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**REPORT FOR WESTERN GREAT LAKES PALEOECOLOGY STUDY, GLOBAL CLIMATE
CHANGE INITIATIVE: ISLE ROYALE**

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EXECUTIVE SUMMARY

Information about past and current rates and directions of change at Isle Royale can be used to assess how to best manage the island according to National Park Service objectives, to predict if the island's vegetation will be more or less susceptible to anticipated climatic changes than mainland vegetation, and as a baseline for measuring if future changes will be more accelerated than current changes and if there are any precedents for such change.

Several sediment cores were collected from lakes on Isle Royale. A long (about 9500 yr BP) and a short core were collected from Lily Lake, in a northern hardwoods forest on the southwestern end of the island. Another long (about 8500 yr BP) and short core were collected from Lake Ojibway, in a boreal forest on the northeastern end of the island. A short core was collected from Wallace lake, also in a boreal forest on the northeastern end of the island. The island is relatively inaccessible, and its climate is influenced by Lake Superior. Its southwestern end has a mantle of glacial till, which the northeastern end lacks. Thus, these cores provide opportunities to:

- 1) Determine whether the timing or rates of change on the island differ from those from similar mainland sites.
- 2) Determine whether rates of change have differed on the island according to substrate type.
- 3) Compare vegetation composition on the island before and after European settlers arrived in the region.

The cores were subjected to loss-on-ignition, macrofossil, charcoal, pollen, and other analyses. Pollen analysis reveals that vegetation at all three lakes has been stable for at least the past 200 years, showing only slight, possibly regional, changes after settlement. Despite their different substrates, vegetation change throughout the Holocene appears gradual at both Lily Lake and Lake Ojibway, though the timing of changes and the composition of their modern forests differ. Their Holocene vegetation composition records are in harmony with other records of Holocene vegetation change in the upper Midwest. The Isle Royale records indicate, however, that both the mid-Holocene dry interval and the impacts of European settlement were perhaps less severe on

the island than at more continental sites.

In gross appearance, the pollen records from lakes on Isle Royale are similar to one another and to those of mainland sites. They show major changes during the mid-Holocene, at about 3,000 years before present, and after European settlement of the region. Yet they differ from one another and from the mainland in the timing of some of these changes, in the nature and magnitude of the changes, and in the rate of change. These subtle differences are highlighted by examining the differences in rates of change at the various sites. Rates of change on the island are lower than rates of change for several other lakes of the same latitude as Isle Royale but with more continental climates. Within the island, rates of change are lower at bedrock-underlain Lake Ojibway than at till-underlain Lily Lake.

TECHNICAL REPORT

INTRODUCTION

Isle Royale is located in western Lake Superior, about 24 km south of the Canadian shore (Fig. 1). The island is 72 x 14 km, composed of parallel ridges and valleys of Precambrian basaltic lava interbedded with sandstone and conglomerates (Huber 1973, 1975). The valleys contain numerous lakes, swamps, and streams. Unlike the northeastern end of the island, the southwestern end has a mantle of glacial till; this difference in substrate may have influenced the development of two broad forest types on the two ends of the island. The southwestern end supports a deciduous, northern hardwoods forest, especially at higher elevations, while the northeastern end and much of the periphery of the island support a more coniferous, boreal forest. Because Isle Royale is relatively inaccessible and, since 1940, incorporated into the National Park system, it is likely less disturbed than much of the mainland. To date, little paleoecological research has been conducted at Isle Royale (but see Potzger 1954 and Raymond et al. 1975).

Pollen analytical data from the island contributes to our understanding of the development of vegetation as influenced by microclimate, substrate, and settlement impacts. These factors are highlighted at Isle Royale because 1) the island's climate is moderated compared to regional climate because of Lake Superior's influence; 2) there are sharp substrate differences between the northeastern and southwestern ends of the island; and 3) the island's relative isolation may have buffered the impact of European settlement on the vegetation. The rate at which vegetation changes in response to natural and anthropogenic forces such as global warming likely depends on such factors. By examining past rates of change at sites differing in these factors, researchers might better predict which sites are more sensitive and will show more rapid change under forecasted global change scenarios. This study addresses the following hypotheses:

1. The climate-modifying effect of Lake Superior will be reflected in slower rates of vegetation change on Isle Royale than on mainland sites.
2. Within the island, the vegetation surrounding Lily Lake, because of its clayey till substrate, will initially change faster than that surrounding Lake Ojibway, without the thicker till soils. Following disturbance, however, the changes at Lake Ojibway will occur at a faster rate.
3. Because of its relative inaccessibility and current status as a National Park, the effects of post-European-settlement disturbance on the vegetation will be visible, but less marked at Isle Royale than at mainland sites.

The effect of the Great Lakes on temperature is to reduce average summer temperatures and raise average winter temperatures, and to reduce the number of days of either extreme heat or cold, compared to sites not influenced by the lakes (Changnon and Jones 1972, Eichenlaub 1979, Kopeck 1965). If this effect has been consistent throughout the Holocene it would likely dampen the rate of change on lake-influenced sites. To determine whether the lake effect influenced the rate of vegetation change, the Isle Royale pollen records were compared to pollen records from the mainland at similar latitude but with more continental climates than Isle Royale.

Substrate has been shown to have a marked effect on vegetation composition (Brubaker 1975). To determine if it also affects rates of change, the histories of Lily Lake and Lake Ojibway, which are presumably under the influence of the same regional and lake-effect climate, were compared. Because of the lack of soil development near Lake Ojibway, vegetation change there was expected to initially be slower than at Lily Lake. For the same reason, however, the vegetation near Lake Ojibway was expected to be more sensitive to disturbance and show periods of rapid change following disturbance.

Finally, to determine the impact of European settlement, pre- and postsettlement vegetation changes at Isle Royale were finely examined using short cores.

METHODS

Field

Using a square-rod piston corer, long sediment cores were obtained in the winters of 1992 and 1993 from the centers of Lily Lake, on the till-underlain southwestern end, and Lake Ojibway, on the bedrock-underlain northeastern end of the main island of Isle Royale. In the summer of 1993, the vegetation surrounding the lakes was surveyed in four (north, south, east, west) 500-m transects beginning at the edge of each lake.

Laboratory Processing of Sediment Cores

Both cores are composed of organic gyttja overlying inorganic glacial clay. The cores were subsampled for radiocarbon dating (five dates were obtained from Lily Lake and six from Lake Ojibway), loss-on-ignition analysis (2 cm² every 20 cm along each core), pollen analysis (1 cm² every 10 cm along each core, except for fifteen samples taken at 5-cm intervals from the Lake Ojibway core), and chemical assay charcoal analysis (1 cm² every 10 cm along each core).

Loss-on-ignition analyses were carried out using standard methods (Dean 1974) to determine the organic, inorganic, and carbonate content of the sediment. Pollen was chemically extracted using modified standard methods (Faegri and Iversen 1975), including the addition of *Lycopodium* spores for use in calculating pollen influx values (Stockmarr 1971). Between 500 and 1000 arboreal pollen grains were counted for each sampled level of the cores. Appendices A and B present the raw data of pollen types counted for each level of the cores. Charcoal analysis was performed using the chemical assay technique (Winkler 1985).

Data Analysis

Appendix C details the quantitative treatment of the pollen data and the selection of the methods used. To describe relationships among the pollen spectra from each core, the data were ordinated. Because of tradeoffs in the assumptions and distance measures employed by each one (Beals 1984, Gauch 1982), several ordination techniques available with PC-ORD software (McCune and Mefford 1995) were tested. These included Bray-Curtis, principal components

analysis, detrended correspondence analysis, and nonmetric multidimensional scaling.

Analysis of the rates of vegetation change was modified from methods developed by Jacobson et al. (1987). Composite pollen spectra representing 200-year intervals were interpolated using rectangular integration, an appropriate method when observations exceed estimates (e.g., when data points less than 200 years apart are used to estimate pollen percentages spaced 200 years apart) (Davis 1986). Following Overpeck et al. (1985) squared chord distance (rather than chord distance) was used to measure the degree of dissimilarity between adjacent composite pollen spectra.

