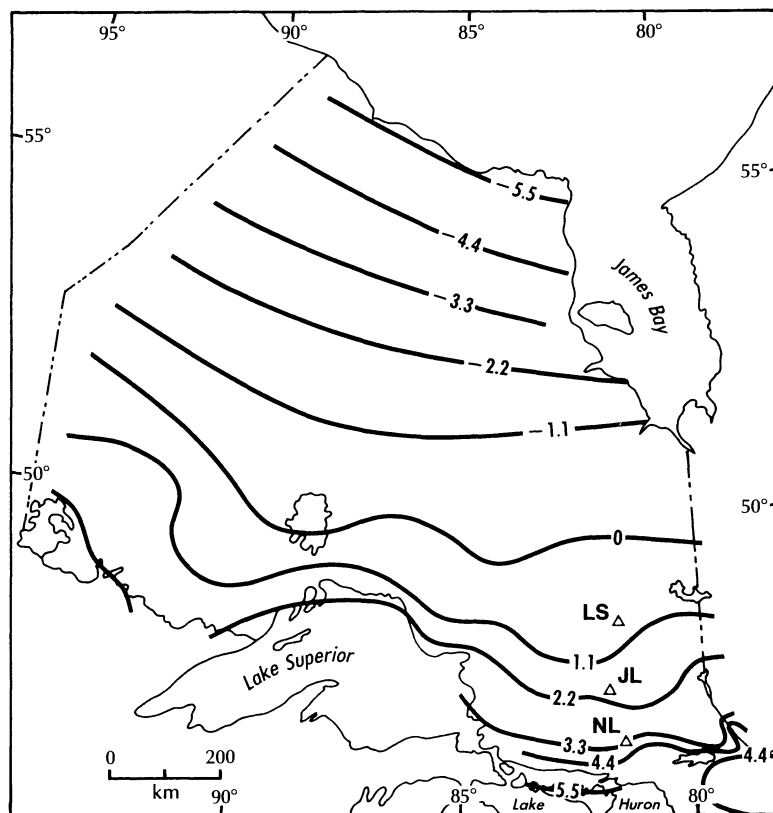


FIG. 2. Isotherms of mean annual temperatures ($^{\circ}\text{C}$) in northern Ontario, after Chapman and Thomas (1968), and the location of the three study sites (Δ): Nina Lake (NL), Jack Lake (JL), and Lake Six (LS).

THE STUDY REGION

The part of Ontario between Lake Huron and James Bay (here referred to as northern Ontario) encompasses the ecotone between the boreal forest and the Great Lakes–St. Lawrence forest (Rowe 1972). The boreal forest is dominated by white spruce (*Picea glauca*), black spruce (*P. mariana*), balsam fir (*Abies balsamea*), and jack pine (*Pinus banksiana*) on uplands, often associated with deciduous hardwoods such as white birch (*Betula papyrifera*), aspen (*Populus tremuloides*), and balsam poplar (*P. balsamifera*); and by black spruce and tamarack (*Larix laricina*) in the lowlands (Rowe 1972). The Great Lakes–St. Lawrence forest consists of mixed associations or mosaics of boreal and temperate tree taxa, often differentiated into “interpenetrating climaxes” (Braun 1950: 338) along topo-climatic and edaphic gradients (Hills 1959). Characteristic dominants include white pine (*Pinus strobus*), red pine (*P. resinosa*), hemlock (*Tsuga canadensis*), beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), and sugar maple (*Acer saccharum*) (Rowe 1972). The ecotone between these two forest regions is a diffuse vegetation transition that generally parallels the height of land separating the Arctic watershed from the Great Lakes watershed (Fig. 1). At least fourteen important thermophilous hardwood species (*Fagus grandifolia*,

Betula alleghaniensis, *Acer saccharum*, *A. rubrum*, *Ostrya virginiana*, *Ulmus americana*, *U. rubra*, *Quercus macrocarpa*, *Q. rubra*, *Fraxinus americana*, *F. nigra*, *F. pennsylvanica*, *Tilia americana*, *Populus grandidentata*) and four conifers typical of the Great Lakes–St. Lawrence forest (*Pinus strobus*, *P. resinosa*, *Tsuga canadensis*, *Thuja occidentalis*) reach their northern limits in this region (Little 1971; Fig. 1); some of them penetrate into the southern part of the boreal forest. The whole region, therefore, is a tension zone where the temperate flora merges with the boreal and subarctic flora of North America (Nichols 1935, Braun 1950).

The position of the ecotone is controlled by continent-scale atmospheric circulation phenomena. The southern border of the boreal forest coincides generally with the mean January position of the Arctic Front, which separates the cold, dry, Arctic airstreams from the relatively warm, moist, Pacific airstreams (Bryson, 1966). A steep climatic gradient exists in the region. Northern Ontario belongs to the Dfb climate of Köppen (Eichenlaub 1979) or the C'2 (warm microthermal) thermal province of Thornthwaite (Hare 1950). It has cold-to-severe winters, cool-to-moderately warm summers, and a humid-to-perhumid moisture regime. Precipitation ranges from ≈ 900 mm in the extreme southeast to < 760 mm in the central and northwestern part.

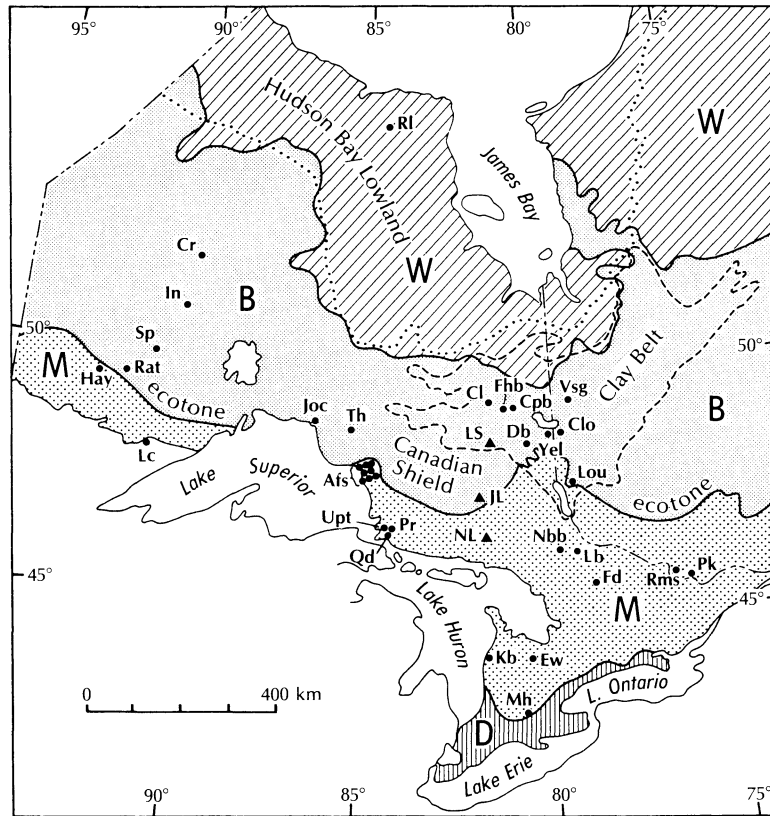


FIG. 3. Major physiographic divisions (broken lines) and vegetation regions (shaded and identified by uppercase letters) in northern Ontario and adjacent areas, modified from Rowe (1972), Prest (1970), and Saarnisto (1974); and the location of some of pollen study sites mentioned in the text. D = deciduous forest, M = Great Lakes–St. Lawrence forest, B = boreal forest, W = boreal woodland; Sites of this study (\blacktriangle): NL = Nina Lake, JL = Jack Lake, LS = Lake Six; Other sites (\bullet): Afs = Alfies Lake and 7 other lakes (Saarnisto 1975), Cl = Crates Lake (Liu 1982), Clo = Lac Clo (Richard 1980), Cpb = Cochrane peat bog (Ignatius 1956), Cr = Cristal Lake (Bjorck 1985), Db = Drinkwater bog (Ignatius 1956), Ew = Edward Lake (McAndrews 1981), Fd = Found Lake (McAndrews 1981), Fhb = Frederick House River bog (Terasmae and Hughes 1960b), Hay = Hayes Lake (McAndrews 1982), In = Indian Lake (Bjorck 1985), Jock = Jock Lake (Saarnisto 1975), Kincardine bog (Karrow et al. 1975), Lb = Lac Bastian (Bennett 1987), Lc = Lake of the Clouds (Craig 1972), Lou = Lake Louis (Vincent 1973), M = Maplehurst Lake (Mott and Farley-Gill 1978), Nbb = North Bay bog (Terasmae 1968), Pk = Pink Lake (Mott and Farley-Gill 1981), Pr = Prince Lake (Saarnisto 1974), Qd = Quadrangle Lake (Terasmae 1967), Rat = Rattle Lake (Bjorck 1985), Ri = R Lake (McAndrews et al. 1982), Rms = Ramsay Lake (Mott and Farley-Gill 1981), Sp = Sioux Pond (Bjorck 1985), Th = Thane Lake (Terasmae 1967), Upt = Upper Twin Lake (Saarnisto 1974), Vsg = Val St. Gilles bog (Terasmae and Anderson 1970), Yel = Lac Yelle (Richard 1980). - - - = provincial boundaries of Ontario.

Mean annual temperature decreases poleward from 5°C along the north shore of Lake Huron to -1° just south of James Bay (Fig. 2). The steepest temperature gradient occurs in the southern part of the region, where mean annual temperature drops by 4° over a distance of 200 km (Chapman and Thomas 1968). The ecotone generally follows the 2.2° isotherm.

The steep climatic gradient is also reflected by a compressed vegetation zonation. The boreal forest, stretching across the continent from Alaska to Labrador–Newfoundland, reaches its southernmost distribution (about 47° N) in northern Ontario and adjacent Quebec (Fig. 3). Also, the width of the boreal forest is most compressed latitudinally in this region, compared with west-central Canada and eastern Quebec. Baldwin

(1962) observed that the transition from Great Lakes–St. Lawrence forest to subarctic forest is completed within a distance of 400 km in northern Ontario, whereas the same transition extends over 800 km in Scandinavia. The steep climatic gradient and the compressed vegetation zonation suggest that pollen records sensitive to late-Quaternary climatic and vegetational changes can be obtained from this region.

Northern Ontario had a complex deglaciation history during the final phase of the Late Wisconsin Glaciation. The Laurentide Ice Sheet retreated to north of Lake Huron shortly before 11 000 BP. It built two massive morainic belts: (1) the Cartier moraine, during the Algonquin Stadial from 11 000 to 10 100 years ago; and (2) the Chapleau moraine, located farther north

and dating from 9500 BP (Saarnisto 1974). As the ice retreated north of the continental water-divide, two huge proglacial lakes, glacial Lakes Barlow and Ojibway, were formed, which existed until ca. 7900 BP (Terasmae and Hughes 1960a, Vincent and Hardy 1979). The northern part of Lake Ojibway was overridden by ice during the Cochrane readvance, which occurred in two phases at 8200 BP and 7975 BP (Hardy 1977). The ensuing collapse and disintegration of the ice saddle over Hudson Bay resulted in the invasion of the Tyrrell Sea and the rapid draining of Lake Ojibway (Mayewski et al. 1981).

This complex deglaciation history has resulted in a variety of landforms and soils. By far the greatest physiographic contrast exists between the Canadian Shield and the Clay Belt (Fig. 3). The Canadian Shield, composed of Precambrian metamorphic rocks, occupies a rolling upland between 300 m and 450 m above sea level. It is covered by a thin and discontinuous layer of coarse, sandy till derived from the crystalline bedrock (Boissonneau 1968). The predominant soils are humo-ferric podzols, which are generally well drained, acidic, and nutrient poor (Clayton et al. 1977). The Clay Belt, generally between 150 m and 300 m above sea level, is a flat-to-undulating lacustrine plain composed largely of varved or massive clay deposited in glacial Lakes Barlow and Ojibway. The northern part of the Clay Belt is blanketed by a calcareous, clay-rich till deposited by the Cochrane ice (Boissonneau 1966). The soils of the Clay Belt are predominantly gleysols, which are base rich and calcareous (Clayton et al. 1977). Because of poor drainage, the Clay Belt supports extensive muskegs dominated by black spruce. Upland habitats are confined to eskers and sandy outwash plains, which are locally extensive and often support forests dominated by jack pine. The occurrence of these physiographic variations can provide favorable conditions for evaluating the effects of landform and substrate on vegetational changes.

Compared with adjacent regions, northern Ontario is not well explored palynologically. Although pollen diagrams have been published from at least 22 sites in northern Ontario and adjacent Quebec (Fig. 3), many have inadequate dating control and are only cursorily interpreted in terms of regional vegetational history; some only contain a partial Holocene sequence. Most of the existing pollen study sites are aligned along two broad transects. An eastern transect occurs along the Ontario-Quebec border (Ignatius 1956, Karlstrom 1956, Terasmae and Hughes 1960b, Terasmae 1968, Terasmae and Anderson 1970, Vincent 1973, Richard 1980, Bennett 1987). The western transect occurs mainly along the east shore of Lake Superior (Terasmae 1967, Saarnisto 1974). A series of other sites (Craig 1972, McAndrews 1982, Bjork 1985) farther to the west of Lake Superior forms an additional transect outside my study region. The transect reported here is located in the central part of northern Ontario, where

little palynological work has been published before except for an abbreviated pollen percentage diagram from Jack Lake (Liu and Lam 1985).

METHODS

My transect, ≈ 220 km long, was placed to parallel the steepest climatic gradient north of Lake Huron. The three lakes along the transect were chosen so that they are 60–80 km apart and situated in different vegetation or physiographic regions. All are small lakes <6 ha in size, and have inlet and outlet streams. Most of their pollen is expected to be derived from extralocal and regional sources, although some local and extralocal components might be brought in by fluvial transport (Peck 1973, Jacobson and Bradshaw 1981). Nina Lake (46°36' N, 81°30' W), the southernmost site, is in the Great Lakes-St. Lawrence forest. Jack Lake (47°19' N, 81°46' W) is in the Canadian Shield section of the boreal forest, just north of the ecotone. Lake Six (48°24' N, 81°19' W), the northernmost site, is also in the boreal forest but is within the Clay Belt. Differences in their vegetational histories are expected to reflect climatic as well as physiographic and edaphic controls.

Water depth was measured by sonar, and sediments in each of the three lakes were cored near their deepest parts by means of a square-rod piston sampler (Wright 1967). The wet sediment cores were sampled for pollen analysis at 10-cm intervals by packing each sediment sample into a 0.9-mL measuring spoon. The samples were chemically processed to concentrate pollen grains and spores by standard pollen extraction techniques (Faegri and Iversen 1975). At least 400 grains were counted in each sample except those from basal sandy sediments. The pollen sum consisted of all taxa except Cyperaceae, aquatics, and pteridophyte spores. Two *Lycopodium* tablets, each containing $10\,850 \pm 200$ spores, were added to each sample for estimating pollen concentration and influx values (Stockmarr 1971). Identification of pollen and spores was made with the aid of the modern reference collection at the Botany Department of the Royal Ontario Museum, Canada, and by consultation with published works (Kapp 1969, Richard 1970a, b, McAndrews et al. 1973, Bassett et al. 1978). Nomenclature of pollen taxa follows McAndrews et al. (1973). The pollen of *Pinus strobus*, the only haploxylon pine species in eastern North America, was distinguished from that of *P. banksiana* and *P. resinosa* by the presence of distal verrucae (McAndrews et al. 1973). The pollen of the latter two diploxylon pine species could not be separated easily, and was lumped under *P. banksiana/resinosa*. At selected levels at least 20 *Picea* pollen grains were measured and statistically assigned to either *P. glauca* or *P. mariana* according to the discriminant functions derived by Birks and Peglar (1980). The pollen stratigraphies were divided into local pollen assemblage zones and subzones (sensu Hedberg 1972) with the aid of three constrained agglomerative and divisive techniques (CONSLINK,

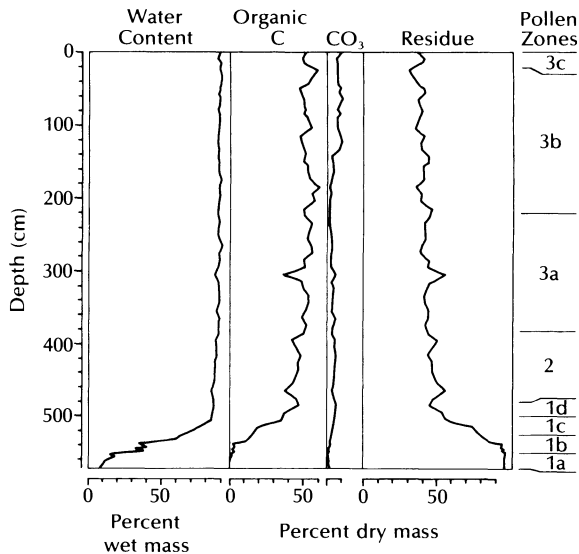


FIG. 4. Loss-on-ignition analysis of the sediments from Nina Lake. Water content is expressed as percent of wet mass; organic carbon (C), carbonates (CO_3) and residue contents are expressed as percent of dry mass.

SPLITINF, SPLITLSQ) developed by Gordon and Birks (1972).

After sampling for pollen, each core was cut into 20-cm sections for macrofossil analysis. Each sample, 250 mL in volume, was washed through a 325- μm sieve to concentrate macrofossils. Macrofossil identifications were made with the aid of published manuals (Martin and Barkley 1961, Montgomery 1977) and the modern reference collection at the Royal Ontario Museum. The sediments were heated at 105°, 550°, and 1000°C, respectively, to determine their water contents, organic matter contents, and carbonate contents (Dean 1974). Nine C-14 dates, three from each core, were determined by the radiocarbon dating laboratory at the University of Waterloo (Waterloo, Ontario, Canada).

Discriminant analysis was used to aid the interpretation of the three pollen stratigraphies in terms of vegetational changes (Liu and Lam 1985). In this previous study we used a modern pollen data set that consisted of 121 surface samples derived from five vegetation regions in northeastern North America—the deciduous forest, Great Lakes–St. Lawrence forest, boreal forest, boreal woodland, and tundra; our discriminant functions correctly classified 95% of our surface samples to the five vegetation regions (Liu and Lam 1985). The same modern pollen data set and the same discriminant functions were used in this study. The discriminant analysis results are summarized by two parameters. (1) The Vegetation Zonal Index (VZI), which ranges from 1.0 to 5.0, identifies a pollen sample with one of the five vegetation regions. (2) The $P(X_i|H_k)$ probability, conveniently referred to as the Probability of Modern Analog (PMA), compares a pollen sample

with the statistical centroid of the pollen samples classified to the same group; a low probability thus suggests that the sample does not resemble the “average” or “typical” pollen assemblage of its designated vegetation region. It should be noted that the PMA is not an exhaustive test for modern analogs because it does not directly compare the fossil sample with each individual surface sample, as is the case with dissimilarity coefficient techniques (Overpeck et al. 1985) or other multidimensional scaling techniques (Prentice 1980) and correlation coefficient techniques (Ogden 1969, Davis et al. 1975). Thus a low PMA does not preclude the possibility that the fossil sample might resemble individual surface samples that are themselves atypical of their own group (and thus strictly speaking would have a modern analog), but it is a useful supplement to the VZI in detecting fossil samples that deviate from the palynological “signatures” of their assigned vegetation groups.