These squared chord distances were calculated between successive 200-year composite pollen spectra from an east-west transect of lakes within a degree of latitude of Isle Royale and having various degrees of continentality. Pollen data from mainland lakes were obtained from the North American Pollen Database. Coefficients of continentality were obtained from a map of the Great Lakes region prepared by Kopec (1965) using Conrad's coefficient of continentality (Fig. 2). In this index, 100% corresponds to a completely continental climate and 0% corresponds to a completely maritime climate. If the lakes did not exist, it is estimated that sites in the Great Lakes region would have coefficients of continentality of about 60% (Kopec 1965). The analysis included Alfies Lake, Ontario ($47^{\circ} 53' \text{ N}$, $84^{\circ} 52' \text{ W}$; coefficient of continentality 43%) (Saarnisto 1974), the Isle Royale lakes ($89^{\circ} 55' \text{ N}$, 89° W ; coefficient of continentality 37-38%), Lake of the Clouds, Minnesota (48° N , 91° W ; coefficient of continentality 50%) (Craig 1972), and Myrtle Lake, Minnesota ($47^{\circ} 58' \text{ N}$, $93^{\circ} 23' \text{ W}$; coefficient of continentality 56%) (Janssen 1968) (see Fig. 2).

RESULTS

Radiocarbon and ^{210}Pb Chronology

Lily Lake. Five radiocarbon dates were obtained on the long core from Lily Lake (Figure 3). The date at the transition from inorganic clay to organic gyttja sediment (8.87 - 8.88 m; 9420 $\pm$ 90 yr B.P.) was obtained from the AMS facility at the University of Arizona. The remaining dates were obtained from Geochron Laboratories in Cambridge, Massachusetts. The short core was dated by ^{210}Pb by D. Engstrom from the University of Minnesota (Figure 3) and covers the years 1850 A.D. to the present.

Lake Ojibway. Eight radiocarbon dates were obtained on the long core from Lake Ojibway (Figure 4). These dates were obtained from the National Ocean Sciences AMS Facility at Woods Hole, Massachusetts. The oldest date, at the transition from inorganic clay to organic gyttja sediment (8.46 m) was 8790 $\pm$ 40 yr B.P. The short core was dated by ^{210}Pb by D. Engstrom from the University of Minnesota and covers the years 1800 A.D. to the present.

Wallace Lake. The Wallace Lake short core was dated by ^{210}Pb by D. Engstrom of the University of Minnesota and covers the years 1400 A.D. to the present.

Sediment Chemistry

Lily Lake. The Lily Lake long core is composed of organic gyttja to a depth of 8.87 meters below the lake surface; at this point there is a transition to inorganic glacial clay sediment (Figure 5). The loss-on-ignition analysis of the core (Figure 6) indicates that organic matter increases from less than 5% to about 15% at the transition level (about 9500 yr B.P.), and continues to increase rapidly, reaching levels of about 70% by 7.7 m (about 8000 yr B.P.), and remaining high to the top of the core (Figure 6). At 5.9 m (about 5000 yr B.P.), carbonates increase abruptly from below 3% to about 20%, and they remain at high levels to the top of the core. With this sudden increase in carbonates, the gradual decline of inorganics (from highs of over 90% near the bottom of the core) sharpens dramatically; inorganics drop from almost 40% at 6.1 m to 4% at 5.9 m. They fluctuate through the remainder of the core, ranging from about 4% up to 23%. The increase in carbonates might indicate increased atmospheric dustiness associated with the mid-Holocene warm interval and subsequently with settlement.

Lake Ojibway. The Lake Ojibway long core is composed of organic gyttja to a depth of 8.46 meters below the lake surface; at this point there is a transition to inorganic glacial clay sediment. The loss-on-ignition analysis of the core (Figure 7) indicates that organic matter increases from less than 1% to 15% at the transition level (about 8800 yr B.P.), then continues to increase, stabilizing at levels between 40% and 50% by 7.5 m (about 6800 yr B.P.). Inorganics decrease correspondingly. Carbonates range from less than 1% to less than 4% throughout the core. They are at their highest levels in the glacial clay near the bottom of the core (as the lake is forming) and from 7.7 to 6.5 m (about 7000 to 4500 yr B.P.). The increase in carbonates might indicate increased atmospheric dustiness associated with the mid-Holocene warm interval.

Holocene Vegetation Composition

Lily Lake, long core. Deglaciation near Lily Lake occurred about 9600 to 9400 yr B.P. Since deglaciation, vegetation change near the lake has been gradual, but several pollen zones can be identified (Figure 8).

Zone 1, 9400 - 8800 yr B.P.: This zone represents a forest dominated by spruce and jack pine, with birch increasing near the top of the zone. Relatively high percentages of herbaceous pollen and pteridophyte spores indicate that the forest was somewhat open and moist.

Zone 2, 8800 - 7400 yr B.P.: In this zone, birch and jack pine are dominant, while spruce and herbs decline, alder increases, and fir is constant. This pattern indicates warming climate and a closing forest.

Zone 3a, 7600 - 7400 yr B.P.: This subzone is notable because it is when white pine invades the area and begins a dramatic increase.

Zone 4, 7400 - 3300 yr B.P.: Throughout this time, roughly corresponding to the mid-Holocene warm dry interval identified elsewhere in the upper Midwest (Craig 1972, Fries 1962, Janssen 1968, Webb et al. 1983, Winkler et al. 1986), pines dominate the area surrounding Lily

Lake. Early in the zone, other tree species decline or remain at low levels. At about 4300 yr B.P., however, this begins to change. Maple becomes established and begins to increase near the lake, birch begins to recover, and spruce, fir, oak, and elm increase slightly. Pines, particularly white pines, begin their decline.

Zone 5, 3300 - 100 yr B.P.: In this zone, patterns beginning near the end of the previous zone become well established. Pine decline and birch increase are the most striking events. Spruce, fir, and alder continue to recover, while most other taxa remain constant. The modern forest is established during this period.

Zone 6, settlement: Although Lily Lake is remote from direct European settlement, an increase in ragweed pollen marks settlement of the region.

Lily Lake, short core. The Lily Lake short core (Figure 9) provides an opportunity to examine recent vegetation changes at a fine time scale. The core dates to about 1850 A.D., very shortly before European settlement of the region. It mirrors the top section of the long core in its high percentage of birch pollen, followed by jack pine pollen, then some spruce and fir. Very little change is apparent in the short core, perhaps because it extends only to about the time of settlement. A small rise in ragweed pollen is detectable after about 1890 (the approximate time of European settlement). It is possible that the ragweed rise is so small because some settlement impacts were already taking place by 1850, the date of the core.

Lake Ojibway, long core. Deglaciation near Lake Ojibway occurred about 9000 - 8800 yr B.P., as many as 800 years after Lily Lake. As at Lily Lake, vegetation change since deglaciation has been gradual at Lake Ojibway, but pollen zones can be identified (Figure 10).

Zone 1, 8800 - 6800 yr B.P.: This zone represents a forest dominated by birch and jack pine. A short interval near the bottom of the zone indicates that spruce started out as an important component of the forest, but it is not as common as at Lily Lake, and it declines quickly. Herbaceous pollen remains relatively high through most of this zone, declining near the top. This indicates that the forest remained fairly open until near the end of this zone.

Zone 2, 6800 - 3500 yr B.P.: At the bottom of this zone, both jack and white pine increase dramatically, commencing a period of pine dominance roughly corresponding with the mid-Holocene warm interval reported elsewhere in the upper Midwest. Birch, spruce, fir, alder, and herbs decline, while other taxa remain fairly constant. Near the end of this zone, however, the declining taxa begin to recover and the pines begin to decline.

Zone 3, 3500 - 100 yr B.P.: In this zone, patterns beginning near the top of the previous zone become well established. Pines continue to gradually decline, and birch, spruce, fir, and alder continue to recover. A modern forest, in which pine, birch, spruce, and fir dominate, is established during this period.

Zone 4, settlement: As at Lily Lake, European settlement of the region is marked by an increase of ragweed pollen at Lake Ojibway.

Lake Ojibway, short core. As at Lily Lake, the short core at Lake Ojibway mirrors the top of the long core, with moderate amounts of birch, pine, spruce, fir, and alder pollen (Figure 11). The core is a bit older than the Lily Lake short core, dating to just before 1800 A.D. Again, little vegetation change is evidenced by the pollen in the core, due perhaps to its short time scale. Yet some changes after 1890, the approximate time of European settlement of the region, are suggestive. For instance, there is a slight rise in ragweed pollen, a common settlement indicator, and a slight drop in white pine pollen, perhaps due to logging in the region or even on the island.

Wallace Lake, short core. The short core taken at Wallace Lake is older than the other short cores collected, dating to about 1400 A.D. (Figure 12). Despite its age, the pollen from this core also indicates little vegetation change during that time. There is, however, a clear rise in ragweed pollen; as in the other cores, it begins slightly before 1890. The pollen percentages are much like those in the Lake Ojibway short core. This is to be expected because the modern vegetation surrounding both lakes is similar.