RESULTS

Nina Lake

Nina Lake (unofficial name) (46°36' N, 81°30' W; elevation 380 m) is situated on the western limit of Windy Lake Provincial Park \approx 38 km west of Sudbury, Ontario. It is a small lake, \approx 100 \times 230 m, and \approx 7.2 m deep near the center. The lake is connected with other small lakes by an inlet and an outlet stream. It occupies a rock basin of unknown origin.

Nina Lake lies within the Sudbury–North Bay section of the Great Lakes–St. Lawrence forest (Rowe 1972), but because of human disturbance, fire, and proximity to an extensive sandy outwash plain, the local vegetation around Nina Lake is quite boreal in character. According to forest resources inventory data, the forest within a 1-km radius of Nina Lake contains \approx 40% jack pine, 30% white birch, 10% balsam fir, 10% aspen, and 10% miscellaneous trees such as white pine, white spruce, and red maple (Ontario Department of Lands and Forests, Forest Stand Map, Cascaden Township, 1980 inventory). *Nymphaea odorata* and *Carex* spp. are common aquatic plants in the lake.

The 5.75-m core was mainly composed of detrital gyttja except at the lowermost 30 cm, where clay, sand, and gravel occurred (Fig. 4). Sedimentation rates calculated from the three C-14 dates are fairly uniform (Table 1). The basal date of 9510 ± 100 BP is slightly younger than the expected age of deglaciation for this area south of the Cartier moraine, which according to Saarnisto (1974) was formed 11 000–10 100 yr ago. The reason for the delay in organic sedimentation is unclear. The fact that the lake is embedded in Precambrian bedrock rather than glacial drift implies that delayed melting of buried ice block (Wright 1980) is not a likely explanation.

Pollen stratigraphy.—The Nina Lake pollen stratig-

TABLE 1. Radiocarbon dates and sedimentation rates for the cores from Nina Lake, Jack Lake, and Lake Six.

Core depth (cm)	Uncorrected age (yr BP)	¹³ C (%)	Laboratory number	Sedimentation	
				Depth (cm)	Rate (cm/yr)
Nina Lake					
221-229	3960 ± 90	-31.8	WAT-811	0-225	0.0568
382-390	7380 ± 100	-30.3	WAT-699	225-386	0.0471
524-534	9510 ± 100	-30.0	WAT-695	386-529	0.0671
Jack Lake					
160-171	3450 ± 60	-30.9	WAT-809	0-165	0.0478
321-329	7490 ± 90	-29.9	WAT-700	165-325	0.0396
372-381	9270 ± 100	-30.4	WAT-706	325-377	0.0343
Lake Six					
135-143	3190 ± 60	-30.8	WAT-810	0-139	0.0436
216-225	5040 ± 70	-30.7	WAT-697	139-221	0.0438
290-298	6970 ± 100	-34.7	WAT-549	221-294	0.0409

raphy is divided into three local pollen assemblage zones and seven subzones, as follows (Figs. 5, 6, 7).

1. *Zone NL-1 (Picea pollen assemblage zone): 485-572 cm; ca. 9800-8900 BP.*—This zone is characterized by maximum frequencies of *Picea* pollen, about 7-31% (Fig. 6). Discriminant analysis of the size statistics of *Picea* pollen at one level (529 cm) indicates

that 95% are *P. glauca* type. Although size measurement of *Picea* pollen was not made at other levels in this zone, it was noted during counting that most of the spruce pollen grains present were large, suggesting white spruce. This zone is divided into four subzones based on variations in other pollen taxa.

a) Subzone NL-1a or the NAP subzone (545-572

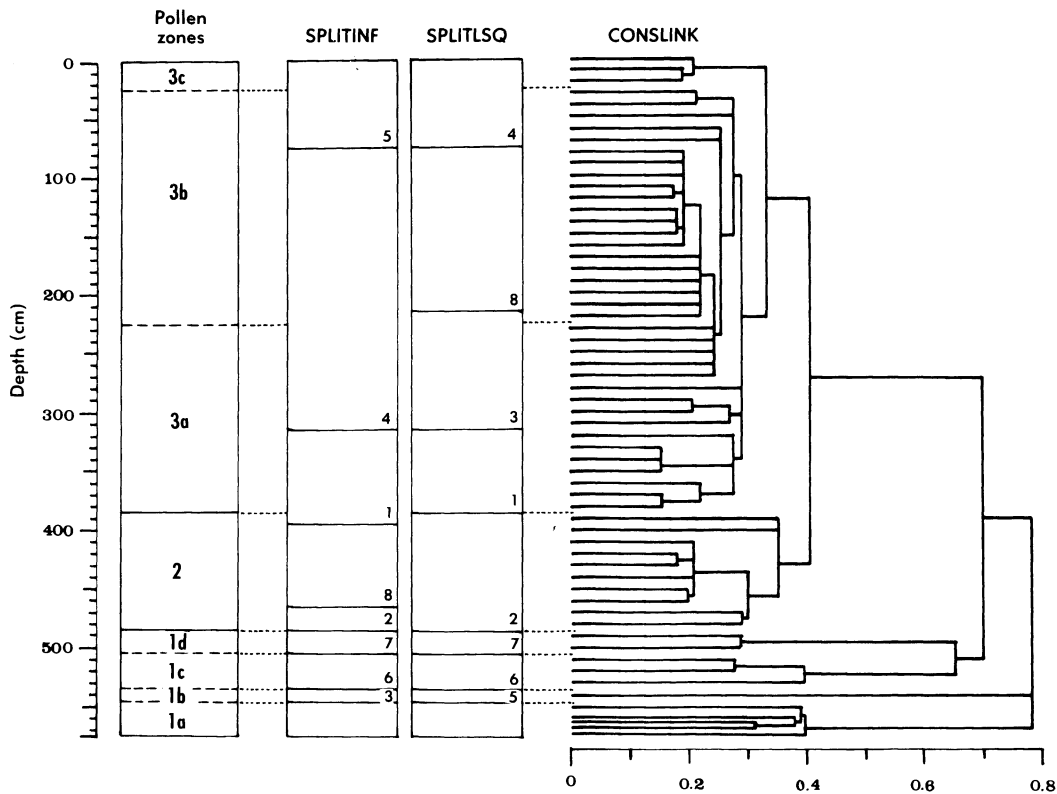


FIG. 5. Results of three numerical zonation procedures and the pollen zones delineated for Nina Lake. The number above each division for SPLITINF and SPLITLSQ indicates the order of the numerically derived division (e.g., 1 = primary division, 2 = secondary division, etc.).

NINA LAKE
POLLEN PERCENTAGE DIAGRAM

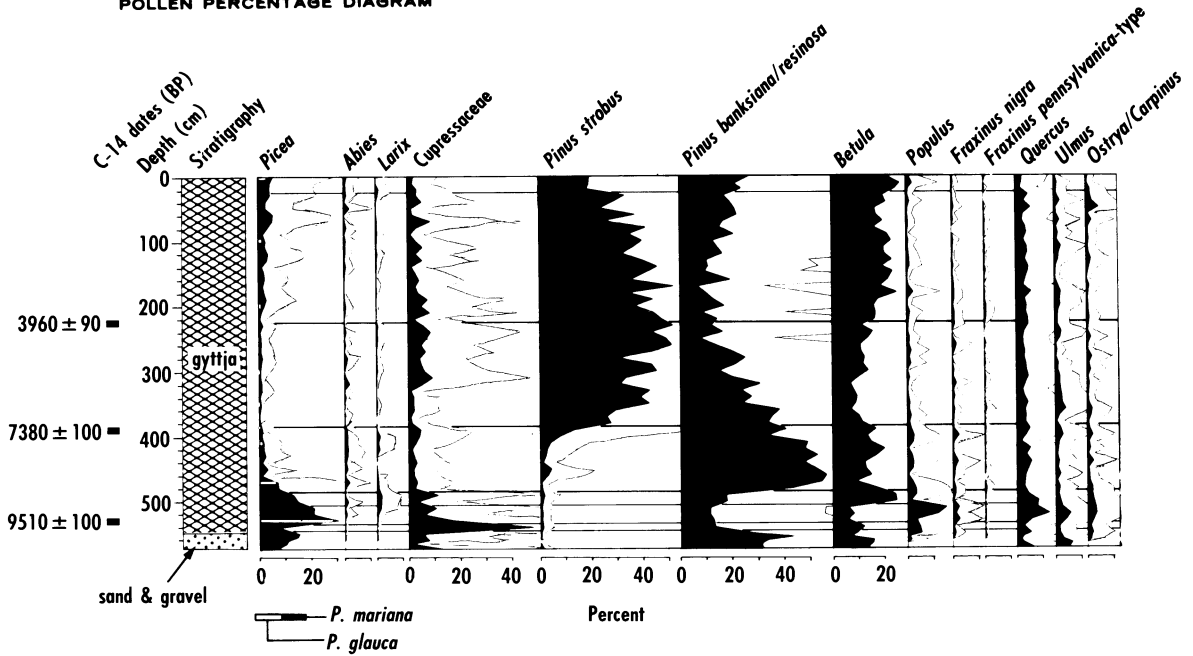


FIG. 6. Pollen percentage diagram for Nina Lake. The scale of the unshaded silhouettes is exaggerated by 5 ×.

NINA LAKE
POLLEN INFLUX DIAGRAM

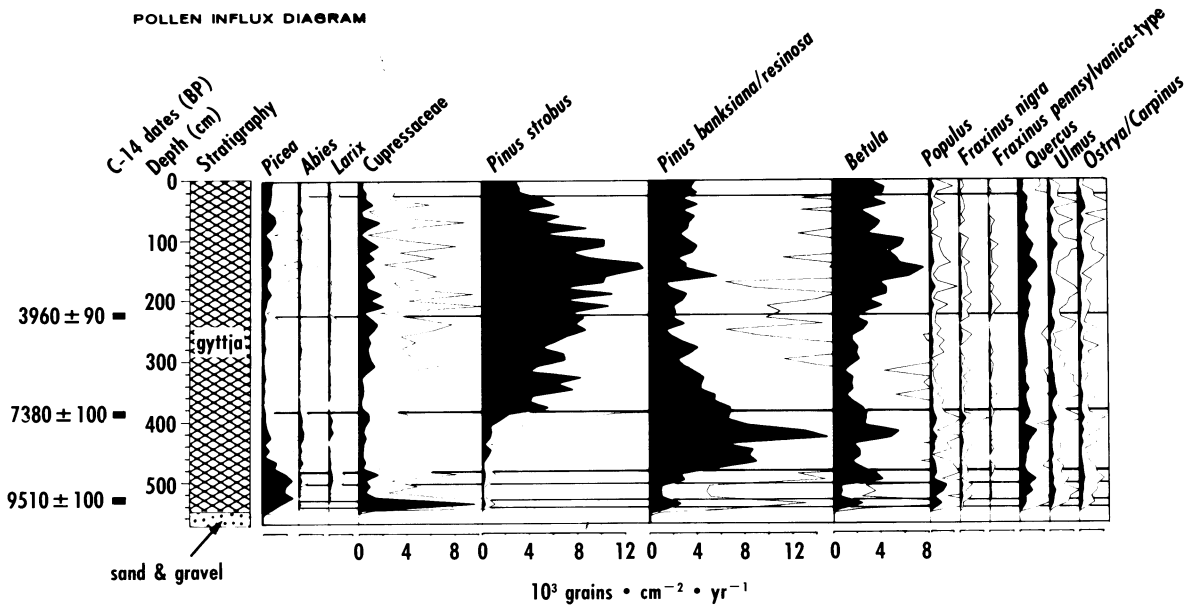


FIG. 7. Pollen influx diagram for Nina Lake. The scale of the unshaded silhouettes is exaggerated by 5 ×.

cm; Fig. 6) has high percentages of *Pinus banksiana/resinosa* pollen (29–44%) and distinct peaks of *Salix*, *Artemisia*, Gramineae, and Cyperaceae pollen. This subzone is confined to coarse minerogenic sediments in which pollen concentrations are extremely low ($<0.1 \times 10^3$ grains/cm³, except at the uppermost level).

b) Subzone NL-1b, the Cupressaceae pollen subzone (535–545 cm), is characterized by a prominent peak in Cupressaceae pollen, in both percentages and concentration values. Although this subzone is defined by only one sample, the results were reproducible in a duplicate sample taken from a parallel core, thus con-

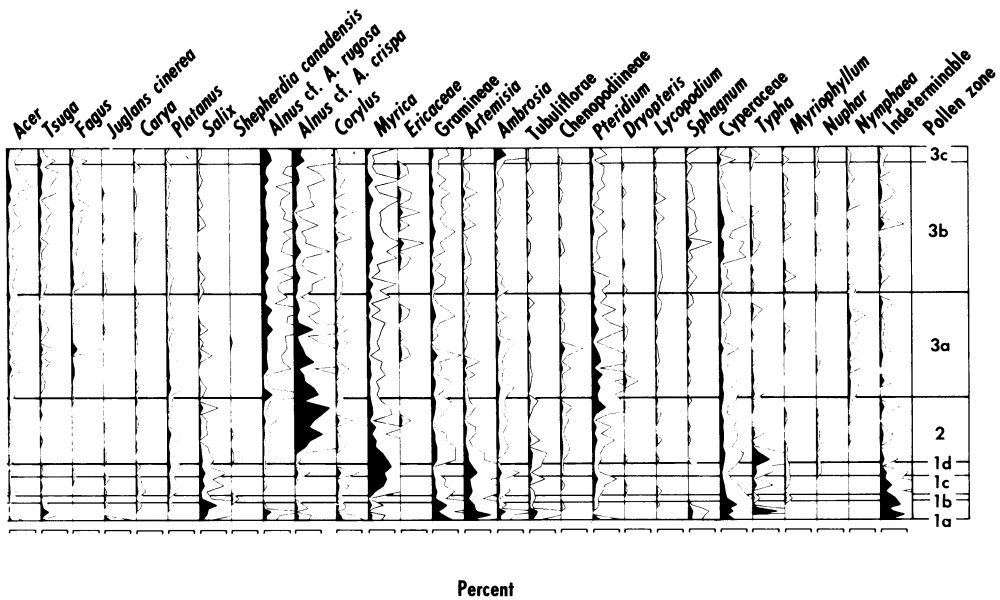


FIG. 6. Continued.

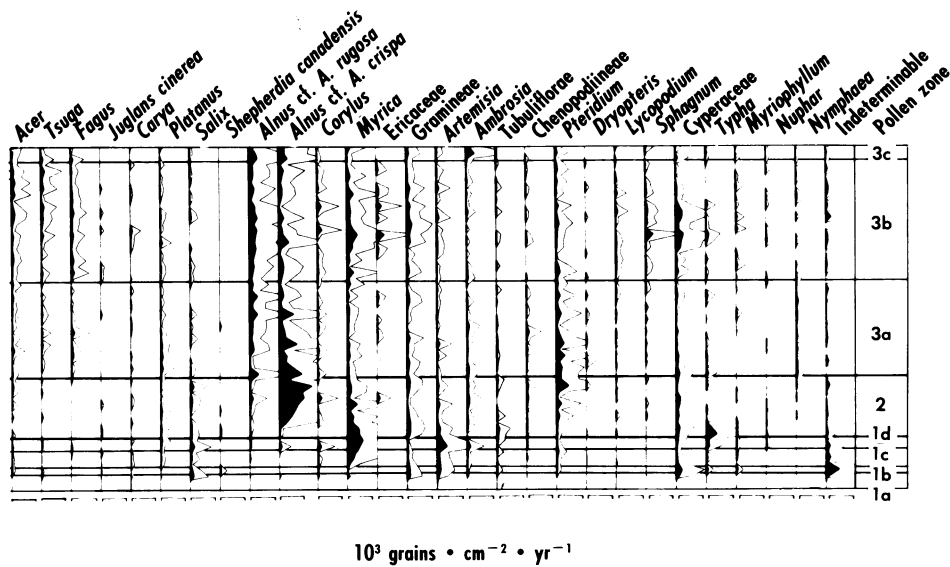


FIG. 7. Continued.

firming that the Cupressaceae pollen peak is not an artifact of the analysis. The percentages of *Pinus banksiana/resinosa* pollen decrease sharply from 29% to 11% in this and the overlying subzones.

c) In subzone NL-1c or the *Populus* subzone (505–535 cm), both *Populus* (4–15%) and *Picea* (21–31%)

pollen occur in maximum frequencies. Pollen percentages for *Myrica*, *Quercus*, *Ulmus*, *Ostrya/Carpinus*, and *Fraxinus* also increase. Pollen influx (Fig. 7) is in the order of $8.2\text{--}9.0 \times 10^3 \text{ grains} \cdot \text{cm}^{-2} \cdot \text{yr}^{-1}$.

d) Subzone NL-1d, or the *Betula* subzone (485–505 cm), contains high percentages of *Betula* pollen

NINA LAKE MACROFOSSIL DIAGRAM

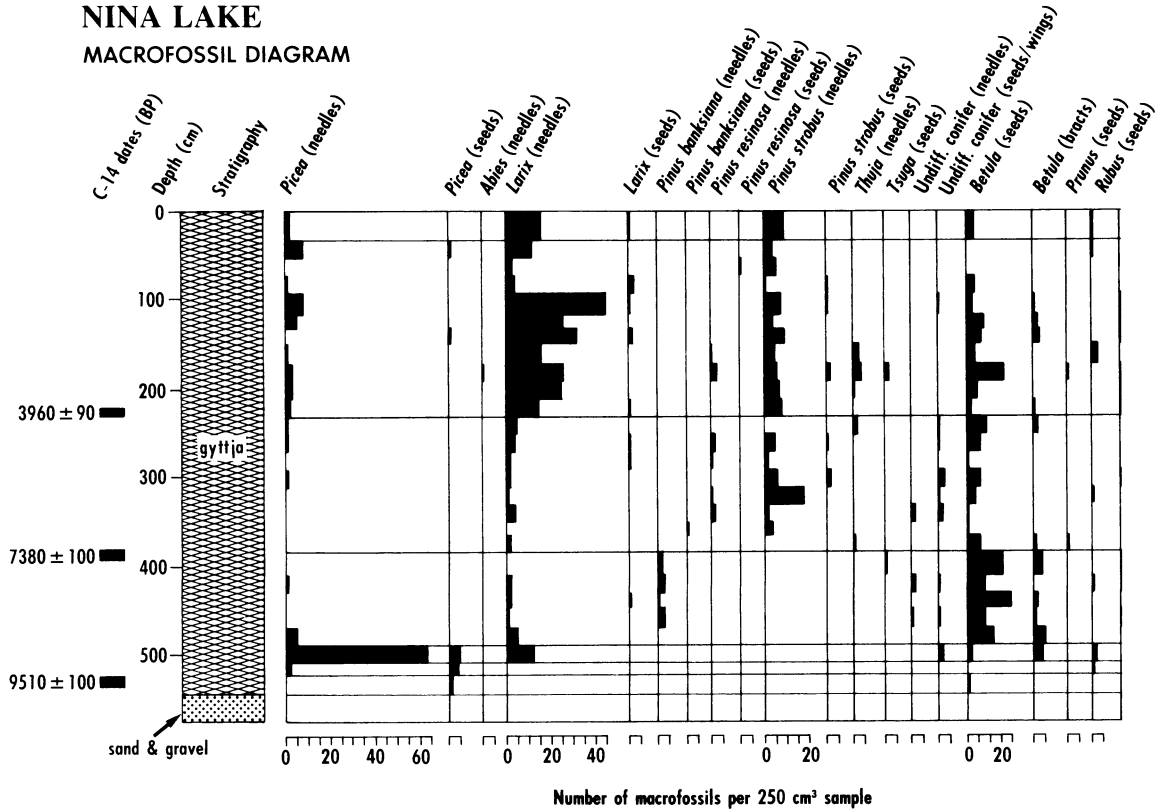


FIG. 8. Macrofossil diagram for Nina Lake.

(25%), while *Picea* pollen declines in percentage. Pollen influx values have increased to $14.0\text{--}16.5 \times 10^3$ grains·cm⁻²·yr⁻¹.

2. *Zone NL-2 (Pinus banksiana/resinosa pollen assemblage zone): 385–485 cm; 8900–7400 BP.*—The pollen of *Pinus banksiana/resinosa* increases dramatically across the zone 1–2 boundary to >30% in zone 2. The pollen of *Alnus cf. crispa* also increases from <1% in zone 1 to >10% here. *Picea* pollen declines through this zone to <2%, a typical value for the rest of the core. *P. glauca* is still the predominant type in the lower part of this zone, but the proportion of *P. mariana* increases near the top. *Betula* decreases slightly in pollen percentages. Pollen influx values are typically in the order of 30×10^3 grains·cm⁻²·yr⁻¹.

3. *Zone NL-3 (Pinus strobus pollen assemblage zone): 0–385 cm; 7400–0 BP.*—The pollen of *Pinus strobus* increases dramatically at the base of this zone to >50% in the middle. The pollen of *Fagus*, *Tsuga*, and *Acer* also occur more consistently. Three subzones are recognized.

a) Subzone NL-3a (225–385 cm) is characterized by increasing *P. strobus* percentages, a concomitant decline in *P. banksiana/resinosa* pollen, and minimum frequencies for *Picea*.

b) Subzone NL-3b (25–225 cm) is recognized by decreasing *P. strobus* percentages, while *Picea*, *Pinus banksiana/resinosa*, and *Betula* increase.

c) Subzone NL-3c (0–25 cm) is delimited by the

Ambrosia rise, and a further decrease in *P. strobus* pollen abundance.

Macrofossil stratigraphy.—The sediments from Nina Lake contain a rich macrofossil record of both upland and aquatic plant taxa (Fig. 8). The basal coarse minerogenic sediments of subzone NL-1a do not contain any macrofossils. Subzone NL-1b marks the first appearance of *Picea* and *Betula* seeds, but macrofossils of Cupressaceae are absent. Despite the peak in *Picea* pollen percentages in subzone NL-1c, *Picea* macrofossils are most abundant in the overlying subzone NL-1d, together with frequent *Larix* needles.

Pinus banksiana needles are confined to the sediments of pollen zone NL-2. *Betula* macrofossils are most frequent in this pollen zone. *Picea* and *Larix* needles are present but less frequent than in the zone below. A seed of *Tsuga canadensis* was found at the top of zone NL-2.

Pollen zone NL-3 is characterized by the consistent occurrence of *Pinus strobus* needles. Macrofossils of *P. resinosa*, *Thuja*, *Tsuga*, and *Abies* are also present sporadically. *Betula* seeds occur consistently but are less common than in the underlying zone. *Picea* and *Larix* needles are infrequent in subzone NL-3a but increase significantly in subzone NL-3b. Subzone NL-3c seems to contain a less diverse assemblage of macrofossils; otherwise it is indistinguishable from the other two subzones.

A diverse macrofossil assemblage of upland and wet-

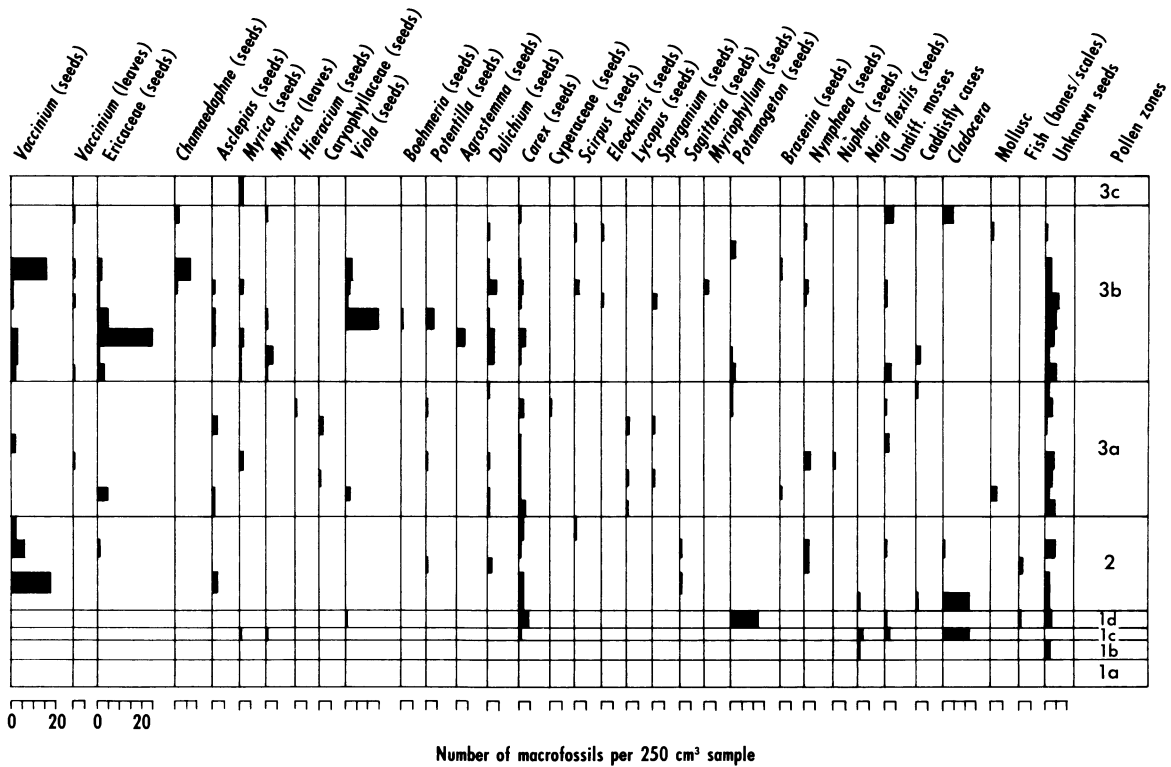


FIG. 8. Continued.

land non-arboreal plants as well as aquatics was found in the sediments of Nina Lake. Macrofossils of *Myrica*, *Rubus*, *Viola*, *Carex*, *Potamogeton* and *Najas flexilis* are already present in zone NL-1. Zone NL-2 includes an additional list of *Vaccinium*, *Asclepias*, *Potentilla*, *Nymphaea*, *Sagittaria*, *Scirpus*, and *Dulichium*. Zone NL-3 contains the richest assemblage. Aquatic and wetland taxa appearing for the first time in zone NL-3 include *Nuphar*, *Brasenia*, *Myriophyllum*, *Sparganium*, *Lycopus*, and *Eleocharis*. Moreover, macrofossils of *Myrica*, *Viola*, *Vaccinium*, *Chamaedaphne*, and *Ericaceae* are very well-represented in subzone NL-3b, although they are already present in the sediments below.

Discriminant analysis. — Except at one level (565 cm), pollen zone NL-1 has VZIs of about 3.0 coupled with near-zero PMAs, suggesting a boreal forest without modern analog (Fig. 9). The anomalous sample is classified as tundra but has the boreal forest as its second most probable group, and has a PMA of 0. The anomaly undoubtedly indicates a no-analog pollen assemblage (Liu and Lam 1985). In zone NL-2, the VZIs remain at 3.0 but the PMAs increase to >0.5, indicating the establishment of a boreal forest with modern characteristics.

The VZIs drop abruptly from 3.0 to 2.0 across the boundary between zone NL-2 and zone NL-3. The shift signifies the replacement of boreal forest by Great Lakes–St. Lawrence forest. VZIs of 2.0–<2.5 occur

throughout zone NL-3 despite some slight increases towards the top, suggesting that Great Lakes–St. Lawrence forest has persisted around Nina Lake since it was established 7400 years ago.

Jack Lake

Jack Lake (47°19' N, 81°46' W; elevation 430 m) is situated in Paudash Township ≈40 km south of Gogama. It is one of a series of small lakes connected by a small tributary of the Spanish River system. The lake is 260 × 200 m; maximum water depth was measured to be ≈5.0 m near the center. It lies in coarse sandy and bouldery till on the rolling Canadian Shield upland, south of the occurrence of calcareous drift on the shield (Karrow and Geddes 1987). Bedrock exposures are common in the vicinity. Much wetland development occurs along margins of lakes and streams.

Jack Lake occupies an ecotonal location between the boreal forest and the Great Lakes–St. Lawrence forest. The exact position of the diffuse ecotone is hard to determine in the field, but, based on Rowe's (1972) map, Jack Lake lies within the Missinaibi–Cabonga section of the boreal forest, perhaps <20 km north of the ecotone. The surrounding vegetation is transitional in character. White birch, balsam fir, white spruce, aspen, and jack pine are the most common dominants in the upland forests, but sugar maple and yellow birch are present in several hardwood stands in the vicinity (Ontario Ministry of Natural Resources, Forest Stand

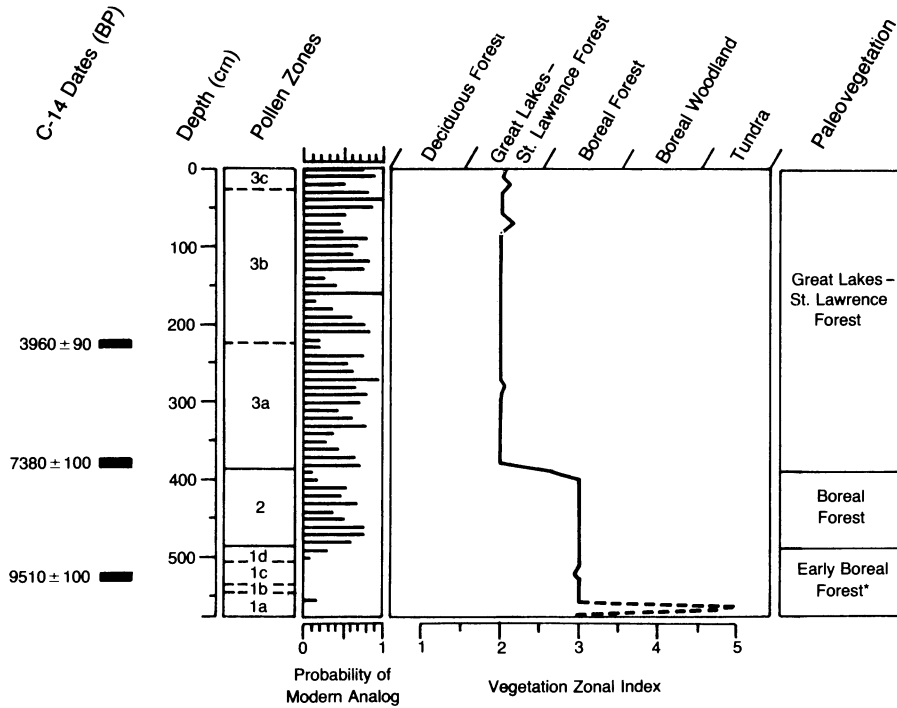


FIG. 9. Discriminant analysis results for the pollen stratigraphy from Nina Lake. Paleovegetation inferred to be without regional modern analog is marked with an asterisk.

Map, Paudash Township, 1974 inventory). White pine is also locally common, as are black spruce, alder, and willow in the lowlands. *Carex* spp., *Sagittaria latifolia*, and *Nymphaea odorata* are common in the littoral zone along the lake margin.

The core from Jack Lake was 4.80 m long, including 86 cm of coarse sand, silt, and clay at the base. The rest of the core is mainly dark-brown gyttja with 40–50% organic matter content (Fig. 10). A C-14 date of 9270 ± 100 BP was obtained from the organic sediments 13 cm above the sharp lithologic contact at 394 cm. By extrapolation, Jack Lake started accumulating organic sediments ≈ 9500 yr ago. The lake basin was probably formed shortly before that, perhaps some 9800 yr ago, assuming that it may have taken several hundred years for the 86 cm of basal minerogenic sediments to accumulate. This estimated age for Jack Lake is compatible with the chronology of the Chapleau moraine 20 km to the north, which was formed by a glacial readvance ≈ 9500 yr ago (Saarnisto 1974). Sedimentation rates calculated from the three C-14 dates are very uniform throughout the organic sediments of the core (Table 1).

Pollen stratigraphy.—The lowermost 30 cm of coarse sand in the core from Jack Lake did not contain pollen. The remaining 450 cm of the pollen stratigraphy is divided into four local pollen assemblage zones and four subzones (Figs. 11, 12, 13).

1. *Zone JL-1 (Picea pollen assemblage zone): 398–450 cm; ca. 9800–9500 BP.*—This pollen zone is restricted to the basal minerogenic sediments. It contains

high percentages of *Picea* pollen (up to 33%) (Fig. 12). Almost all is *P. glauca* type. Two subzones are delineated.

a) Subzone JL-1a, or the NAP subzone (415–450 cm), has relatively high percentages of non-arboreal pollen, including Cyperaceae (13%), *Artemisia* (8%), Tubuliflorae (4%), and *Pteridium* (7%), as well as having peaks in the pollen percentages of *Pinus banksiana/resinosa* (20–50%), *Quercus* (4–12%), and *Ulmus* (4–

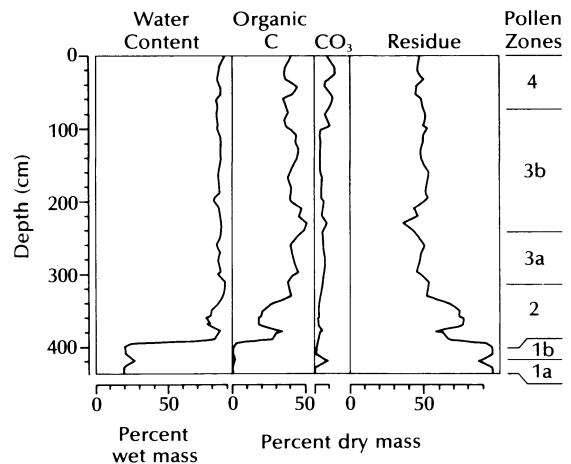


FIG. 10. Loss-on-ignition analysis of the sediments from Jack Lake. Water content is expressed as percent of wet mass; organic carbon (C), carbonates (CO₃) and residue contents are expressed as percent of dry mass.

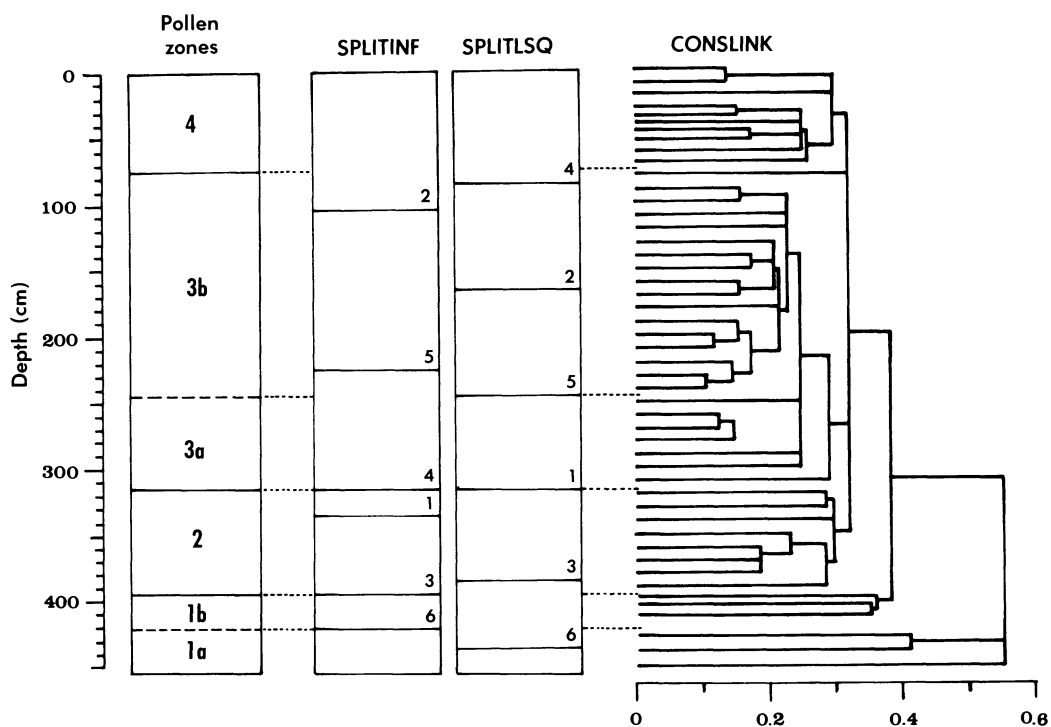


FIG. 11. Results of three numerical zonation procedures and their comparison with the pollen zones delineated for Jack Lake. The number above each division for SPLITINF and SPLITLSQ indicates the order of the numerically derived division (e.g., 1 = primary division, 2 = secondary division, etc.).

8%). Pollen concentrations are extremely low, only $0.3\text{--}0.6 \times 10^3$ grains/cm³.

b) Subzone JL-1b, or the *Populus-Larix* subzone (398–415 cm), has maximum pollen percentages of *Picea* (up to 33%), *Populus* (5–8%), and *Larix* (5%), but *Pinus banksiana/resinosa* pollen declines to <30%. Total pollen concentrations, $\approx 5.0 \times 10^3$ grains/cm³, are about an order of magnitude higher than in the underlying subzone.