Ordination Analyses

Ordination summarized relationships among the sampled levels of each core by depicting similar samples near one another and dissimilar samples farther apart. Appendix C details selection of ordination techniques. Although all of the tested techniques revealed the same patterns in the data, detrended correspondence analysis (DCA; Hill and Gauch 1980) and nonmetric multidimensional scaling (NMDS; Kruskal 1964a, 1964b) provided the clearest, most efficient analyses, and the following is based on DCA results.

Lily Lake. The first axis separates mid-Holocene samples with large pine percentages from the others, particularly those with a relatively large percentage of weedy pollen types, which generally have peaks in the early Holocene and the late Holocene. The most dissimilar samples on this axis are samples 50 (6808 yr B.P.) and 68 (9504 yr B.P.). The second axis separates early-Holocene samples having high percentages of spruce and many of the weedy species from late-Holocene samples having high percentages of birch, other northern hardwoods trees and shrubs, and a few weeds. The most dissimilar samples on this axis are samples 2 (416.1 yr B.P.) and 68 (9504 yr B.P.) (Fig. 13).

Lake Ojibway. The first axis separates mid-Holocene samples with high pine pollen percentages from the other samples, particularly those high in pollen from spruce and from a variety of relatively uncommon taxa tending to peak in the late Holocene. The most dissimilar samples on this axis are samples 14 (1148 yr B.P.) and 40 (6642 yr B.P.). The second axis separates samples high in spruce, maple, and hemlock pollen (i.e., late-Holocene samples) from samples having high percentages of weedy or uncommon pollen types (early-to-mid-Holocene samples). The most dissimilar samples on this axis are samples 5 (471 yr B.P.) and 45 (7630 yr B.P.) (Fig. 14).

Rates of Change Analyses

Squared chord distances from adjacent, 200-year-interval pollen spectra at five lakes within a degree of latitude of Isle Royale but with varying degrees of continentality indicate that the Holocene rate of vegetation change was lower at more lake-influenced sites, especially Isle Royale (Fig. 15).

Within the island, rates of vegetation change were consistently lower at Lake Ojibway, on the poorer soils, than at Lily Lake, on the richer soils (Fig. 15).

DISCUSSION

Substrate Influence

The areas surrounding Lily Lake and Lake Ojibway have several similarities in their vegetation histories, but the timing and rate of the changes differs, and the composition of the modern forest differs. The Lily Lake area was probably the first part of the island to be deglaciated. An open spruce-jack pine forest developed immediately, but by the time the Lake Ojibway area was deglaciated (about 800 years later), this forest had become a more closed jack pine-birch forest. At Lake Ojibway, there is only a very brief period in which the spruce-jack pine forest appeared; it was quickly replaced by the jack pine-birch forest seen simultaneously at Lily Lake.

At both lakes, white pine pollen is present only in trace amounts at the bottom of the core. At both lakes, it increases sharply. But the sharp increase occurs earlier (7400 yr B.P.) at Lily Lake than at Lake Ojibway (6800 yr. B.P.). Overall pine dominance also begins earlier at Lily Lake. Pine decline appears to begin slightly earlier at Lake Ojibway (3500 yr B.P. vs. 3300 yr B.P.), but it is more gradual and less complete than at Lily Lake. The maple increase that occurs at 4300 yr B.P. at Lily Lake is barely detectable at Lake Ojibway.

At both lakes, forests much like those seen today were established shortly before 3000 yr B.P. Birch dominates at Lily Lake; at Lake Ojibway it shares dominance with pine, spruce, and fir.

This evidence supports the hypothesis that rapid changes will occur early at Lily Lake, where soil development had a head start because of the glacial till substrate. The appearance of and increase in white pine, and the period of pine dominance, occur much earlier at Lily Lake, maples become established there, and the replacement of pine dominance by birch and other hardwood dominance is extensive. The second aspect of the substrate hypothesis (that change will be more rapid at Lake Ojibway following disturbance) is not supported; changes appear to be consistently more gradual at Lake Ojibway.

Settlement Impact

Despite Isle Royale's remote location and current legal protection, there is some evidence of European settlement impacts at each of the lakes. The Lily Lake short core records changes since 1850 A.D., very shortly before European settlement of the region (estimated at 1890 A.D.). Nevertheless, some settlement-related vegetation changes are apparent, notably the slight increase in ragweed and chenopod pollen after 1890. Lily Lake is the most remote lake in this study, and its short core is the youngest; therefore detection of these settlement impacts is surprising. Lake Ojibway's short core dates from 1800 A.D. and also shows a slight increase in ragweed pollen after 1890. The Wallace Lake short core dates from 1400 A.D. This diagram shows a marked rise in ragweed pollen, and suggests that ragweed and chenopod pollen began to rise around 1800 A.D. and continued to rise past 1890. An examination of the percent of ragweed pollen in the short cores shows a rising trend after 1850 A.D. in each core (Fig. 16). The sharpness of the trend corresponds with the age of the short core and accessibility of the lakes (i.e., sharpest at Wallace Lake, with the oldest short core and the greatest accessibility; shallowest at Lily Lake, with the youngest short core and least accessibility).

Thus, there have been changes in the vegetation composition at Isle Royale since European settlement. The results support the hypothesis that European settlement has had some impact on Isle Royale, but less than on the mainland.

Lake Effect

To determine whether vegetation development at Isle Royale differs from that on the mainland, pollen records from similar latitudes were obtained from the North American Pollen Database. Comparisons were made across an east-west transect of regional lakes at 47° 5'N to 48° 5'N latitude [including Alfies Lake (Saarnisto 1974), the Isle Royale lakes, Lake of the Clouds (Craig 1972), and Myrtle Lake (Janssen 1968)]. In overall compositional pattern, the Isle Royale lakes integrate well with regional lakes, all recording vegetation shifts at approximately 7000 and 3000 yr B.P. according to the authors' interpretations of the pollen diagrams. Evidence for the mid-Holocene dry interval tends to be stronger and the degree of change suggested more extreme towards the west. For instance, Lake of the Clouds and especially Myrtle Lake contain prairie elements in their mid-Holocene pollen records. At all of the sites, spruce pollen declines to very low amounts or disappears during the mid-Holocene, returning to some extent around 3000 yr B.P. This spruce decline, however, is least pronounced at the Isle Royale sites, perhaps because the lake influence kept summer temperatures cool enough to permit some spruce survival on the island while other spruce populations were destroyed.

Yet ordination analyses highlight the unique character of pollen spectra from the mid-Holocene at Isle Royale. The Isle Royale evidence supports regional evidence indicating that the mid-Holocene was a time of warm, dry climate (Baker 1992, Bartlein et al. 1984, Webb et al. 1983, Winkler et al. 1986), possibly useful as an analog for vegetation changes that will result from global warming.

Thus, vegetation changes are recorded at similar times and interpreted in similar ways at

all of the sites. These changes likely reflect a response to a strong regional forcing factor, probably changing climate (i.e., the peak of the mid-Holocene warm dry period and its subsequent reversal). There are differences among the sites in the composition of the vegetation before and after these changes, and in the magnitude and rate of the changes. These differences are more subtle than the gross similarities. They suggest that Isle Royale's climate is buffered by Lake Superior enough to slow down, but not prevent, vegetation changes brought on by warming climate.

REFERENCES

- Baker, R.G., L.J. Maher, C.G. Chumbley, and K.L. Van Zant. 1992. Patterns of Holocene environmental change in the Midwestern United States. *Quaternary Research* 37:379-389.
- Bartlein, P.J., T. Webb III, and E. Fleri. 1984. Holocene climatic change in the northern Midwest: Pollen-derived estimates. *Quaternary Research* 22:361-374.
- Beals, E.W. 1984. Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. *Advances in Ecological Research* 14:1-55.
- Brubaker, L.B. 1975. Postglacial forest patterns associated with till and outwash in north central upper Michigan. *Quaternary Research* 5:499-528.
- Changnon, S.A. and D.M.A. Jones. 1972. Review of the influences of the Great Lakes on weather. *Water Resources Research* 8:360-371.
- Craig, A.J. 1972. Pollen influx to laminated sediments: A pollen diagram from northeastern Minnesota. *Ecology* 53:47-57.
- Davis, J.C. 1986. *Statistics and Data Analysis in Geology*, 2nd ed. John Wiley and Sons, New York.
- Dean, W.E. Jr. 1974. Determination of carbonate and organic matter in calcareous sediments and sedimentary rocks by loss on ignition: Comparison with other methods. *Journal of Sedimentary Petrology* 44:242-248.
- Eichenlaub, V. 1979. *Weather and Climate of the Great Lakes Region*. University of Notre Dame Press, South Bend, IN.
- Fægri, K. and J. Iversen. 1975. *Textbook of Pollen Analysis*. Hafner Press, New York.
- Fries, M. 1962. Pollen profiles of late Pleistocene and recent sediment from Weber Lake, Minnesota. *Ecology* 43:295-308.
- Gauch, H.G., Jr. 1982. *Multivariate Analysis in Community Ecology*. Cambridge University

Press, Cambridge.

- Hill, M.O. and H.G. Gauch, Jr. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42:47-58.
- Huber, N.K. 1973. Glacial and postglacial geologic history of Isle Royale National Park, Michigan. Geological Survey Professional Paper 754-A.
- Huber, N.K. 1975. *The Geologic Story of Isle Royale National Park*. Bulletin 1309, Geological Survey, Washington, D.C.
- Jacobson, G.L., T. Webb III, and E.C. Grimm. 1987. Patterns and rates of vegetation change during the deglaciation of eastern North America. In, W.F. Ruddiman and H.E. Wright, Jr., eds. *North America and Adjacent Oceans Since the Last Glaciation*. Geological Society of America, Inc., pp. 277-288.
- Janssen, C.R. 1968. Myrtle Lake: A late- and postglacial pollen diagram from northern Minnesota. *Canadian Journal of Botany* 46:1397-1408.
- Kopec, R.J. 1965. Continentality around the Great Lakes. *Bulletin of the American Meteorological Society* 46(2):54-57.
- Kruskal, J.B. 1964a. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29:1-27.
- Kruskal, J.B. 1964b. Nonmetric multidimensional scaling: a numerical method. *Psychometrika* 29:115-129.
- McCune, B. and J. Mefford. 1995. *PC-ORD: Multivariate Analysis of Ecological Data*.
- Overpeck, J.T., T. Webb III, and I.C. Prentice. 1985. Quantitative interpretation of fossil pollen spectra: dissimilarity coefficients and the method of modern analogs. *Quaternary Research* 23:87-108.
- Potzger, J.E. 1954. Post-Algonquin and post-Nipissing forest history of Isle Royale, Michigan. *Butler University Botanical Studies* 9:200-209.
- Raymond, R.E., R.O. Kapp, and R.A. Janke. 1975. Postglacial and recent sediments of inland lakes of Isle Royale National Park, Michigan. *Michigan Academician* 7:453-465.
- Saarnisto, M. 1975. Stratigraphical studies on the shoreline displacement of Lake Superior. *Canadian Journal of Earth Science* 12:300-319.
- Steigerwaldt, W. and M. Meyer. 1979. Vegetation and fuel type mapping of Isle Royale. University of Minnesota Institute of Agriculture, Forestry, and Home Economics. Remote

Sensing Laboratory Research Report 79-1.

Stockmarr, J. 1971. Tablets with spores used in absolute pollen analysis. *Pollen et Spores* 13:615-621.

Webb, T. III, E.J. Cushing, and H.E. Wright, Jr. 1983. Holocene changes in the vegetation of the Midwest. In, H.E. Wright, ed., *Late Quaternary Environments of the United States. Vol 2: The Holocene*. University of Minnesota Press.

Winkler, M.G. 1985. Charcoal analysis for paleoenvironmental interpretation: a chemical assay. *Quaternary Research* 23:313-326.

Winkler, M.G., A.M. Swain, and J.E. Kutzbach. 1986. Middle Holocene dry period in the northern Midwestern United States: Lake levels and pollen stratigraphy. *Quaternary Research* 25:235-250.

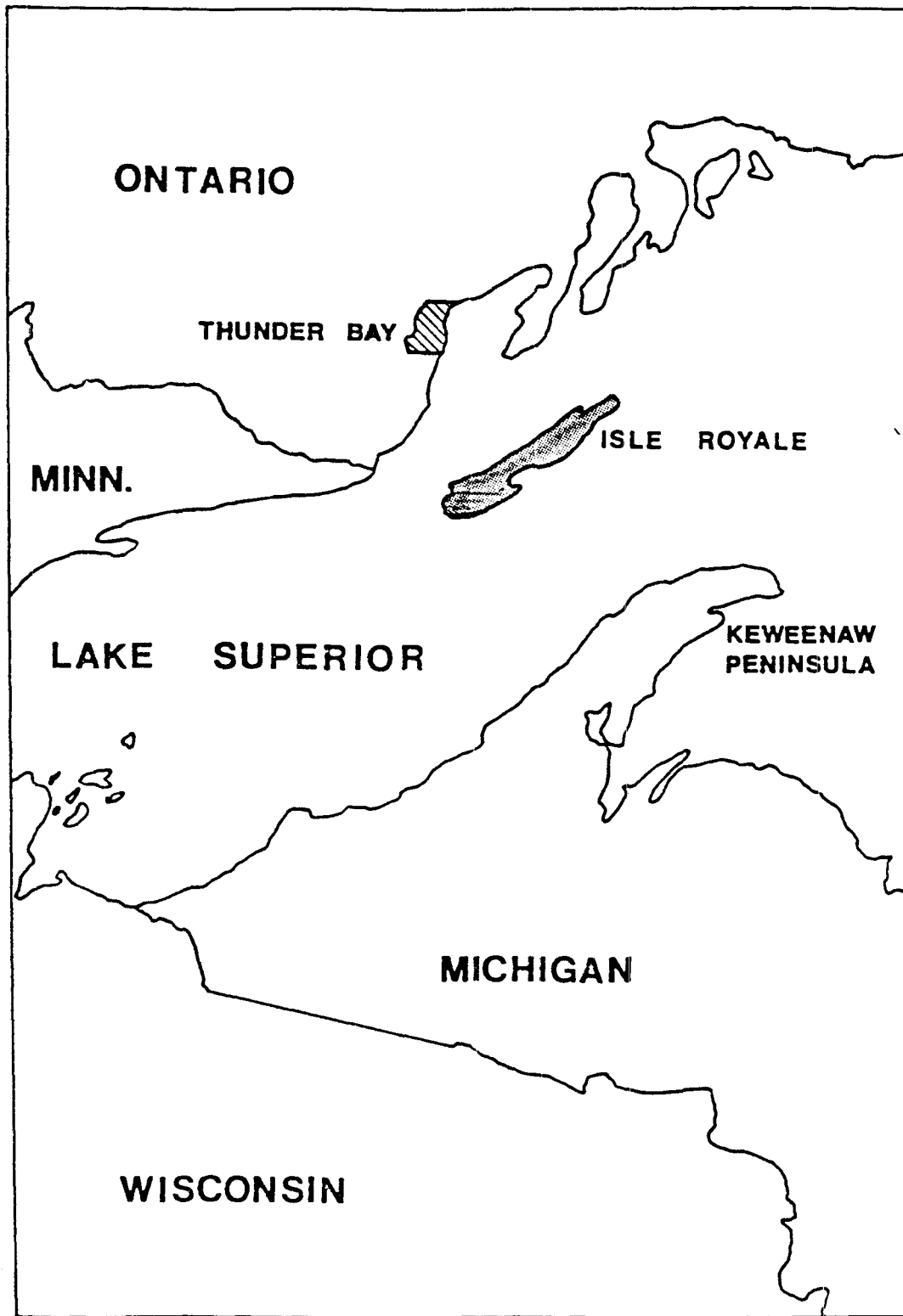


Figure 1. Location of project area.
(from Steigerwaldt and Meyer 1979)