2. Zone JL-2 (*Pinus banksiana/resinosa* pollen assemblage zone): 315–398 cm; 9500–7300 BP.—Total pollen concentration increases by almost two orders of magnitude across the boundary between pollen zones JL-1 and JL-2. Pollen influx values (Fig. 13) also exceed 10×10^3 grains·cm⁻²·yr⁻¹ in the organic sediments of zone JL-2. *P. banksiana/resinosa* pollen increases sharply to 30–54%, while *Picea* pollen declines to <10%. *Picea glauca* remains the predominant pollen type at the base of this zone, but the proportion of *P. mariana* type increases upward. *Betula* pollen percentages are generally high but variable (10–25%).

3. Zone JL-3 (*Pinus strobus* pollen assemblage zone): 75–315 cm; 7300–1400 BP.—This zone is characterized by high pollen percentages for *P. strobus* (10–50%) and Cupressaceae (3–12%). *P. banksiana/resinosa* pollen percentages decline sharply from a peak of >50% in the preceding zone to <20% here. Total pollen influx values also are highest, generally exceeding 20×10^3 grains·cm⁻²·yr⁻¹. It is divided into two subzones.

a) Subzone JL-3a (245–315 cm) contains maximum percentages of *P. strobus*, while *Betula* pollen declines to low percentages (10%). The pollen of *Alnus* cf. *rugosa* also increases distinctly.

b) Subzone JL-3b (75–245 cm) shows a steady decline in the *P. strobus* pollen curve, while pollen percentages of Cupressaceae, *Betula*, and *Picea* are increasing.

4. Zone JL-4 (*Pinus banksiana/resinosa-Betula* pollen assemblage zone): 0–75 cm; 1400–0 BP.—This zone contains higher percentages of *P. banksiana/resinosa* (20–35%) and *Picea* (5–13%) than the preceding zone. *Betula* pollen declines slightly but remains abundant ($\approx 25\%$). Despite some fluctuations, *P. strobus* percentages continue to decline to <10% at the top. Total pollen influx is reduced slightly in this zone.

Macrofossil stratigraphy.—The macrofossil record preserved in the sediments of Jack Lake is not as rich as that from Nina Lake (Fig. 14). The basal inorganic sediments in zone JL-1 are virtually devoid of macrofossils except for a few seeds of aquatic macrophytes and undifferentiated conifers. Macrofossils of *Larix*, *Picea*, and *Betula* begin to appear in abundance in zone JL-2, along with seeds of *Najas flexilis*, *Potamogeton*, *Carex*, and *Lycopus*. A needle of *Pinus banksiana* was found at the top of zone JL-2. Many needles and seeds of *Pinus strobus* are present in subzone JL-3a and the lower part of subzone JL-3b, but decrease sharply upward. Seeds of *Alnus crispa* and *Sagittaria* also begin

JACK LAKE

POLLEN PERCENTAGE DIAGRAM

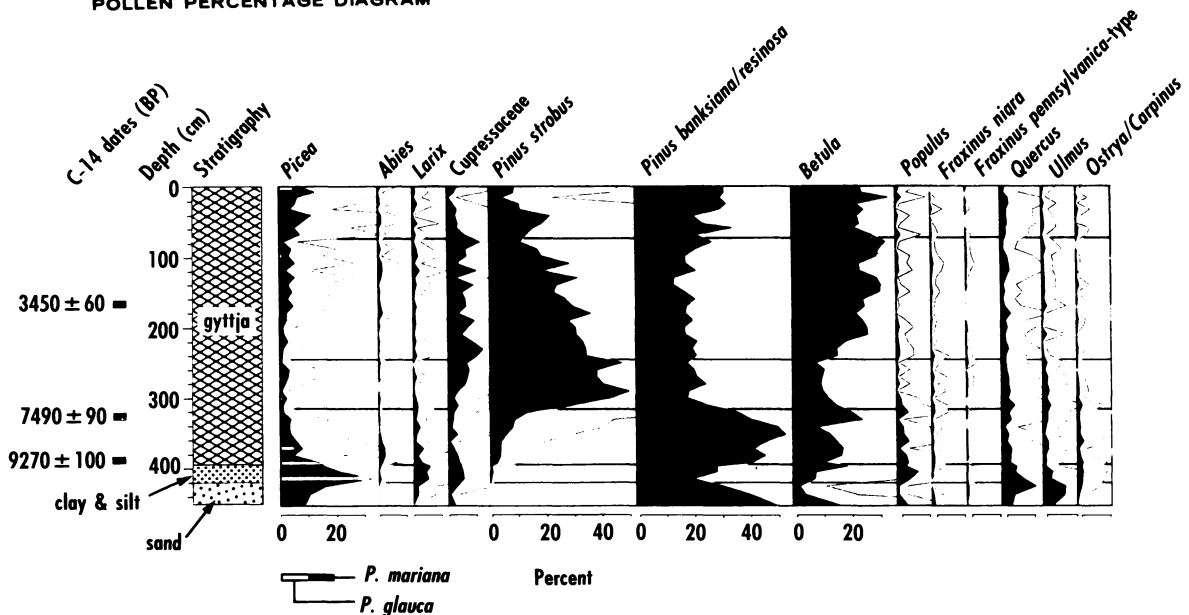


FIG. 12. Pollen percentage diagram for Jack Lake. The scale of the unshaded silhouettes is exaggerated by 5 ×.

JACK LAKE

POLLEN INFLUX DIAGRAM

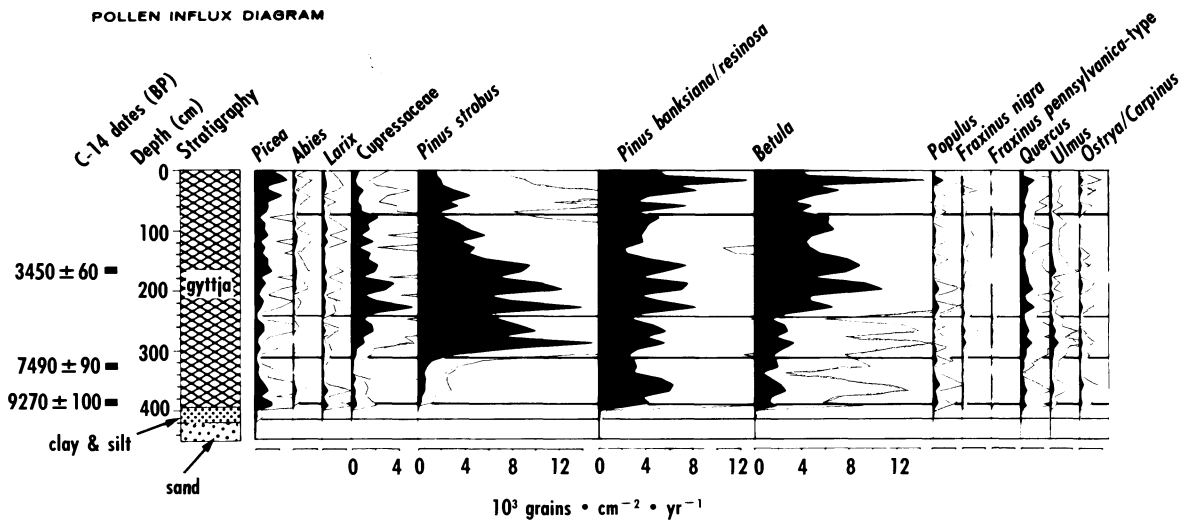


FIG. 13. Pollen influx diagram for Jack Lake. The scale of the unshaded silhouettes is exaggerated by 5 ×.

to appear in subzone JL-3a. *Picea*, *Larix*, and *Betula* macrofossils are least frequent in subzone JL-3a, but increase in subzone JL-3b. Zone JL-4 is characterized by the virtual absence of *P. strobus* macrofossils; otherwise it is broadly similar to zone JL-3.

Discriminant analysis.—VZIs of 4.0–3.0 and near-zero PMAs in zone JL-1 suggest that the early post-glacial vegetation around Jack Lake was a boreal forest or boreal woodland without modern analog (Liu and

Lam 1985) (Fig. 15). The no-analog interpretation is reinforced by an anomalous sample at 423 cm, which is classified as boreal forest but has tundra as its second most probable group (Liu and Lam 1985). PMAs rise to high values in zone JL-2, suggesting that the boreal forest became similar to the modern one in overall composition. A shift of VZIs from 3.0 to 2.0 across the boundary between zones JL-2 and JL-3 signifies the replacement of boreal forest by Great Lakes–St.

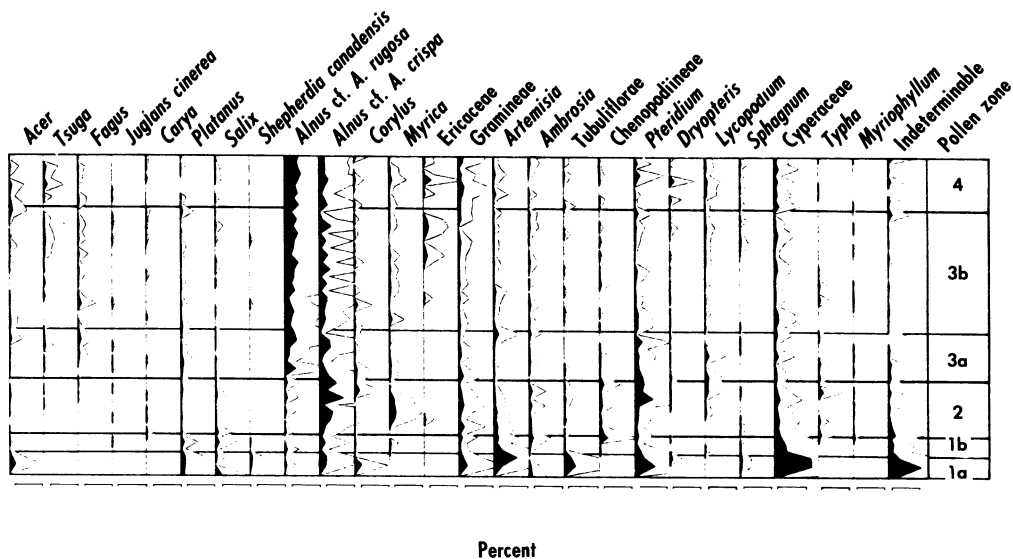


FIG. 12. Continued.

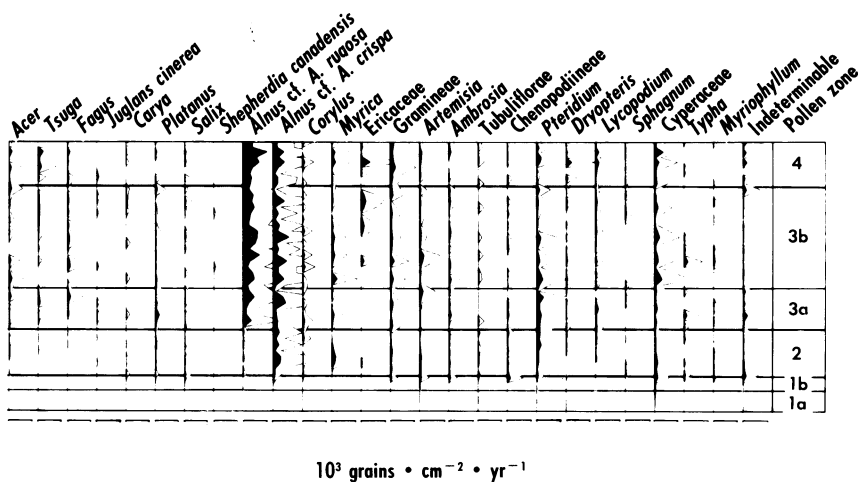


FIG. 13. Continued.

Lawrence forest. VZIs of 2.0–2.5, indicating Great Lakes–St. Lawrence forest, prevail in subzone JL-3a and the lower part of subzone JL-3b. The VZI reverts to 3.0 again at 120 cm (interpolated to 2600 BP), suggesting that boreal forest was reestablished as the ecotone retreated southward across Jack Lake. Fluctuating VZIs between 2.0 and 3.0 in the upper part of subzone JL-3b and in zone JL-4 are consistent with the transitional character of the modern vegetation around Jack

Lake near the boreal forest/Great Lakes–St. Lawrence forest ecotone (Liu and Lam 1985).

Lake Six

Lake Six (48°24' N, 81°19' W; elevation 305 m) is situated in Deloro Township ≈8 km south of Timmins. It is the lowest member of a group of eight small lakes draining into a tributary of the Mattagami River. The lake is roughly oval, ≈340 × 230 m, and has a

JACK LAKE MACROFOSSIL DIAGRAM

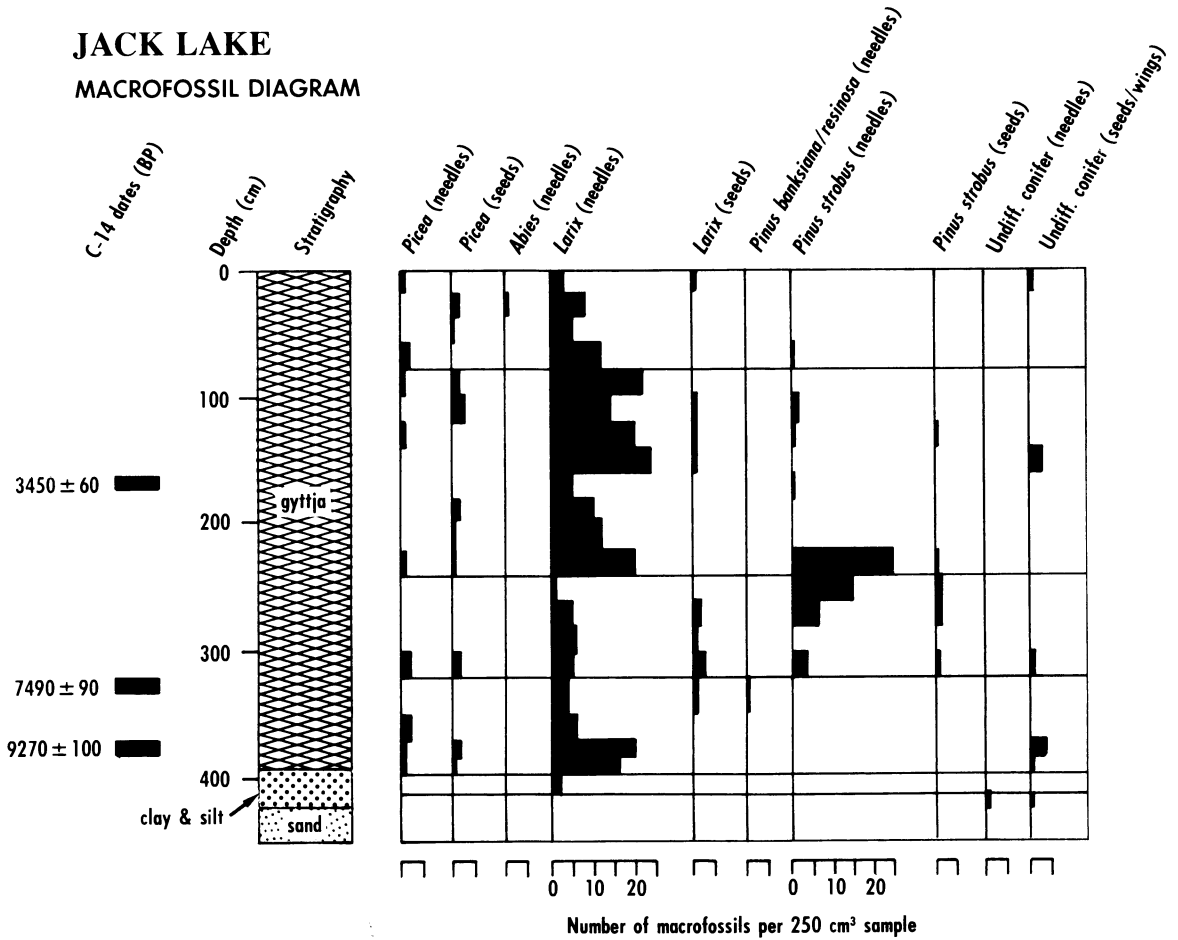


FIG. 14. Macrofossil diagram for Jack Lake.

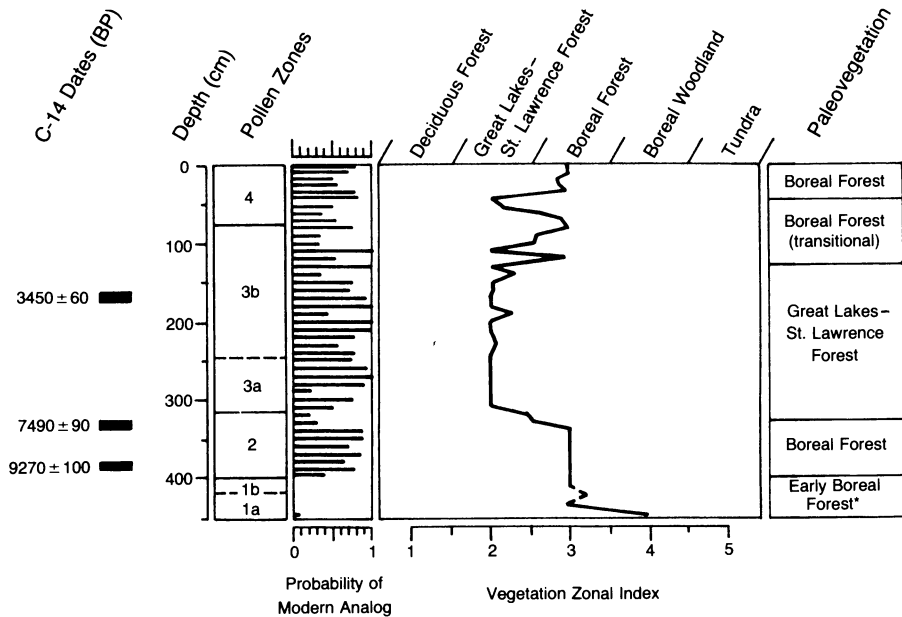


FIG. 15. Discriminant analysis results for the pollen stratigraphy from Jack Lake. Paleovegetation inferred to be without regional modern analog is marked with an asterisk (after Liu and Lam 1985).