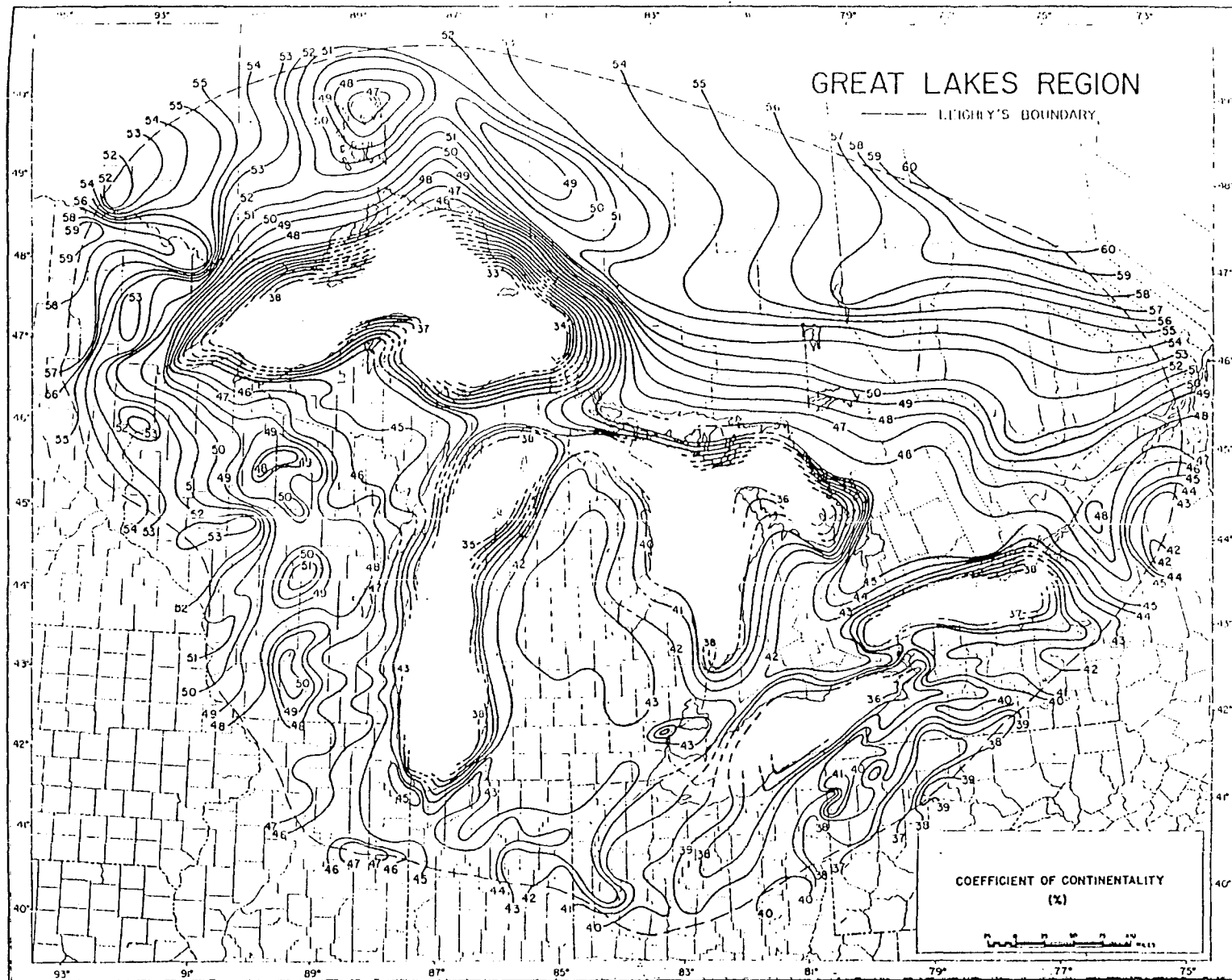


Figure 2: Location of study sites and their degree of continentality (from Kopec 1965).

Lily Lake

Isle Royale National Park

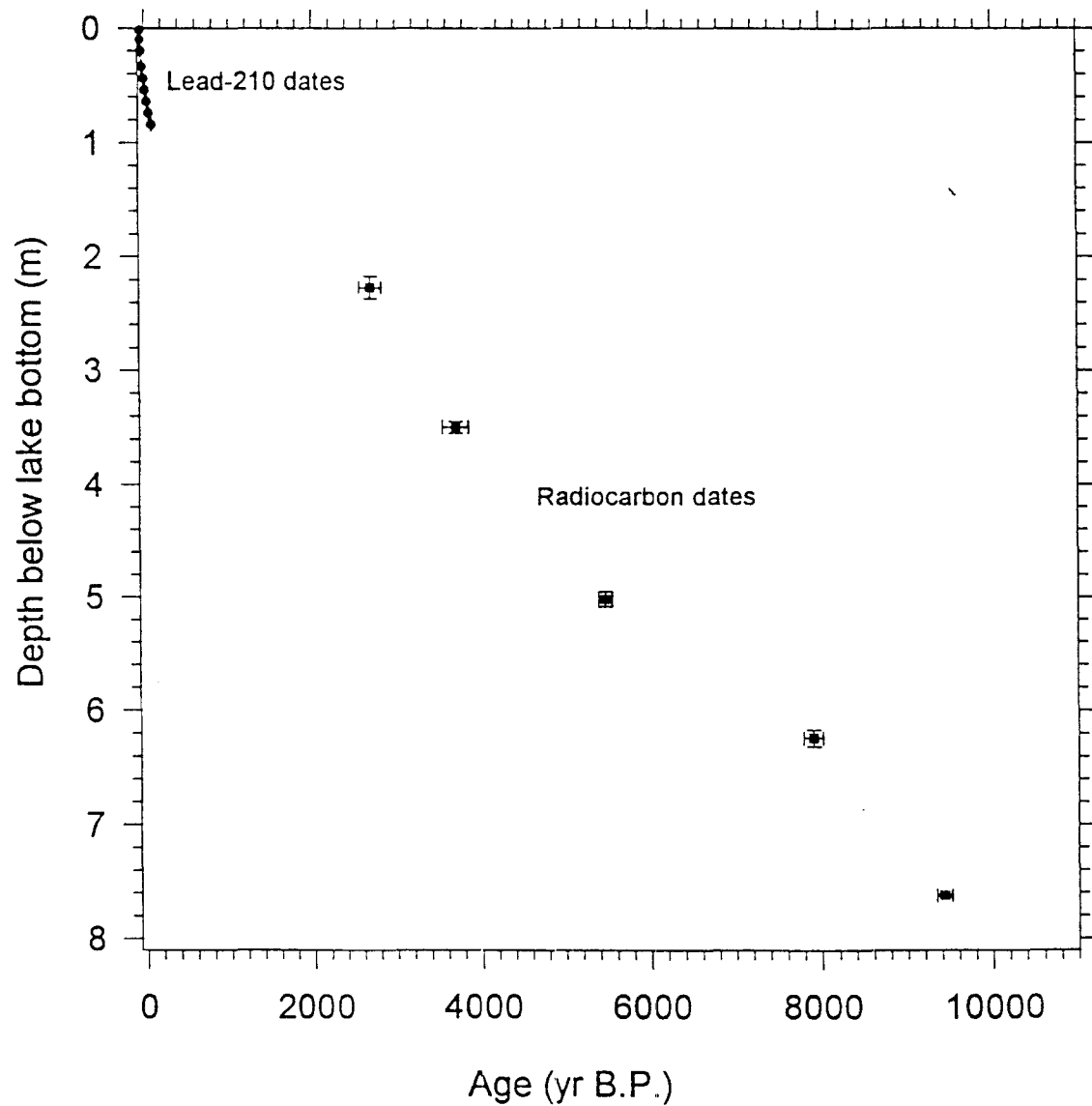


Figure 3: Radiocarbon dates for Lily Lake.

Lake Ojibway

Isle Royale National Park

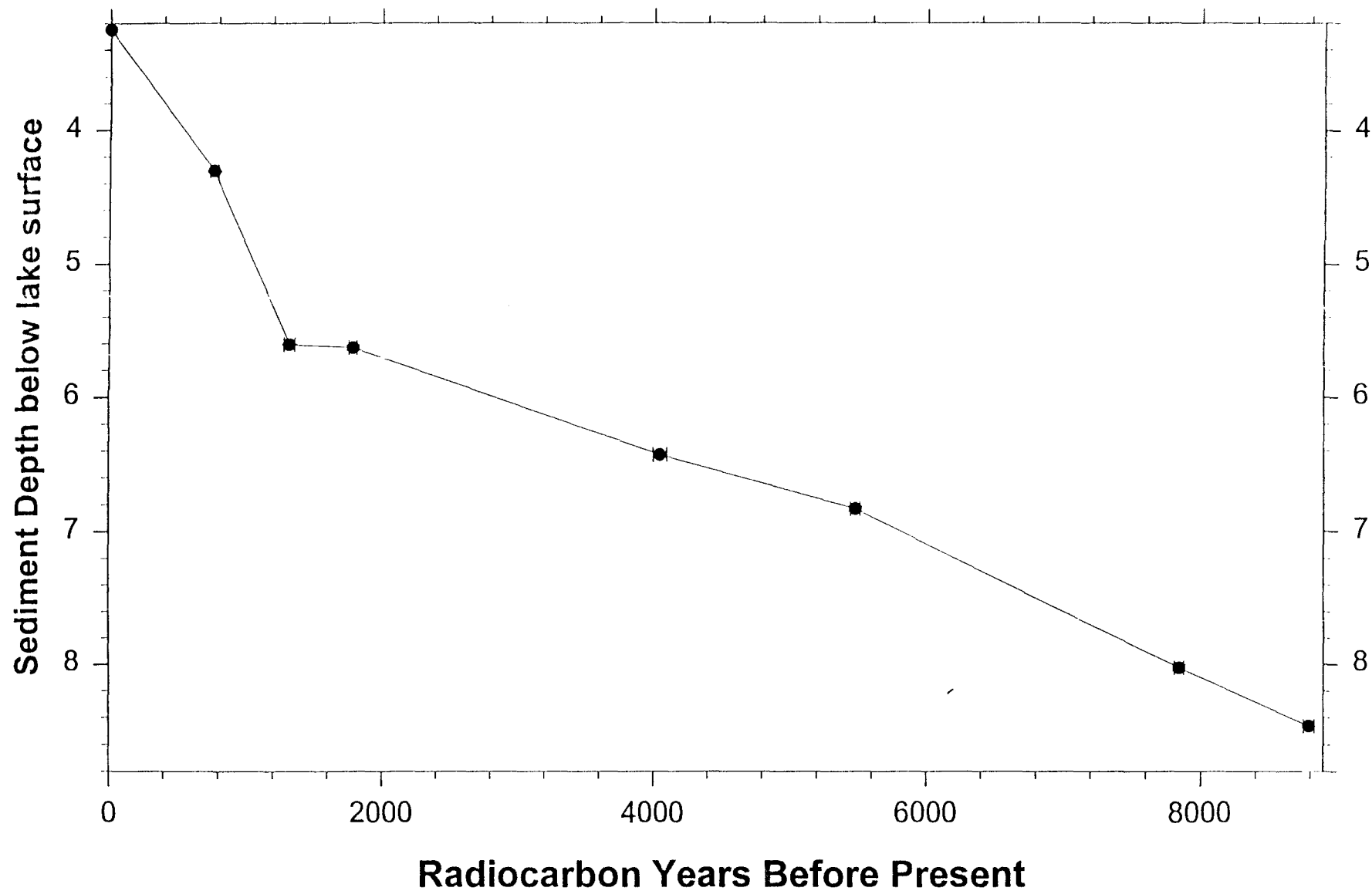


Figure 4: Radiocarbon dates for Lake Ojibway.

Lily Lake, Isle Royale N.P.

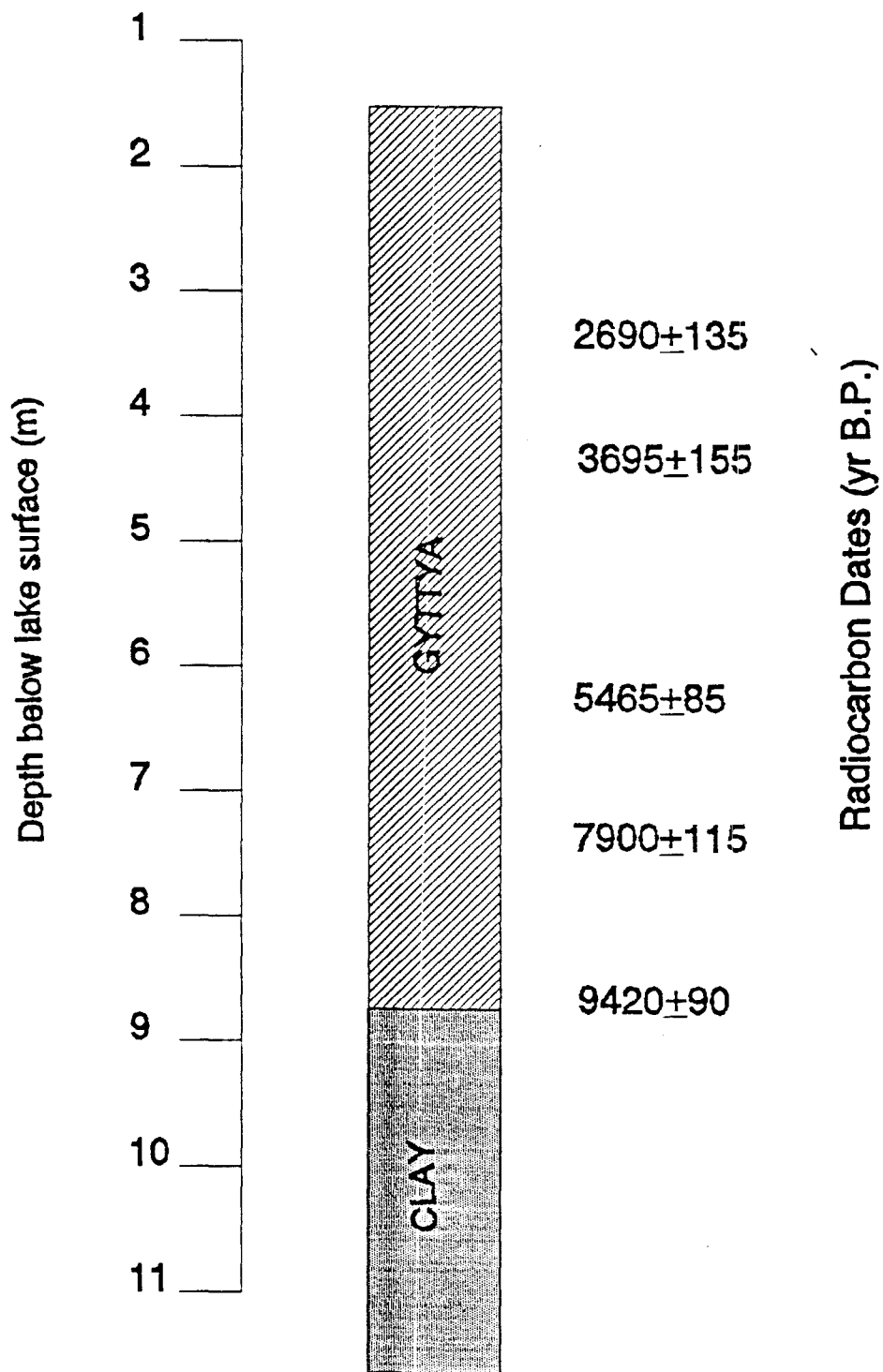


Figure 5: Composition of Lily Lake long core.

Lily Lake, Isle Royale N.P.