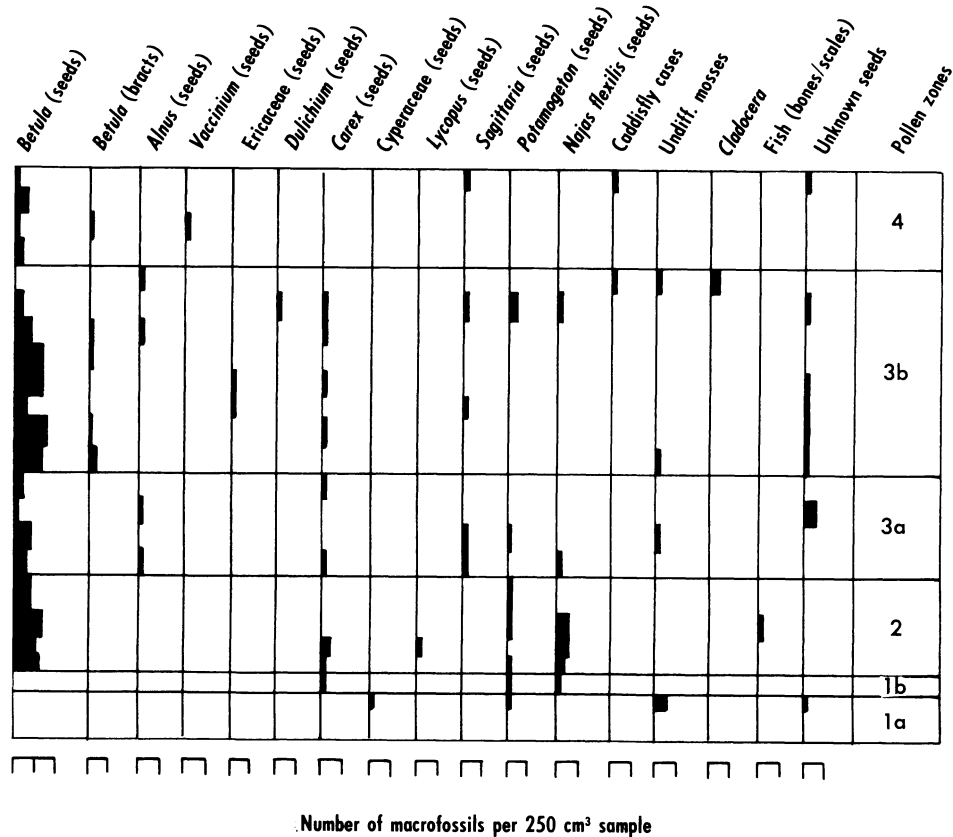


FIG. 14. Continued.

surface area of 6.0 ha. The deepest part is 12.8 m (unpublished limnological survey data, Ontario Ministry of Natural Resources). Physiographically Lake Six is situated near the southern edge of the Clay Belt lowlands, only 18 km north of the more rolling upland areas of the Canadian Shield. Locally the lake basin is developed on a sandy outwash plain amid Barlow-Ojibway lacustrine deposits. The outwash plain was formed by wave erosion of an esker system and re-deposition of the sands in the shallows along the south shore of the proglacial lake (Boissonneau 1966). The shape of the lake suggests that it might have originated as kettles in the esker.

Lake Six is situated near the transition between the Missinaibi-Cabonga section and the Northern Clay section of the boreal forest (Rowe 1972). The forest in the vicinity of Lake Six contains a mosaic of pure and mixed stands dominated by jack pine, aspen, and black spruce. Forests on sandy outwash and eskers are dominated by jack pine, but black spruce, aspen, and balsam poplar are more common in the surrounding lowlands of clayey substrates. Black spruce, often associated with tamarack or northern white cedar, is especially prominent in peatlands and along river valleys. White spruce, balsam fir, and white birch are only minor

components of the forests. Thermophilous tree communities are absent around the lake, but individual trees of white pine, red pine, red maple, green ash, and yellow birch were observed in a mesic forest stand developed on coarse till on the Canadian Shield upland only some 20 km to the south, probably one of the

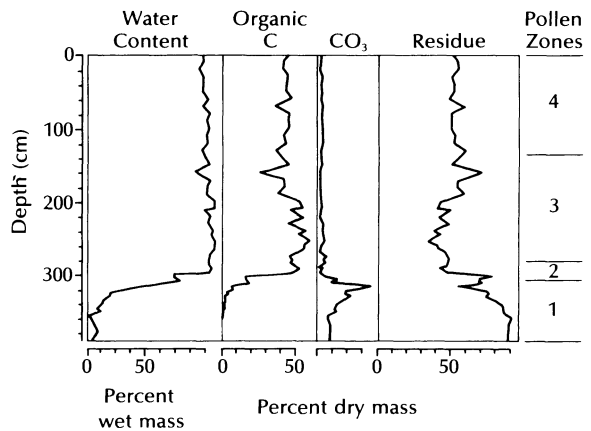


FIG. 16. Loss-on-ignition analysis of the sediments from Lake Six. Water content is expressed as percent of wet mass; organic carbon (C), carbonates (CO₃) and residue contents are expressed as percent of dry mass.

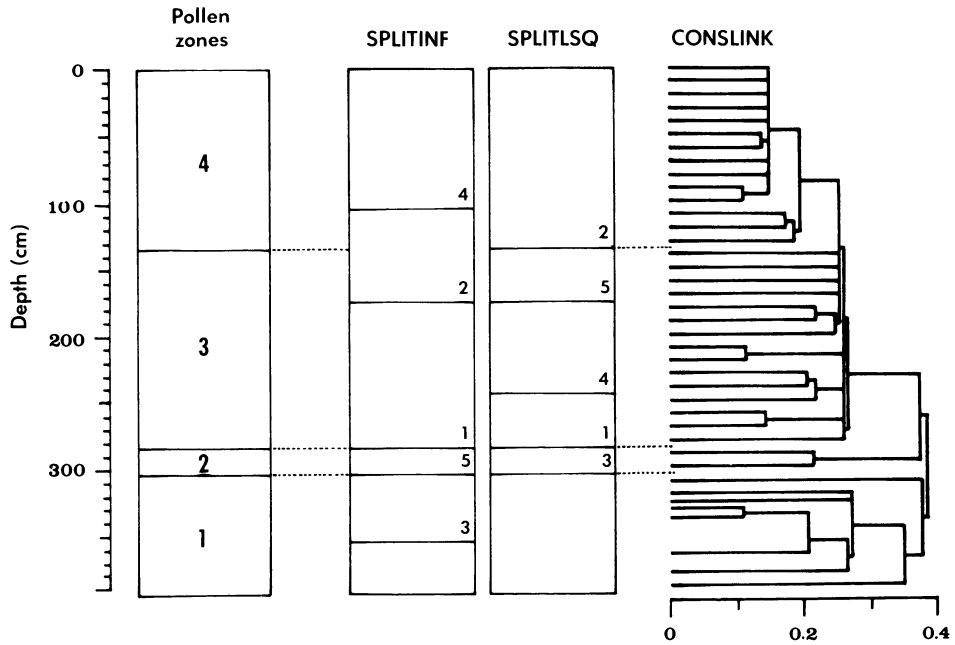


FIG. 17. Results of three numerical zonation procedures and their comparison with the pollen zones delineated for Lake Six. The number above each division for SPLITINF and SPLITLSQ indicates the order of the numerically derived division (e.g., 1 = primary division, 2 = secondary division, etc.).

northernmost locations in Ontario where these thermophilous species occur in association. Lake shore communities around Lake Six include *Salix* spp., *Alnus rugosa*, and *Myrica gale*. *Nuphar* is common in the littoral zone.

The 3.9-m core from Lake Six contains 315 cm of dark-brown gyttja overlying 75 cm of unlaminated sand, silt, and clay (Fig. 16). The basal inorganic sediments are calcareous, probably derived from outwash materials that surround the lake basin. They were probably

LAKE SIX
POLLEN PERCENTAGE DIAGRAM

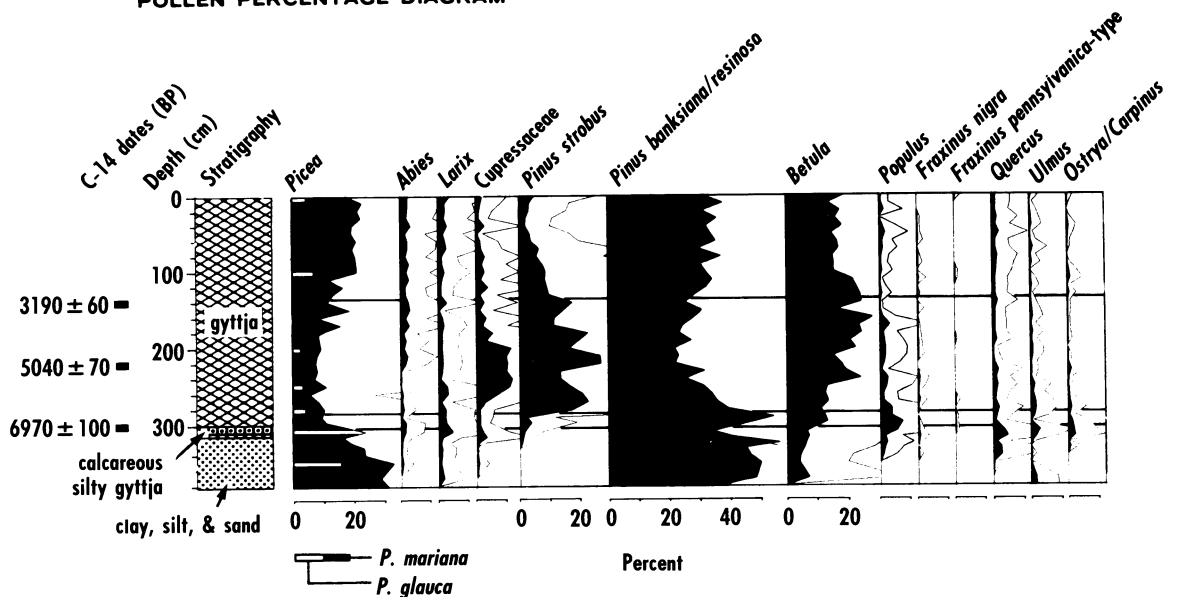


FIG. 18. Pollen percentage diagram for Lake Six. The scale of the unshaded silhouettes is exaggerated by 5×.

not deposited in the bottom of glacial Lake Ojibway. They are overlain conformably by calcareous silty gyttja (300–315 cm) that is transitional between the two depositional units. A C-14 date of 6970 ± 100 BP was obtained from above the calcareous silty gyttja (Table 1). The date is in agreement with basal dates of 6730 ± 200 BP and 6970 ± 310 BP obtained from peat stratigraphies from Drinkwater peat bog and Frederick House River bog in the same general vicinity within the Ojibway lacustrine clay plain (Ignatius 1956, Terasmae and Hughes 1960b). By extrapolating this date downward to the base of the calcareous silty gyttja, it is reasonable to infer that the lake basin was formed at least 7500 yr ago, shortly after the draining of Lake Ojibway. Sedimentation rates are fairly constant at about 0.04 cm/yr over the last 7000 yr (Table 1).

Pollen stratigraphy.—Four local pollen assemblage zones are recognized for Lake Six (Figs. 17, 18, 19).

1. **Zone LS-1** (*Picea*–*Pinus banksiana/resinosa* pollen assemblage zone): 300–380 cm; ca. 7500–7100 BP.—This zone includes both the basal inorganic sediments and the calcareous silty gyttja above them. Pollen concentrations are very low (≈ 250 grains/cm³) in the basal sand and silt, but increase to $>100 \times 10^3$ grains/cm³ in the overlying calcareous silty gyttja. The pollen assemblage is dominated by *Picea* (17–33%) and *Pinus banksiana/resinosa* (35–57%). In one sample from the basal inorganic sediments at 350 cm, the pollen of *Picea glauca* and *P. mariana* are almost equally represented. But in the calcareous silty gyttja, at 309 cm, 95% of the *Picea* pollen in the sample is classified by discriminant analysis to be *P. glauca*. Non-arboreal pollen and spore taxa such as Cyperaceae, Gramineae, *Artemisia*, *Ambrosia*, Tubuliflorae, Chenopodiineae, *Pteridium*, and *Sphagnum* occur at their maximum percentages in this zone. Pollen preservation is gen-

erally poor, as suggested by the large number of indeterminate grains.

2. **Zone LS-2** (*Pinus banksiana/resinosa*–*Populus pollen assemblage zone*): 285–300 cm; ca. 7100–6800 BP.—Total pollen influx continues to increase sharply to $>15 \times 10^3$ grains·cm⁻²·yr⁻¹ in this zone. Pollen percentages (Fig. 18) and influx rates (Fig. 19) for *Pinus banksiana/resinosa* (48–55%) and *Populus* (4–7%) reach their highest values. *Picea* pollen declines in percentages but its influx remains high. *P. glauca* and *P. mariana* types are equally represented.

3. **Zone LS-3** (*Pinus strobus*–*Betula*–*Cupressaceae pollen assemblage zone*): 135–285 cm; 6800–3100 BP.—*Pinus strobus* pollen increases sharply from 2% to $>20\%$ across the zone 2–3 boundary, and remains abundant ($>10\%$) in this zone despite some fluctuations. *Betula* pollen increases steadily from 11% to 29% at the top. The pollen of *Cupressaceae* is prominent (11%) in the middle of this zone, but falls to background values above the 200 cm level. Total pollen influx reaches maximum values, $\approx 15\text{--}25 \times 10^3$ grains·cm⁻²·yr⁻¹.

4. **Zone LS-4** (*Pinus banksiana/resinosa*–*Picea pollen assemblage zone*): 0–135 cm; 3100–0 BP.—This zone is marked by steadily increasing pollen percentages and influx values of *P. banksiana/resinosa* (29–38%) and *Picea* (12–23%); whereas *P. strobus* pollen drops from its mid-Holocene maximum to $<3\%$ near the top of the profile. *Betula* decreases slightly in relative and absolute frequencies but remains fairly abundant ($>15\%$). Total pollen influx also declines somewhat to $\approx 10\text{--}20 \times 10^3$ grains·cm⁻²·yr⁻¹.

Macrofossil stratigraphy.—Macrofossils are virtually absent in zone LS-1 except for a few seeds of *Betula*, *Larix*, *Sagittaria*, and *Potamogeton* near the top of the zone (Fig. 20). *Picea* needles occur most frequently in zone LS-2, along with macrofossils of *Larix*, *Betula*,

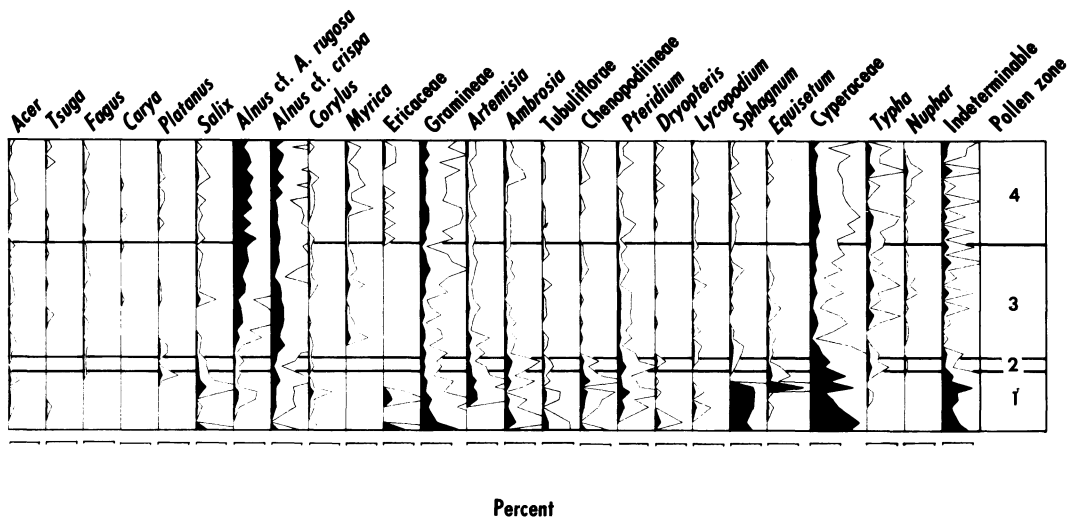


FIG. 18. Continued.

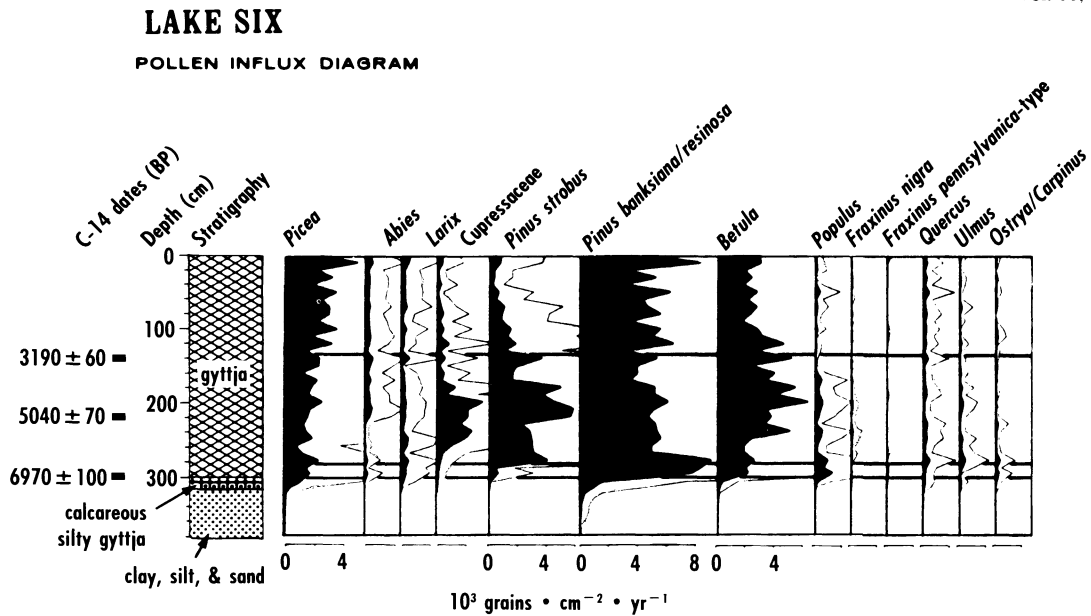


FIG. 19. Pollen influx diagram for Lake Six. The scale of the unshaded silhouettes is exaggerated by $5\times$.

Alnus crispa, and some aquatics. These taxa are also very common in zone LS-3. *Pinus banksiana* needles, notably absent in zone LS-2, are present in the lower part of zone LS-3. Also remarkable is the occurrence of *Pinus strobus* and *Thuja* seeds in the middle part of zone LS-3. Macrofossils of aquatic plants are well represented in zone LS-3, including *Najas flexilis*, *Sagittaria*, *Carex*, *Lycopus*, *Potamogeton*, *Myriophyllum*, *Polygonum*, and *Eleocharis*. Zone LS-4 can be distinguished from zone LS-3 by the absence of *Pinus strobus*, *P. banksiana*, *Thuja*, *Alnus crispa*, *Mentha*, and *Najas flexilis*, and the first appearance of *Myrica* and *Sparganium*.