Loss-on-Ignition

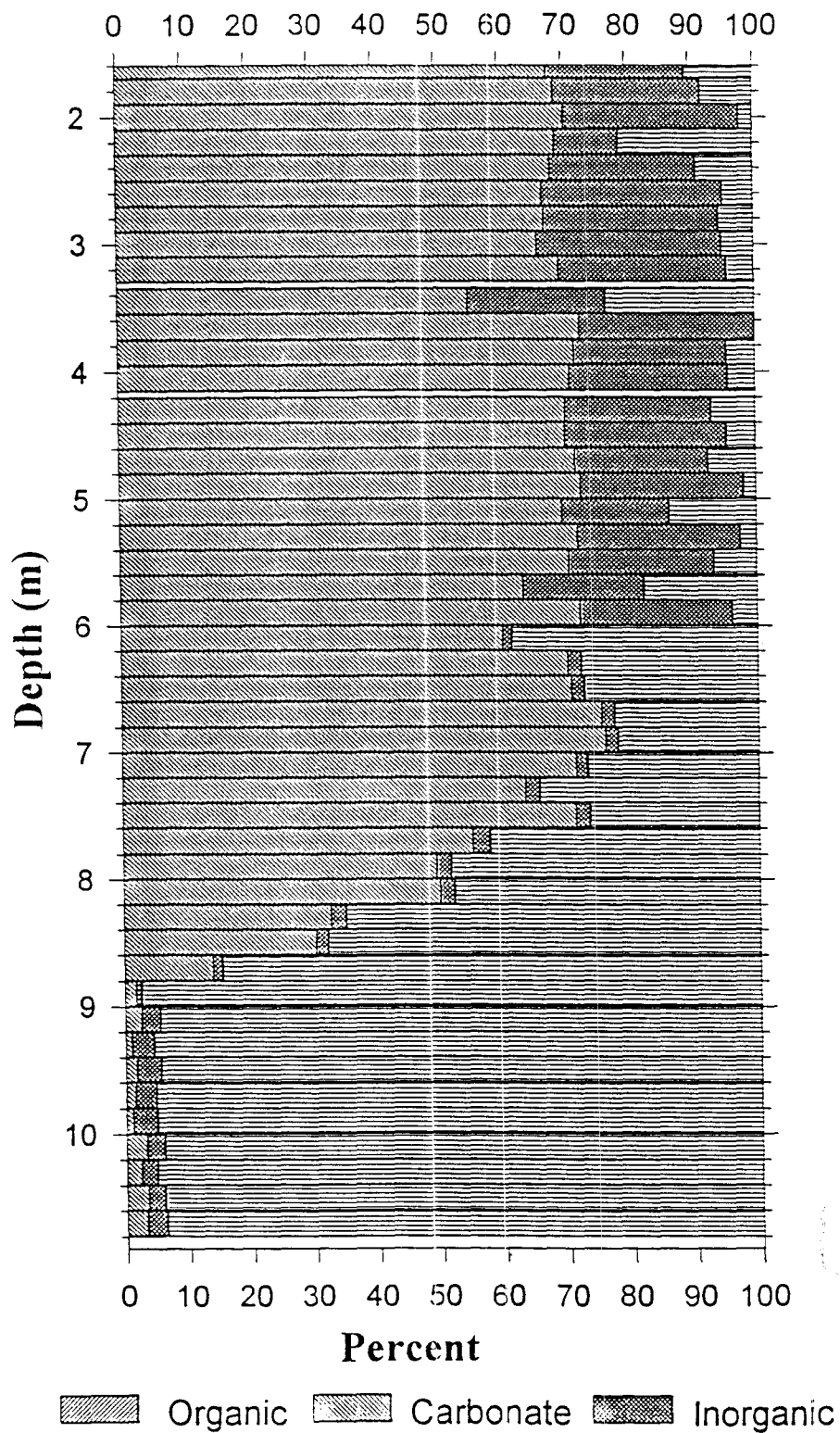


Figure 6: Loss-on-ignition of Lily Lake long core.

Lake Ojibway, ISRO

Loss on Ignition

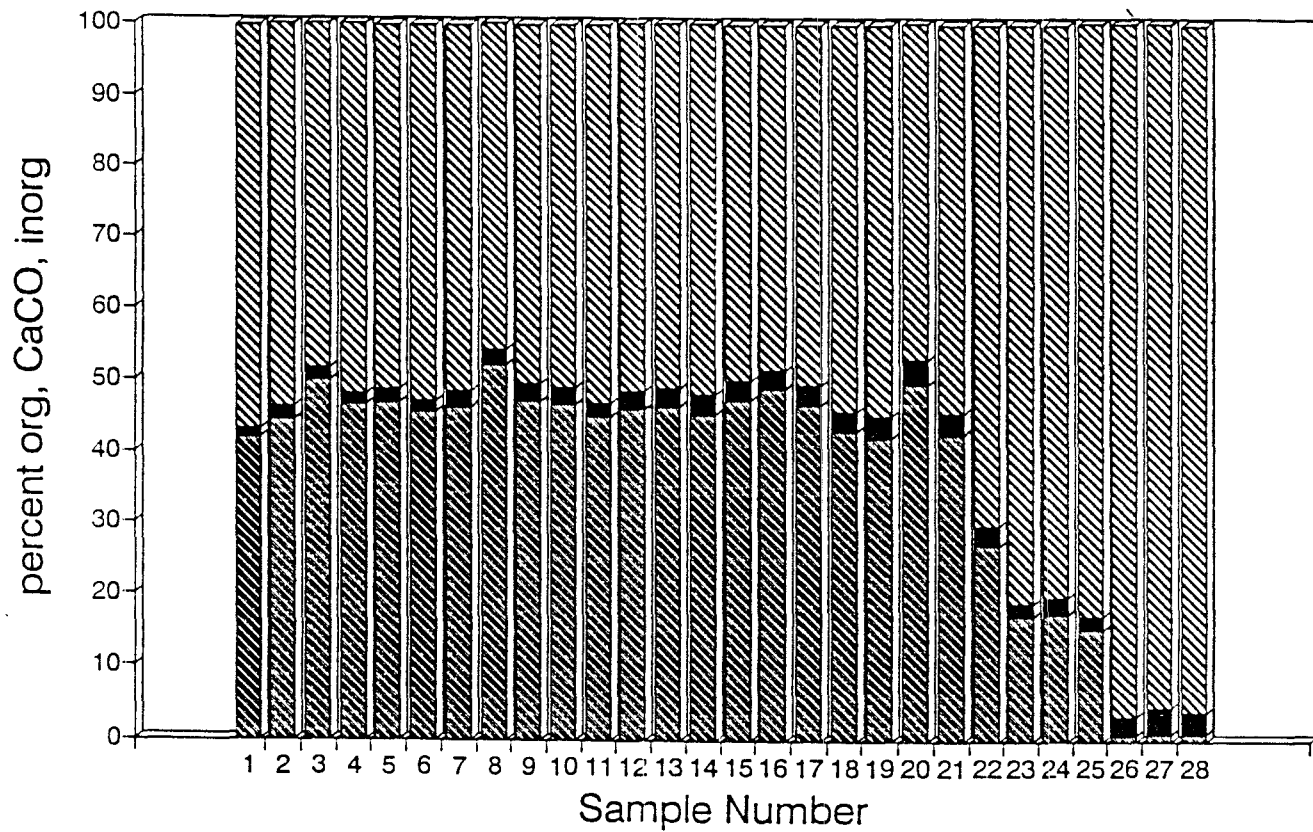


Figure 7: Loss-on-ignition of Lake Ojibway long core.

Lily Lake, Isle Royale
 Pollen analyst: Robyn Talbot

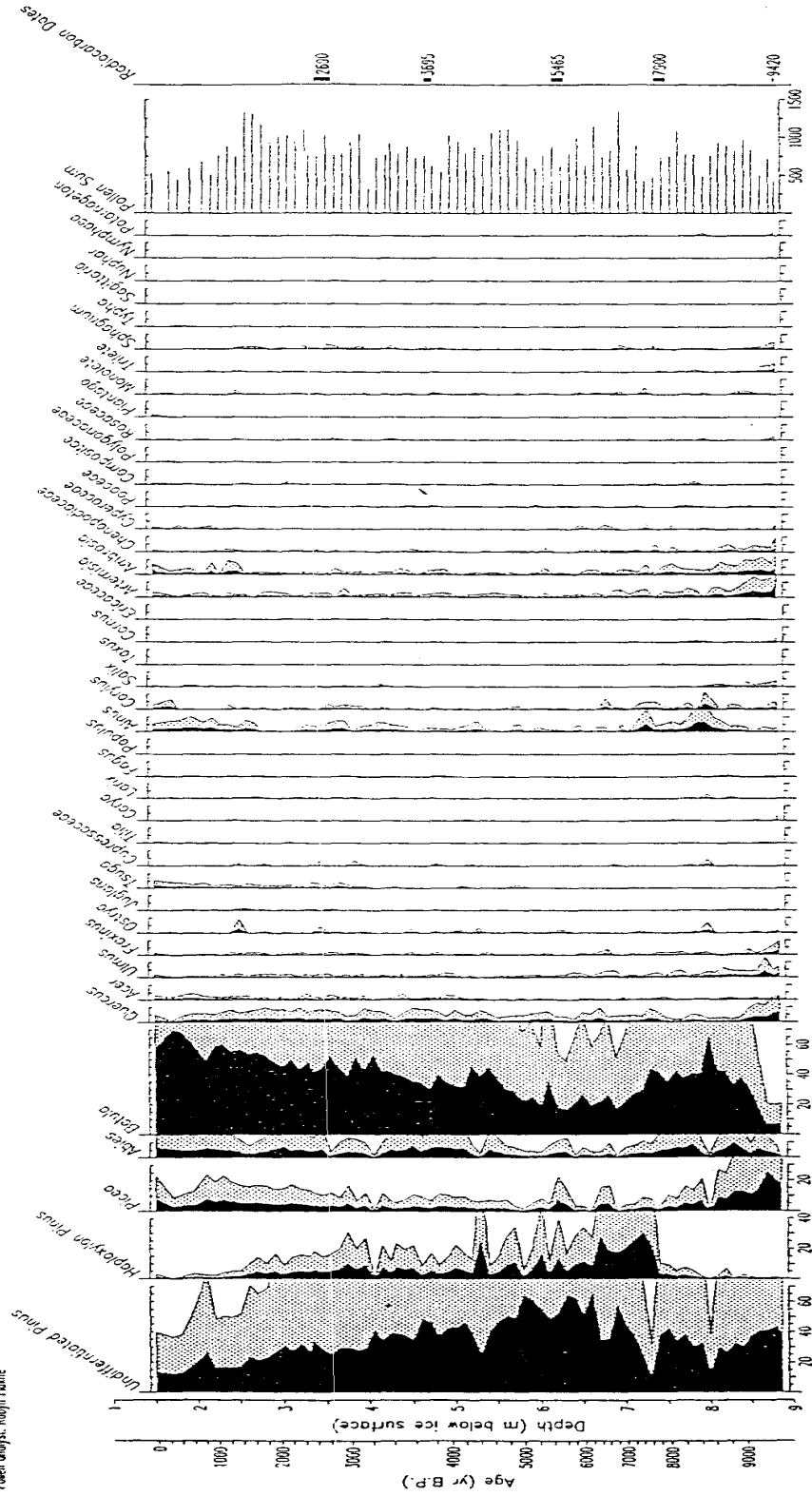


Figure 8: Lily Lake long core pollen diagram.