Discriminant analysis.—The VZIs range from 4.0 at the lowermost level to ≈ 3.0 in the rest of zone LS-1, indicating transition from a brief phase of boreal woodland to a boreal forest (Fig. 21). PMAs are low (< 0.15) but significantly above 0, implying that the pollen assemblage is unlike that typical of the modern boreal forest. In zone LS-2, VZIs of 3.0 and high PMAs suggest a boreal forest with modern analog. The VZIs are at or slightly below 3.0 in most of zone LS-3, indicating a boreal forest of transitional character. At several levels (270–280 cm, 180–190 cm, 140 cm) the VZIs drop to ≤ 2.5 , suggesting encroachment upon the boreal forest by Great Lakes–St. Lawrence forest. However, the inconsistent occurrence of these lower values implies that Great Lakes–St. Lawrence forest was probably never fully developed around Lake Six. VZIs of 3.0 coupled with high PMAs throughout zone LS-4 indicate the establishment of a stable, modern boreal forest.

DISCUSSION

Regional overview

To provide a regional perspective, the three local pollen stratigraphies from Nina Lake, Jack Lake, and Lake Six are correlated schematically in Fig. 22. Despite latitudinal and site-specific differences, the three pollen stratigraphies have some features in common. All three start with a basal pollen zone wholly or partly dominated by *Picea glauca* pollen (zone 1), although the base of the Lake Six stratigraphy is younger than the other two by 2000 yr. *Picea* is clearly the predominant pollen type in the basal zones of Nina Lake and Jack Lake, but it co-dominates with *Pinus banksiana/resinosa* pollen in Lake Six. The basal *Picea* zone is succeeded by a *Pinus banksiana/resinosa* pollen zone (zone 2) in all three pollen records, but *Populus* pollen is more frequent in the Clay Belt site (Lake Six) than at the two upland sites. The overlying *Pinus strobus* zone (zone 3) is the most important pollen zone that differentiates the three sites. The base of this zone is generally time transgressive, being older at Nina Lake (7400 BP) and Jack Lake (7300 BP) than at Lake Six (ca. 6800 BP). Distinctive facies change also occurs within this zone along the transect. *P. strobus* pollen occurs at up to 50% at Nina Lake and Jack Lake. It is more subdued at Lake Six ($< 30\%$) and becomes co-dominant with *Betula* and Cupressaceae pollen. The facies change mimicks the modern vegetation gradient between the northern and southern sites. The upper boundary of this zone is also time transgressive. At

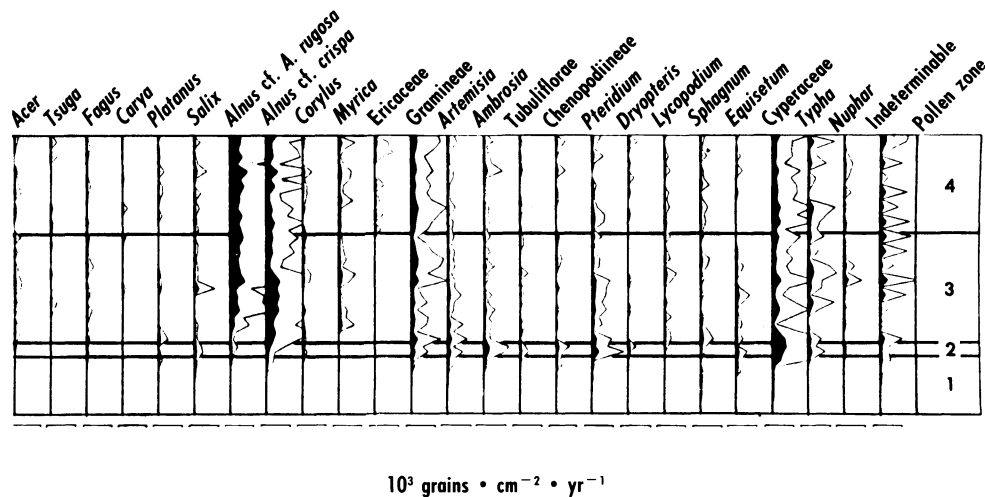


FIG. 19. Continued.

Nina Lake it extends to the top of the sequence. It is replaced at 1400 BP by a *Pinus banksiana/resinosa*–*Betula* pollen zone (zone 4) at Jack Lake, and at 3100 BP by a *P. banksiana/resinosa*–*Picea* zone at Lake Six. Thus the *P. strobus*-dominated pollen zone (zone 3) becomes stratigraphically more compressed from south to north. The time-transgressiveness of the upper and lower zone boundaries is a function of the Hypsithermal northward migration of white pine and its subsequent southward retreat in response to Neoglacial cooling.

The detailed vegetational reconstruction at each site is presented below. The local vegetation histories are synthesized into regional patterns of postglacial vegetational changes in northern Ontario (Fig. 23). These regional patterns will be discussed in the light of several paleoecological problems for the boreal forest and Great Lakes–St. Lawrence forest.

Vegetation history at Nina Lake

Delayed organic deposition in Nina Lake does not permit independent testing of Saarnisto's (1974) postulation that a narrow belt of tundra existed south of the ice front during the Algonquin Stadial (ca. 11 000–10 100 BP). The regional vegetation represented by pollen zone NL-1 (Figs. 6 and 7) is a white spruce-dominated boreal forest that lacks modern analog. Subzones NL-1a and NL-1b probably record primary succession around Nina Lake following lake basin formation. During the time of subzone NL-1a, an open community of pioneer herbs and shrubs (e.g., *Arte-*

misia, Gramineae, *Salix*) developed on the unstable slopes of the newly formed lake basin. The *Pinus banksiana/resinosa* pollen in this subzone are probably overrepresented from regional sources due to very low pollen production from the local vegetation.

The Cupressaceae pollen in subzone NL-1b probably comes from *Juniperus* rather than *Thuja*. *Thuja occidentalis* (the only *Thuja* species in eastern North America) is a long-lived, slow-growing tree that is very shade tolerant; it is not a typical species of early succession (Fowells 1965). *Juniperus* is represented in northern Ontario by two species, *J. communis* and *J. horizontalis*. The main range of *J. horizontalis* occurs north of Nina Lake today (Little 1971), although it is possible that it occurred in the region during the early Holocene. *J. communis*, the more likely candidate, is a heliophytic low shrub that is often a successful pioneer of open slopes and old fields; it cannot compete with other trees and shrubs under closed canopy. Prominent Cupressaceae pollen peaks have also been reported from the late-glacial and early postglacial sediments of Lake Louis (Vincent 1973) and several other lakes in Quebec and Ontario (Richard 1977, McAndrews 1981, McAndrews et al. 1982), and in most cases have been interpreted to represent *Juniperus*. Subzone NL-1b thus likely reflects succession to a heliophytic community dominated by juniper shrubs, along with soapberry (*Shepherdia canadensis*) and willow.

Total pollen influx values of $< 10 \times 10^3$ grains · cm⁻² · yr⁻¹ in subzone NL-1c suggest an open spruce forest around Nina Lake ca. 9500–9200 yr ago. The rarity of

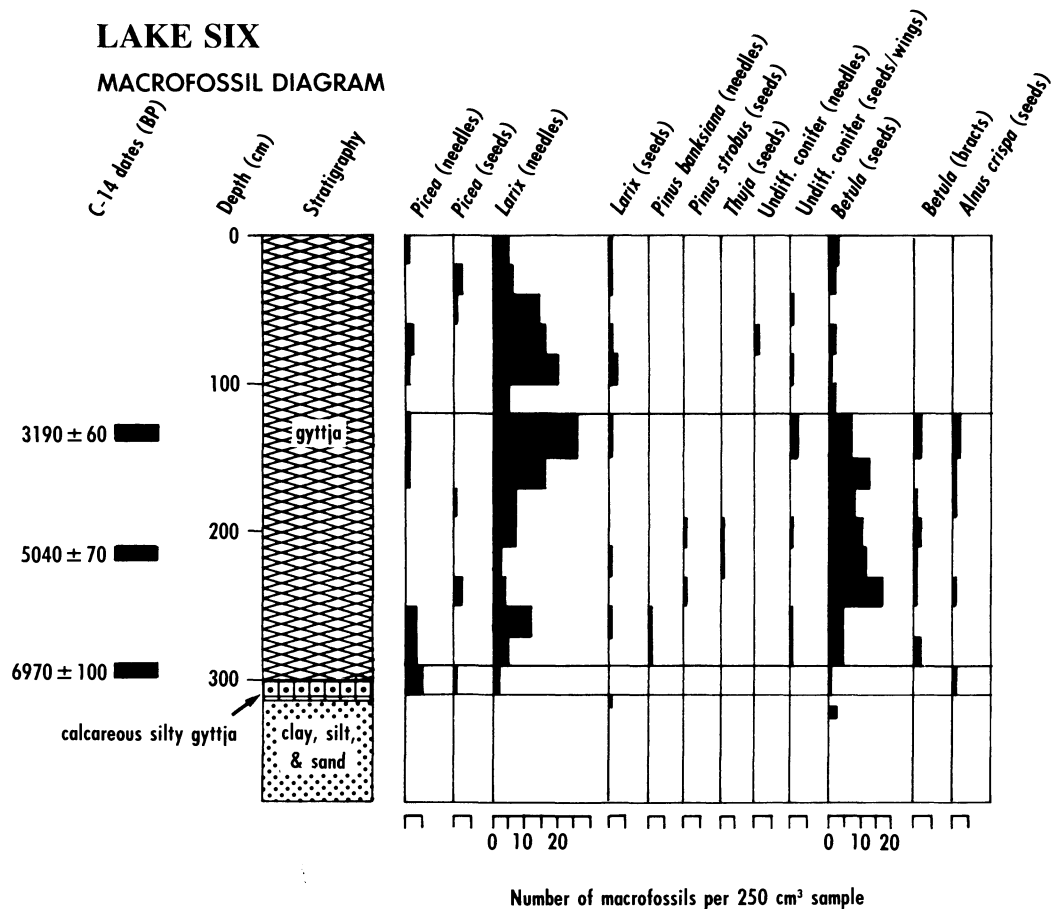


FIG. 20. Macrofossil diagram for Lake Six.

Picea macrofossils in the sediments implies locally small populations. White spruce was the predominant spruce species present; black spruce was either absent or occurred only in insignificant numbers. Jack pine, aspen (*P. tremuloides*), and balsam poplar (*P. balsamifera*) were present and might have been locally common. *Myrica* had already migrated to the site by 9500 BP and rapidly increased in lowland habitats.

Pollen percentages and pollen influx values of some thermophilous hardwoods (*Quercus*, *Ulmus*, *Ostrya/Carpinus*) in subzone NL-1c are sufficiently high to suggest their presence around Nina Lake after 9500 BP. Although the ranges of several species of oak (*Q. rubra*, *Q. macrocarpa*) and elm (*U. americana*, *U. rubra*) extend into the southern part of the boreal forest today (Little 1971), their pollen rarely exceeds 3% in surface samples from the boreal forest of northern Ontario (Liu 1982), much lower than their fossil abundance (up to 12.5% for *Quercus* and 5.9% for *Ulmus*) in subzone NL-1c. The admixtures of thermophilous and boreal forest taxa in the early Holocene vegetation of Nina Lake, a situation without modern analog (as confirmed by PMAs of 0) (Fig. 9), can be explained by a unique combination of climatic and edaphic conditions in front of the Laurentide ice sheet. At 9500 BP

the Laurentide ice front was situated ≈ 100 km north of Nina Lake (Denton and Hughes 1981, Teller 1987). The region of Nina Lake would have been subjected to easterly or northeasterly, anticyclonic wind descending from the ice dome (Kutzbach and Guetter 1986), resulting in a periglacial climate characterized by milder and drier winters and cooler, windier summers than those of the present (Amundson and Wright 1979). In addition, the fresh, base-rich soils newly developed on glacial tills would have been favorable to the growth of thermophilous hardwoods in a predominantly boreal forest.

Betula, probably representing white birch (*B. papyrifera*), increased in abundance during the next 300 yr (ca. 9200–8900 BP; subzone NL-1d). The boreal forest became denser in structure, but white spruce remained dominant.

A closed boreal forest dominated by jack pine, along with spruce, birch, and poplar, prevailed during the time of zone NL-2. Macrofossil evidence suggests that the increase in *Pinus banksiana/resinosa* pollen after 8900 BP is due to the expansion of jack pine rather than red pine. The replacement of white spruce by jack pine was probably caused by a warmer climate. Black spruce also began to occur in lowland habitats. With

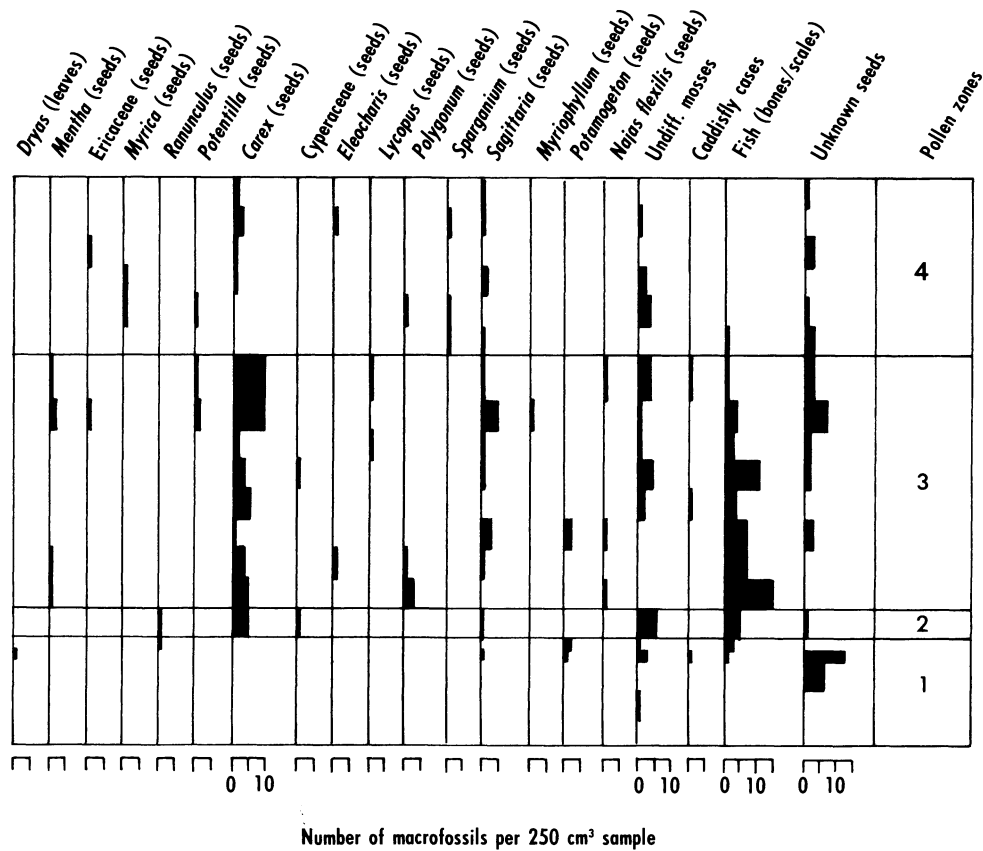


FIG. 20. Continued.

the immigration of *Alnus crispa* around 8600 BP, the boreal forest was essentially similar to the modern one in floristic composition.

The dramatic increase of *P. strobus* pollen at 7400 BP signifies the immigration of white pine to northern Ontario. Once arrived, it vigorously replaced the boreal forest species such as jack pine, spruce, and white birch. Macrofossil evidence suggests that red pine probably arrived at Nina Lake at about the same time. The pollen of *Fagus* and *Tsuga* began to occur consistently at the bottom of zone NL-3 at 0.5% to 1% (Fig. 6), generally exceeding the criterion values determined by Davis et al. (1986) to suggest the local presence of these trees. The presence of *Tsuga* is confirmed by the discovery of a seed at the top of zone NL-2 (Fig. 8). Pollen influx values of $\approx 100\text{--}200$ grains $\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$ for both *Fagus* and *Tsuga* also support that these thermophilous trees migrated to Nina Lake at 7400 BP or shortly thereafter.

The immigration and proliferation of white pine, red pine, hemlock, and beech around 7400 BP effectively transformed the boreal forest into Great Lakes–St. Lawrence forest (Fig. 9). Between 7400 and 4000 BP (subzone NL-3a), white pine proliferated at Nina Lake at maximum population densities due to a warmer

climate. *Betula* pollen also began to increase in the middle of subzone NL-3a, around 6000 BP. Although size statistics on the *Betula* pollen are not available for species determination, it is speculated that at least part of the increase might be due to yellow birch (*B. alleghaniensis*), a thermophilous species. At the same time, northern white cedar became more common, as can be inferred from an increase in Cupressaceae pollen and the presence of *Thuja occidentalis* macrofossils.

Palynological changes in subzone NL-3b record Neoglacial cooling after the Hypsithermal. The trend for *P. strobus* pollen influx percentages is reversed after 4000 BP. Although *P. strobus* pollen influx remains high in the lower part of this subzone, the steady increase in *Picea*, *Pinus banksiana/resinosa*, and *Betula* pollen after 4000 BP signifies an expansion of boreal elements in the forest in response to climatic cooling. *P. strobus* pollen influx declines sharply after ca. 2500 BP. But despite these changes in forest composition, the ecotone has remained north of Nina Lake throughout the last 7400 yr (Fig. 23).

Both white spruce and black spruce were involved in the late-Holocene increase in *Picea* pollen. Wetlands became more widespread, as suggested by the distinct increase in the macrofossil abundance of *Larix*, a typ-

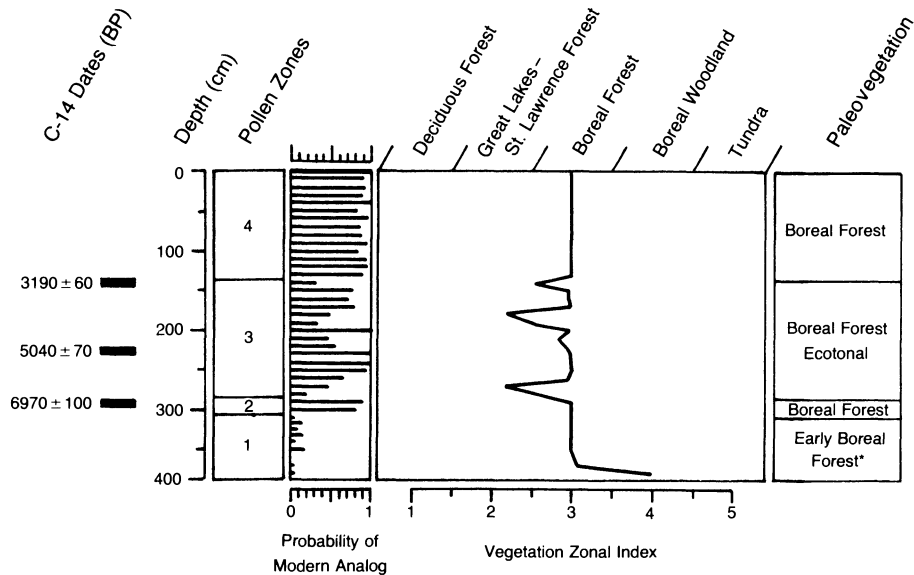


FIG. 21. Discriminant analysis results for the pollen stratigraphy from Lake Six. Paleovegetation inferred to be without regional modern analog is marked with an asterisk.

ical species of ombrotrophic bogs. The greater abundance of *Vaccinium*, *Ericaceae*, and *Chamaedaphne*, all acidophilous shrubs, in the macrofossil record corresponding to subzone NL-3b, suggests that soil leaching and paludification might have contributed to the landscape and vegetation changes in the late-Holocene.

The vegetation of the Sudbury area was profoundly disturbed by human activities, particularly the development of mining and smelting industries, over the last 150 yr (Huhn 1974). This disturbance has favored the spread of ragweed (*Ambrosia*), the tolerant hardwoods such as aspen and white birch, and the fire-adapted jack pine, while white pine was diminished due to logging and pollution. The *Ambrosia* rise in subzone NL-3c is more subdued than at sites in southern Ontario where the population densities of ragweed are much higher (Bassett and Terasmae 1962, McAndrews 1981).

Vegetation history at Jack Lake

The postglacial vegetation history of Jack Lake generally parallels that of Nina Lake despite differences in details. The local vegetation in zone JL-1a (Figs. 12 and 13) probably consisted of an open community of pioneer herbs and shrubs on the unstable slopes around Jack Lake, with white spruce and some jack pine trees in the distant uplands. It is likely that oak and elm were significant components of the regional spruce-dominated boreal forest, although their local presence at Jack Lake cannot be positively determined, due to low pollen concentrations in the basal inorganic sediments. Alternatively, these pollen grains, many of them badly degraded, could have been recycled from older deposits or from melting ice blocks (McAndrews 1984); or they could have been blown in from the south due to long-distance transport. The abundance of *Pteridi-*

um spores in subzone JL-1a seems to imply that the pollen assemblage might have been distorted by processes of differential pollen transport and preservation that typically occur in periglacial environments today (Funder and Abrahamsen 1988).

The pollen spectra in subzone JL-1b suggest increasing tree cover. The local vegetation was probably an open woodland dominated by white spruce, tamarack, and poplar, with heliophytic shrubs such as *Juniperus* and *Shepherdia canadensis* occupying the openings. The tamarack trees in this subzone probably represent upland populations that colonized the newly deglaciated landscape. The absence of black spruce also implies limited wetland development at this time. Near-zero PMAs for the whole of zone JL-1 (Fig. 15) imply that the pollen assemblage does not resemble the typical palynological signature of the regional boreal forest existing in northern Ontario today. But on a more limited scale, the vegetation was probably analogous to the white spruce-tamarack association, an edaphic climax, that exists on the recent alluvial flats of northern Manitoba (Ritchie 1957) (discussed in Paleocology of the Early Postglacial White Spruce-dominated Boreal Forest, below).

By the time organic sedimentation began in Jack Lake ca. 9500 yr ago, the climate had already become too warm for the regional spruce forest to persist. A closed boreal forest dominated by jack pine, similar in composition to the present one, ensued (zone JL-2; 9500–7300 BP). Initially white spruce, balsam fir, and tamarack remained common, but after ca. 8500 BP they, too, became scarce. White birch was an important component throughout this period. Black spruce began to appear in quantities after ca. 8900 BP, probably a function of soil development. *Alnus crispa* probably immigrated to Jack Lake around this time, although

its arrival time cannot be more precisely determined because its pollen percentage record was probably masked by long-distance transport in pollen zone JL-1. *Myrica* was also present after 9200 BP.

The boreal forest at Jack Lake was transformed into a Great Lakes–St. Lawrence forest when white pine immigrated ca. 7300 yr ago and proliferated until 5500 BP (subzone JL-3a). *Alnus rugosa* probably arrived at about the same time. The increase in Cupressaceae pollen in subzone JL-3a is interpreted to suggest an expansion of *Thuja* after ca. 6500 BP (discussed in Hypsithermal *Thuja* expansion in the Clay Belt, below). The history of hemlock and beech is less clearly interpretable in the pollen record. The pollen of both species began to occur more or less consistently at the bottom of zone JL-3a, though generally at <0.5% and with influx values of <150 grains·cm⁻²·yr⁻¹ (Figs. 12 and 13). These values are only marginal to establish their presence locally at Jack Lake some 7000 yr ago (Davis et al. 1986). Today Jack Lake lies outside the northern limits for both hemlock and beech (Little 1971). It is likely that their pollen in zone JL-3 was blown in from marginal, scattered populations that were already present near Nina Lake around this time.

Both pollen and macrofossil data suggest that *Betula* increased significantly during 5500–1400 BP (subzone JL-3b), replacing white pine in the mixed forest. It is not certain which species of birch was involved. The gradual increase in spruce pollen and tamarack macrofossils since 5500 BP signals return to a cooler climate after the Hypsithermal. White pine remained fairly

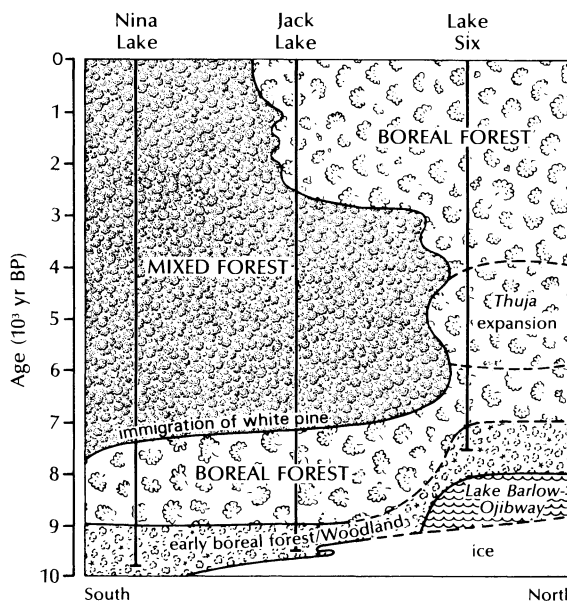


FIG. 23. A temporal-spatial reconstruction of the regional vegetation history of northern Ontario.

common initially, but the sharp decrease in *P. strobus* pollen influx after ca. 3300 BP represents a major contraction of its populations in response to climatic cooling. The cooler climate was also detrimental to the growth of northern white cedar, which became less common after 1400 BP. By the time of zone JL-4, spruce and jack pine had replaced the more thermophilous elements, to the extent that boreal forest was re-established around Jack Lake. Discriminant analysis suggests that the Great Lakes–St. Lawrence forest changed to boreal forest ca. 2600 yr ago (Fig. 15), as the ecotone retreated southward across Jack Lake from its mid-Holocene position. The boreal forest was firmly in place during the last millennium.

Unlike the case of Nina Lake, an *Ambrosia* rise is not evident at the top of the pollen diagram for Jack Lake. Ragweeds are rare or absent near Jack Lake today (Bassett and Terasmae 1962), where the forest remains relatively undisturbed by human activities.

Vegetation history at Lake Six

The postglacial vegetation history of Lake Six differs significantly from those of Nina Lake and Jack Lake in details due to its more northerly location and landform-edaphic contrasts. The formation of Lake Six was delayed until Lake Ojibway was drained, some 7500 yr ago. Zone LS-1 represents the initial phase of lake basin formation, when slope-wash was active and organic productivity in the lake was low. The low pollen-concentration values (Figs. 18 and 19) and the virtual absence of macrofossils (Fig. 20) suggest that the immediate surroundings of the lake basin were sparsely vegetated, and the pollen was probably derived from regional sources. The pollen assemblage thus reflects a regional boreal forest dominated by spruce and jack

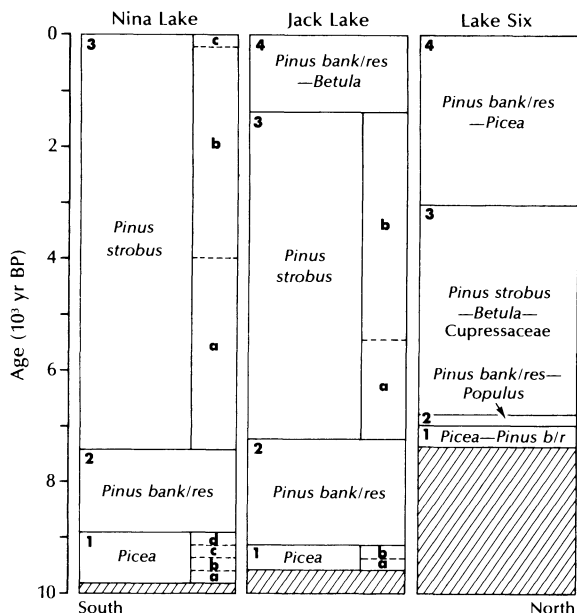


FIG. 22. Relationship of the pollen stratigraphies from Nina Lake, Jack Lake, and Lake Six plotted against time (sediment age). Numbers and small letters within pollen zones denote zone numbers and subzones. Hatched area at the bottom of each stratigraphy denotes time interval beyond the maximum age of the sediment core. *Pinus bank/res* or *Pinus b/r* = *Pinus banksiana/resinosa*.

pine, similar to what Richard (1980) reconstructed for the Barlow–Ojibway lowlands in adjacent Quebec during that period. Both white spruce and black spruce were present in the regional vegetation. Aspen and balsam poplar were probably as common 7000 yr ago as they are in the boreal forest today; the absence of *Populus* pollen in the lower part of zone LS-1 is probably due to its poor preservation in the basal inorganic sediments (Lichti-Federovich and Ritchie 1968).

Given the predominantly “regional” character of the arboreal pollen deposited in the basal inorganic sediments, the high percentages of *Sphagnum* spores in this zone are intriguing. *Sphagnum* moss is most common on wet, acidic, and nutrient-poor substrates, particularly ombrotrophic peatlands, and is usually absent or rare in the early stages of primary succession (Birks 1980a). Its spores, however, have been reported to occur at high percentages in basal lake sediments of Pleistocene to Holocene age from the Canadian Arctic (Rampton 1971, Birks 1980a, McAndrews et al. 1982). Birks (1980a) and Rampton (1971) attributed the abundance of *Sphagnum* spores in the basal sediments of Gull Lake and Antifreeze Pond to redeposition from older deposits. McAndrews (1984) has also found *Sphagnum* spores in meltwater samples from the Devon Ice Cap in northern Canada, thus implying that they might be incorporated in proglacial lake sediments at the time of deglaciation. These interpretations might be applicable to explain the abundance of *Sphagnum* spores in the basal sediments of Lake Six. However, the relatively good preservation conditions of these spores in zone LS-1 suggest that they may be contemporaneous with the sediments. An alternative explanation is that they were brought in by rivers draining the areas south of Lake Six. It has been reported that cryptogam spores are significant components of fluvial pollen transport (Peck 1973). This interpretation, if correct, thus implies that wetland communities, such as black spruce–*Sphagnum* moss muskegs, were already present in the southern part of the Clay Belt prior to 7000 BP.

Pollen and sedimentological changes in the upper part of zone LS-1 provide a good record of the “afforestation phase” (Richard 1977) in the early vegetational history of Lake Six. Pollen concentrations increase by about an order of magnitude as the sediment changes from inorganic clay to calcareous silty gyttja. These changes suggest that the lake basin had begun to stabilize, increasing the organic productivity in the lake itself, and permitting trees to colonize the immediate vicinity of the lake basin. The most significant change occurs in the pollen curve for *Picea*. Accompanying an almost 10-fold increase in spruce pollen influx is a dramatic shift in species ratio from a mixture of *P. glauca* and *P. mariana* to nearly complete dominance by *P. glauca* pollen. This indicates that the basin surroundings were colonized by white spruce, whose pollen thus drowned out the “background” input of black spruce pollen derived from regional sources, thereby

contributing primarily to the increased *Picea* pollen influx at the top of zone LS-1. The sharp decline in *Pinus banksiana/resinosa* pollen percentages at these levels, despite the continually increasing influx of this pollen type, is likewise due to the fact that the regionally derived jack pine pollen was overshadowed by the white spruce pollen derived from local sources.

This early successional white spruce-dominated forest that existed ca. 7100 yr ago was still very open, as indicated by total pollen influx values of 4.2×10^3 grains·cm⁻²·yr⁻¹ calculated from a sedimentation rate extrapolated from that of the immediately overlying sediments. The moderate pollen peaks for heliophytic herbs and shrubs such as *Artemisia*, *Salix*, and Cupressaceae (probably representing *Juniperus*) also attest to abundant forest openings.

The low PMAs (Fig. 21) for zone LS-1 are probably attributed to relatively high percentages of NAP and thermophilous hardwoods. Much of the *Quercus*, *Ulmus*, and *Ostrya/Carpinus* pollen was probably redeposited or derived from long-distance transport.

The afforestation phase at Lake Six lasted only a few hundred years. During the time of zone LS-2 (7100–6800 BP), a closed boreal forest dominated by jack pine and spruce, similar to the modern one, prevailed around Lake Six. Jack pine probably expanded from populations already present in the region, and simply filled the openings in the boreal forest. Despite the decline in *Picea* pollen percentages, macrofossil and pollen influx data suggest that spruce continued to increase in abundance. Changes in *P. glauca/P. mariana* pollen ratios suggest that black spruce began to grow, together with white spruce, around Lake Six after 7000 BP, probably as a result of soil development. This coincides with a change in the sediment from calcareous silty gyttja to gyttja, indicating leaching of the soluble nutrients from the fresh soil. Balsam poplar, aspen, balsam fir, and tamarack were all important components of this closed boreal forest. *Alnus crispa* probably immigrated to Lake Six at this time.

Two major vegetational changes occurred during the mid-Holocene—the arrival of white pine at ca. 6800 BP and the increase in *Thuja* during 6000–4500 BP. The local presence of white pine is confirmed by macrofossil as well as pollen influx data ($2\text{--}6 \times 10^3$ grains·cm⁻²·yr⁻¹) (Figs. 19 and 20). White pine is absent in the vicinity of Lake Six today, but during the mid-Holocene scattered populations must have grown on the surrounding sandy outwash plains due to a warmer climate and favorable soil conditions. That the dramatic increase in Cupressaceae pollen is attributable to *Thuja* rather than *Juniperus* is supported by the occurrence of two fossil seeds of the former species. It probably reflects expansion of *Thuja* populations in the wetlands in response to climatic and hydrological changes during the Hypsithermal (discussed in Hypsithermal *Thuja* Expansion in the Clay Belt, below).

With greater abundance of white pine in the uplands and the proliferation of northern white cedar in the

lowlands, the vegetation around Lake Six was at its maximum diversity during 6800–3100 BP (zone LS-3). *Myrica* and *Alnus rugosa* immigrated to the area about ca. 6500 yr ago. However, boreal conifers such as spruce, jack pine, and tamarack continued to be common and locally predominant, as were white birch, aspen, and balsam poplar. Discriminant analysis suggests that the forest around Lake Six remained predominantly boreal in character (Fig. 21), perhaps broadly similar to the southern part of the boreal forest today. It is likely that the ecotone was positioned along the physiographic boundary between the Clay Belt and the Canadian Shield upland, only some 20 km to the south.

The long-term trend of Neoglacial cooling had already started even before the time of zone LS-4. The slight but distinct increase in *Abies* pollen ca. 5000 yr ago perhaps signals the onset of a climatic change toward cooler and moister conditions. Spruce and jack pine also increased steadily after ca. 4500 BP. *P. strobus* pollen influx declined abruptly after 4000 BP; it never regained its former abundance after another crash at 3100 BP. Since then the continuous range of white pine has probably contracted south of Lake Six, although relict populations still exist in suitable sites in the Clay Belt today (Horton and Bedell 1960).

Significant vegetational changes also occurred in the wetland habitats during the mid- and late-Holocene. Muskegs were already widespread by 6800 BP, if not much earlier, as suggested by substantial increases in the *P. mariana*/*P. glauca* pollen ratio, as well as the abundance of *Larix* macrofossils thereafter. During the mid-Holocene large populations of *Thuja* grew in the wetlands. The lake itself supported a diverse aquatic flora that included *Carex*, *Typha*, *Sagittaria*, *Equisetum*, *Potamogeton*, *Myriophyllum*, *Lycopus*, *Eleocharis*, *Nuphar*, and *Najas flexilis*. Neoglacial cooling decimated the *Thuja* populations after 4500 BP, which were replaced by black spruce and tamarack in the muskegs, and by *Alnus rugosa* in riparian habitats and along lake and bog margins. Coupled with climatic cooling, paludification could also have contributed to the demise of northern white cedar in the late-Holocene. Perhaps after a long period of leaching during the mid-Holocene, the soil had become increasingly depleted of soluble bases, and organic matter had gradually built up in the extensive lowlands in the Clay Belt. As a result, lake and bog waters could have become more acidic and oligotrophic. Decreasing loss-on-ignition values and reduced total pollen influx in the sediments of zone LS-4 attest to lowered biological productivity in the lake itself and in the surrounding forests during the last 3100 yr.

Paleoecology of the early postglacial white spruce-dominated boreal forest

Ecologically the most significant feature of the early postglacial boreal forest was the predominance of white spruce; black spruce was either absent or rare. This

differs significantly from the situation in the modern boreal forest and boreal woodland, where the two spruce species coexist. On a continental scale, the ranges of white spruce and black spruce virtually overlap (Fowells 1965). Within their ranges, white spruce is generally more abundant in the south (e.g., in the Great Lakes–St. Lawrence forest) where it competes successfully with thermophilous hardwoods in fresh, upland sites (Hills 1959), although it is also often the species that forms the northern tree line and penetrates into the tundra along river valleys and on calcareous soils (Hustich 1953, Drew and Shanks 1965). In northern Ontario, black spruce is considerably more abundant than white spruce in the Clay Belt and in the Hudson Bay Lowland (Ketcheson and Jeglum 1972), where edaphic factors favor the former.

Ecologically these two species occupy different niches. White spruce is essentially an upland species, preferring fresh, loamy soils, and is intolerant of fire or water-logged conditions. Black spruce is adapted to acidic and nutrient-poor substrates, poor drainage, and frequent fires, and flourishes well in bogs and wetlands where other species compete less effectively, although within its optimal range it also grows on uplands with white spruce and jack pine (Fowells 1965, Vincent 1965, Sutton 1969, Black and Bliss 1980). The nature of the substrate seems to be the controlling factor that determines the relative abundance of the two species within their distribution limits.

The lack of a regional modern analog for the white spruce-dominated early boreal forest therefore invites the speculation that an important edaphic control that existed during late-glacial and early postglacial times is absent in the modern boreal forest. I hypothesize that the fresh, base-rich soil that must have been widespread over the newly deglaciated land surface was the major controlling factor that favored white spruce over black spruce. Ritchie (1959) has stressed that substrate is the main factor governing the occurrence and performance of white spruce near its northern limit. He has described well-grown, mature white spruce–lichen forests on eskers, floodplain terraces, and recent alluvial deposits in subarctic Manitoba (Ritchie 1957, 1959), which may provide modern analogs for the early postglacial white spruce-dominated boreal forest. Further evidence for the role of white spruce in primary succession comes from the recently deglaciated areas in front of the Klutlan Glaciers in Yukon Territories today, where white spruce were among the first trees to colonize the fresh, base-rich till on the ice-cored moraines (Birks 1980b, Jacobson and Birks 1980). Furthermore, along the recently emerged Hudson Bay coast, white spruce, rather than the regionally dominant black spruce, is notably the species that forms the maritime tree line, apparently because it is more adapted to the nutrient-rich sea-shore environment (Payette et al. 1975, Payette 1976).

The early postglacial white-spruce dominated boreal forest was probably of regional extent, and not unique

to the local environmental setting of Nina Lake and Jack Lake. Pollen and macrofossils identified to *P. glauca* have been reported from late-glacial and early postglacial sediments from the Great Lakes region. Futyma (1981) described a white spruce forest from central Upper Michigan, buried in situ by proglacial lake sediments and dated between $10\,230 \pm 300$ and 9545 ± 225 BP. Abundant white spruce cones and needles, dating to ca. 12 000 BP, were also found in late-glacial sediments from southern Ontario (Terasmae and Matthews 1980, Schwert et al. 1985) and adjacent New York State (Miller 1973, Calkin and McAndrews 1980). In the late-glacial sediments of Crieff Kettle Bog in southern Ontario, Terasmae (in Karrow 1963) reported that *P. glauca* outnumbered *P. mariana* pollen in the ratio of $\approx 6:1$ in the *Picea* pollen peak. The data corroborate pollen and macrofossil records from elsewhere (e.g., Birks 1976, Lamb 1980, 1985, Engstrom and Hansen 1985) that white spruce seemed to be the first colonizers in a primary succession on a newly deglaciated landscape, virtually to the exclusion of black spruce.

An alternative explanation to the edaphic control hypothesis discussed above is that the predominance of white spruce in the early postglacial boreal forest was due to differential migration rates between the two species, i.e., black spruce lagged behind white spruce in their postglacial migration from southern refugia. The postglacial migration patterns of white spruce across North America have been reconstructed recently (Ritchie and MacDonald 1986). They show a steady migration rate of 200–300 m/yr from a full-glacial refugium south of the ice front into the Great Lakes region. By contrast, little is known about the migration patterns of black spruce. Data from Jack Lake (this study) and Lac Yelle (Richard 1980) suggest that by at least 9000 BP black spruce was already present in the Canadian Shield and the Clay Belt of Ontario and Quebec. The data from Lake Six (this study), in fact, suggest that the early white spruce predominance was not due to differential migration. The basal pollen assemblage from this site indicates that black spruce was already present in the regional boreal forest in the southern part of the Clay Belt before 7100 BP. The failure of black spruce to colonize the lake basin slopes during the afforestation phase was most likely due to its inability to compete with white spruce and other hardwoods in a fresh, base-rich soil, and definitely not because of the absence of black spruce propagules in the vicinity.

It is likely that black spruce was present in small populations in the early postglacial white spruce-dominated boreal forest on the Canadian Shield, awaiting soil development to expand its populations. At Nina Lake, black spruce was suppressed for > 1000 yr, even after the demise of the spruce forest due to climatic change. It only increased slightly relative to white spruce after ca. 8500 BP, but by that time the climate had become too warm for spruce to proliferate, and the

spruce forest had been replaced by a jack pine-dominated boreal forest, and subsequently, by a Great Lakes–St. Lawrence forest. Black spruce was never a frequent component of the forest around Nina Lake throughout the Holocene. At Jack Lake, the predominance by white spruce lasted several hundred years, until after ca. 9200 BP when jack pine became dominant. Black spruce seemed to be somewhat more frequent during the late Holocene. However, the initial white spruce-dominated boreal forest at Lake Six was very short-lived. It probably only lasted < 200 yr before it was invaded by black spruce and jack pine. Since then black spruce has been the predominant species in the boreal forest in the vicinity of Lake Six.

The relative increase in black spruce, which occurred at or after the climatically induced demise of the early postglacial spruce forest, was probably due to soil development. The seral changes on calcareous river terraces in northern Manitoba described by Ritchie (1957) may provide a modern analog. In this seral sequence a shrub community of birch and willow was invaded by white spruce and tamarack, which were in turn replaced by black spruce as a result of soil development, peat accumulation, and drainage deterioration. Observations from recently deglaciated areas in Glacier Bay, Alaska, and in the Klutlan moraines in Yukon indicate that, under vegetated conditions, the bases in the soil could be leached out fairly rapidly, with a drop in soil pH from > 8.0 to < 6.0 in < 200 yr (Crocker and Major 1955, Jacobson and Birks 1980). Rapid changes from an early, relatively brief phase of white spruce dominance to a subsequent phase of black spruce dominance also characterize the mid-Holocene vegetation histories at several sites in subarctic Labrador, and have been explained in terms of soil development and paludification (Lamb 1980, 1985, Engstrom and Hansen 1985). Paludification must have been a long-term process favoring black spruce in the Clay Belt during the Holocene.

Hypsithermal ecotonal movements

With the immigration of white pine, beech, and hemlock ca. 7400 yr ago, the boreal forest in the southern part of northern Ontario was transformed into a Great Lakes–St. Lawrence forest. By this time the summer temperature in the northern Midwest was already 1–2°C higher and annual precipitation $\approx 20\%$ lower than the present (Bartlein et al. 1984). White pine continued to expand northward under a favorable climate, vigorously replacing jack pine, white birch, and other boreal elements on its way. This in effect caused a northward advance of the boreal forest/Great Lakes–St. Lawrence forest ecotone. The Hypsithermal movements of the ecotone were depicted remarkably well by the results of discriminant analysis. The ecotone passed Jack Lake ca. 7300 yr ago. During 7000–3000 BP it almost reached the latitude of Lake Six. A reasonable reconstruction is that the ecotone coincided with the northern limit of the Canadian Shield upland,

≈ 140 km north of its present position (Fig. 23). Further caused by the continued expansion of white pine, was northward advance of the ecotone, as would have been constrained by the poor drainage and calcareous clayey soil prevalent in the Clay Belt lowlands, reinforcing the effect of the climatic gradient. Today scattered populations of white pine are present in the Clay Belt but are only confined to upland areas of sandy substrates such as eskers. During the Hypsithermal such habitats probably supported larger populations of white pine, but this species was still absent or rare in the vast stretches of lowland habitats with fine-grained substrates in the Clay Belt.

There is no evidence for Hypsithermal population expansion among other thermophilous tree species such as oak, elm, ash, maple, beech, and hemlock. Their pollen percentages and influx remained fairly constant throughout the mid- and late-Holocene. Their lack of response to the warmer climate during the mid-Holocene might be due to slightly drier conditions (Bartlein et al. 1984) and possibly to increased fire frequency, which would have favored white pine over these mesophytic species. This implies that the species in the Great Lakes–St. Lawrence forest responded individually to Hypsithermal climatic change. The northward advance of the ecotone was largely brought about by the range extension and population expansion of one species, white pine, rather than involving the orderly and proportionate range displacement of every species present south of the ecotone today. This observation is consistent with the individualistic concept of vegetation (Gleason 1926).

Unlike Minnesota and northwestern Ontario, where the Hypsithermal was characterized by increased frequencies of prairie pollen types (Bernabo and Webb 1977, Björck 1985), NAP remained low in the pollen records from northern Ontario during this period. In fact, loss-on-ignition and pollen influx data suggest that the Hypsithermal was probably the time of maximum forest density and organic productivity in northern Ontario. The climate was probably only slightly drier than the present, not enough to open up the forest canopy to simulate the expansion of heliophytic shrubs and herbs. Also, northern Ontario was too far away from the prairie peninsula to receive much prairie pollen input from long-distance transport.

The onset of Neoglacial cooling after the Hypsithermal was signalled by the decrease in the pollen influx of *Pinus strobus*, reflecting the range contraction of white pine and the southward retreat of its populations. This event was time-transgressive. *P. strobus* pollen influx crashed at Lake Six at ca. 4000 BP, at Jack Lake at ca. 3300 BP, and at Nina Lake at 2500 BP. This caused a southward retreat of the ecotone from its Hypsithermal position near Lake Six. Discriminant analysis indicates that the ecotone retreated to the position of Jack Lake ca. 2600 yr ago. It has become stabilized in its present position south of Jack Lake over the last millennium.

Hypsithermal Thuja expansion in the Clay Belt

Other than the elevated pollen frequencies of *P. strobus*, the most significant vegetation change in the mid-Holocene at Lake Six is represented by the prominent peak in Cupressaceae pollen. A prominent mid-Holocene Cupressaceae pollen maximum is a common feature in pollen records from the Clay Belt. It has been reported from Lac Yelle and Lac Clo in the Lake Abitibi region (Richard 1980), and from Crates Lake in northern Ontario ≈ 90 km north of Lake Six (Liu 1982) (Fig. 3). A distinct but less prominent increase in Cupressaceae pollen also occurs in the mid-Holocene sediments of Nina Lake and Jack Lake on the Canadian Shield upland. Thus this represents a vegetation change of regional scale and implies a regional cause, although its magnitude was much greater in the Clay Belt than in the Canadian Shield upland. The Cupressaceae pollen may represent either *Thuja* or *Juniperus*; the pollen of these two taxa cannot be easily distinguished based on morphological criteria (McAndrews et al. 1973). Richard (1980) attributed most of the Cupressaceae pollen at Lac Yelle and Lac Clo to *Juniperus*. At those two sites the sharp increase in Cupressaceae pollen at 6000 BP coincided with an abrupt decline in *P. strobus* pollen, while total pollen influx declined slightly. This has led Richard (1980) to postulate that the climate during 6000–3250 BP was warmer and drier than the present; higher frequencies of fire resulted in a more open forest canopy, thereby permitting the abundant growth of *Juniperus* (probably *J. communis*), a heliophytic shrub, in the openings. This scenario requires a substantial reduction in annual precipitation (or a corresponding increase in the evaporation/precipitation ratio) in order to initiate and maintain an open forest.

However, macrofossil evidence from Lake Six and Crates Lake (Liu 1982) suggests that *Thuja* was probably represented in the Cupressaceae pollen peak (Fig. 20). Strictly speaking, the occurrence of *Thuja* macrofossils in the sediments per se does not preclude the possibility that the Cupressaceae pollen comes from *Juniperus*, because *Juniperus*, being an upland plant, is less likely to be represented in the macrofossil record than is *Thuja*, which is common in riparian and wetland habitats. Nevertheless, pollen data from Lake Six are also inconsistent with the scenario of *Juniperus* proliferation in an open upland forest under a much drier climate. First, the Cupressaceae pollen maximum in Lake Six is contemporaneous with the mid-Holocene maximum in *P. strobus* pollen (Fig. 18), implying that the Cupressaceae plants and white pine coexisted rather than directly competing with each other. Second, total pollen influx reaches maximum values ($16\text{--}27 \times 10^3 \text{ grains}\cdot\text{cm}^{-2}\cdot\text{yr}^{-1}$) typical of closed boreal forest during the time of maximum Cupressaceae pollen at Lake Six (Fig. 19). Third, at neither Lake Six nor the Lake Abitibi sites were the Cupressaceae pollen maxima accompanied by discernible increases in the pollen

of upland herbs and shrubs, as would be expected in an open forest maintained by a higher frequency of fire. Thus I conclude that the mid-Holocene Cupressaceae pollen peak represents *Thuja* expansion in lowland habitats in the Clay Belt.

One plausible explanation for the mid-Holocene *Thuja* pollen peak is that it marks the immigration of *Thuja occidentalis* to the respective sites—only that in the Clay Belt its populations increased rapidly after arrival due to the abundance of favorable lowland habitats and calcareous substrates. The postglacial migration history of *Thuja* in this region is poorly known. Warner (1982) indicated that *Thuja* was already present in Manitoulin Island south of Nina Lake around 10 000 BP and probably immigrated to northern Ontario with other boreal forest elements. The migration hypothesis can be tested by examining the chronology of the mid-Holocene Cupressaceae pollen rise in the region. At Nina Lake, Lake Six, and the two sites near Lake Abitibi (Richard 1980), Cupressaceae pollen began to increase distinctly at 6000 BP, whereas at Jack Lake this occurred at 6500 BP. The apparent synchronicity (or at least the lack of regional time-transgressiveness) over a broad region argues against migration as a probable cause for the *Thuja* expansion. Rather, an environmental change probably occurred at 6000 BP that permitted the expansion of *Thuja* from populations that were already present in northern Ontario.

Thuja occidentalis is a typical species of the Great Lakes–St. Lawrence forest. Although its range extends into the boreal forest and reaches as far north as James Bay (Fig. 1), it grows best and is most common in the southern part of its main range (i.e., the Great Lakes–St. Lawrence forest) where the climate is moderately temperate and moist (Fowells 1965). In terms of habitat requirements *Thuja* is a decided calciphile, growing best on calcareous substrates such as limestone-derived soils. In southern Ontario, where outcrops of Paleozoic carbonate rocks are abundant, it constitutes 7–10% of the trees in the Great Lakes–St. Lawrence forest and can grow both on uplands and in swamps (Dixon 1963, McAndrews 1981). In northern Ontario, *Thuja* rarely constitutes >3% of the trees in the boreal forest (Dixon 1963), and is increasingly confined to the margins of lakes, streams, swamps, and nutrient-rich fens. The depth of the water table and thickness of the peat are critical factors in the occurrence of northern white cedar in swamps and open peatlands. A high water table, poor drainage, and the occurrence of thick, poorly decomposed peat—conditions characteristic of the center of many swamps and open fens—are detrimental to the growth of *Thuja* (Fowells 1965). Thus in northern Ontario *Thuja* tends to be restricted to the margins of large peatlands where the peat is thinner and more well-decomposed, and the internal drainage is better.

I interpret that the mid-Holocene *Thuja* expansion was caused by a warmer and drier climate during the

Hypsithermal. The thermal climate of northern Ontario today is only suboptimal for northern white cedar; its populations would probably have expanded in response to a warmer climate 6000 yr ago. A drier climate would also have lowered the regional water table, thus allowing the *Thuja* populations that were otherwise restricted to the margins of swamps and open peatlands to spread to the center. Peat stratigraphies from the Ontario Clay Belt seem to support this scenario. Terasmae and Hughes (1960b) presented an undated peat stratigraphy from Frederick House River bog (Fig. 3) that contains two woody peat layers. One woody layer near the bottom of this 2.1 m thick peat section overlies Lake Ojibway silty clay and varved clay; the other lies in the middle of the section between thick, medium- to well-decomposed *Sphagnum* peat. A similar peat stratigraphy has also been reported from a nearby locality (Karlstrom 1956), although this profile has a third woody peat layer immediated below the surface. The two lower woody peat layers in Karlstrom's profile were C-14 dated at 6380 ± 350 BP and 5300 ± 300 BP. These three woody peat layers were interpreted by Karlstrom (1956) as recording three episodes of forest invasion into open bog terrains, probably in response to climatic change towards drier conditions. These dates agree well with my interpretation of a warmer and drier climate that permitted *Thuja* to spread across swamps and open peatlands during 6000–4500 BP.

Pollen evidence suggests that the *Thuja* expansion was much more pronounced in the Clay Belt than on the Canadian Shield. This can be explained by the physiographic and edaphic contrasts between the two areas. The abundant calcareous substrates in the Clay Belt were certainly more favorable to the calciphilous *Thuja*, in contrast to the acidic, coarse-grained soils of the Canadian Shield. More importantly, the widespread occurrence of wetlands (swamps, bogs, fens) in the Clay Belt lowland would have provided plenty of suitable habitats for population expansion under favorable climatic and hydrological conditions, whereas on the Canadian Shield *Thuja* expansion would have been largely confined to exposed lakeshores, valley bottoms, and the more limited wetland habitats. On the uplands, northern white cedar would have to face intense competition from white pine, white spruce, white birch, and other hardwoods. The presumably higher frequencies of fire under a drier climate would also have been detrimental to northern white cedar growing on the uplands.

SUMMARY AND CONCLUSIONS

The three pollen and macrofossil stratigraphies along a transect of steep climatic gradient and contrasting landforms have permitted a reconstruction of the postglacial vegetational history of northern Ontario. This study has highlighted several important aspects in the Holocene paleoecology of the boreal forest and Great Lakes–St. Lawrence forest, as summarized below.

1) The early postglacial boreal forest that existed in northern Ontario before ca. 9000 BP is unlike the typical modern boreal forest in several aspects. It was dominated by white spruce with little or no black spruce, a situation paralleled only by white spruce-lichen forests that are confined to local habitats of fresh, nutrient-rich soils today. The prevalence of fresh soil derived from unleached glacial deposits during early postglacial times provided a unique edaphic control of regional scale that is unparalleled in modern environments. In addition, discriminant analysis suggests that the early postglacial boreal forest probably differs from its typical modern counterparts by having more poplar/aspen, more heliophytic herbs and shrubs, and possibly more thermophilous hardwoods, although these pollen assemblages could have been distorted by processes of differential pollen preservation, redeposition, and long-distance transport. This study supports the notion that plant communities without modern analogs are commonplace in late-glacial and early postglacial environments.

2) On the Canadian Shield upland, a warmer and drier climate during the Hypsithermal caused a significant population expansion of white pine, and permitted its range to extend north of its present position. By means of discriminant analysis, it is clearly elucidated that the boreal forest/Great Lakes-St. Lawrence forest ecotone was displaced ≈ 140 km north of its present position during ca. 7000–3000 BP. Its Hypsithermal position probably coincided with the northern boundary of the Canadian Shield. The plant species of the Great Lakes-St. Lawrence forest responded individually to Hypsithermal climatic changes. The northward displacement of the ecotone was largely the result of the population expansion of white pine, while most other thermophilous species showed little evidence of population change or range extension. Neoglacial cooling caused a contraction of white pine populations. The ecotone began to retreat from south of Lake Six at ca. 3100 BP, reaching Jack Lake ≈ 500 yr later. The onset and the termination of the Hypsithermal, as determined by the ecotonal movements across the region, were time-transgressive, as Wright (1976) has contended.

3) The mid-Holocene vegetation history of the Clay Belt contrasts sharply with that of the Canadian Shield upland. This study documents for the first time that *Thuja* populations expanded significantly in the Clay Belt, probably in response to a warmer and drier climate during the Hypsithermal. The *Thuja* expansion was landform selective, much more pronounced in the Clay Belt than on the Canadian Shield upland. The widespread occurrence of wetlands and the abundance of calcareous substrates in the Clay Belt were particularly conducive to the proliferation of *Thuja* under a favorable climate. This study provides an additional example (e.g., see Brubaker 1975) to illustrate that against a background of climatic change, landform and

substrate are important factors determining the character of vegetational change.

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