Exaggeration = 3x

Lily Lake Short Core

3/15/96

Robin Hane

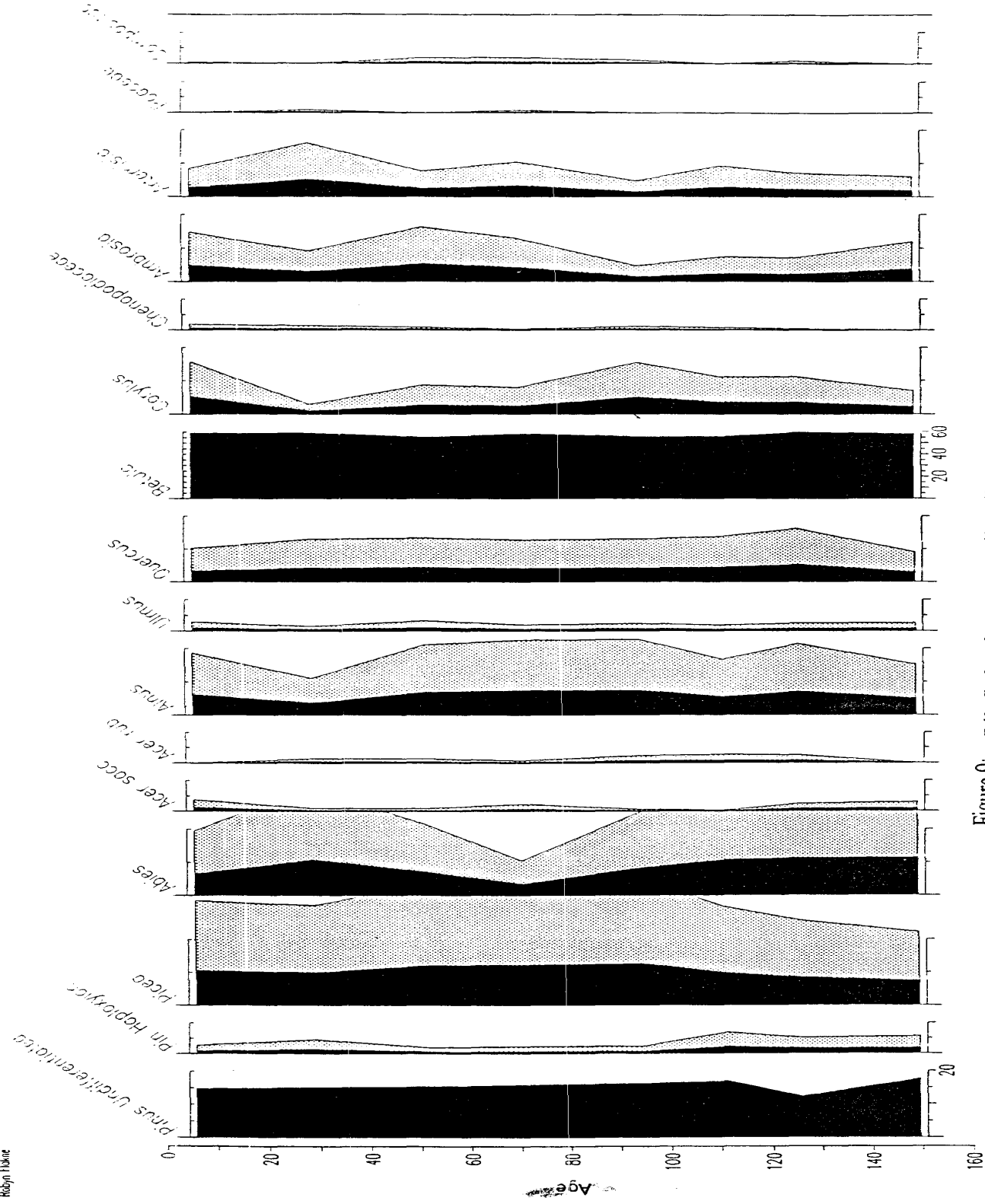


Figure 9: Lily Lake short core pollen diagram.

Lake Ojibway, Isle Royale

Pollen analyst: Robyn Tinkler

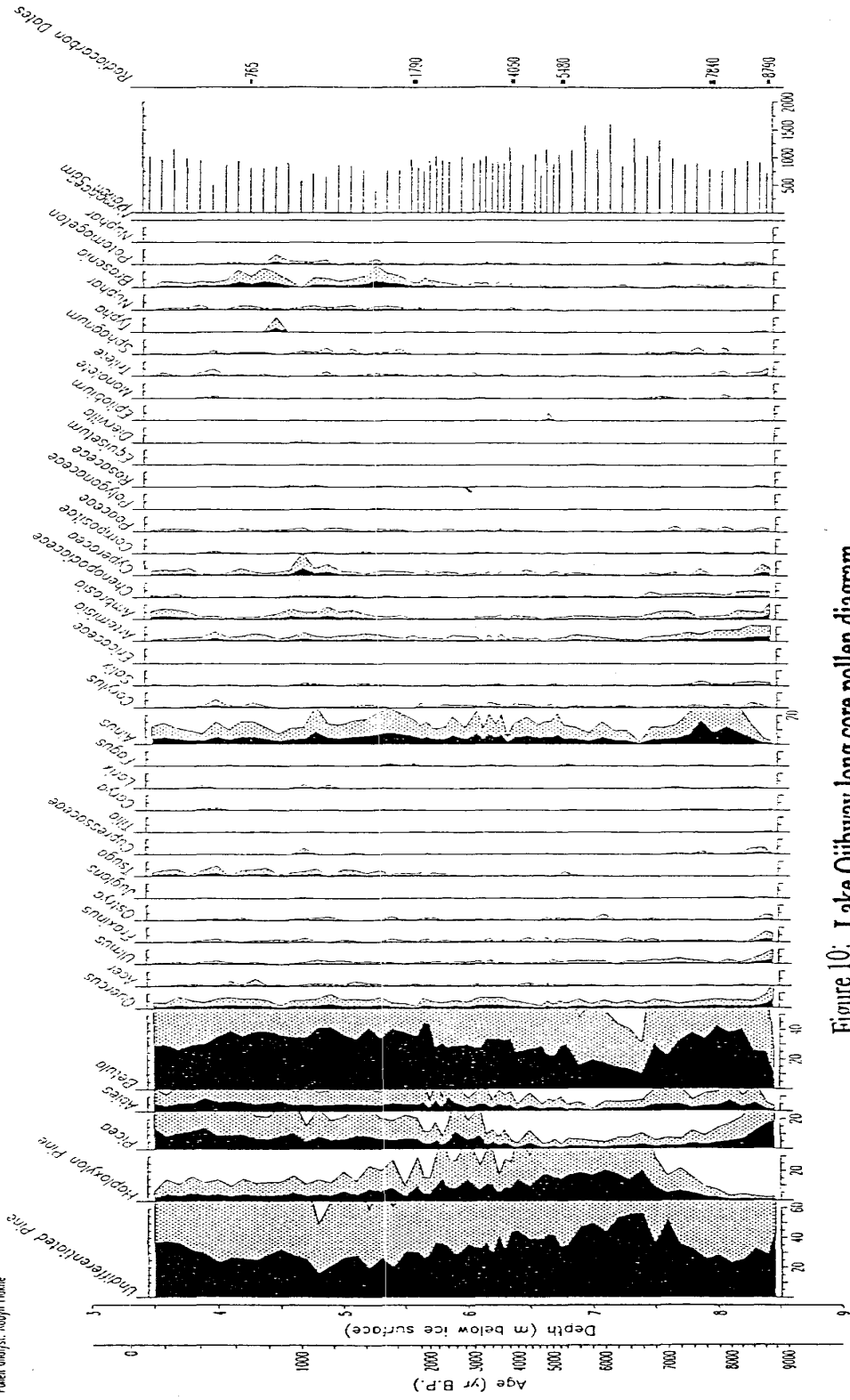


Figure 10: Lake Ojibway long core pollen diagram.

Exaggeration = 3x

Lake Ojibway (11)

Isle Royale

7/2/96

Robyn Flakne

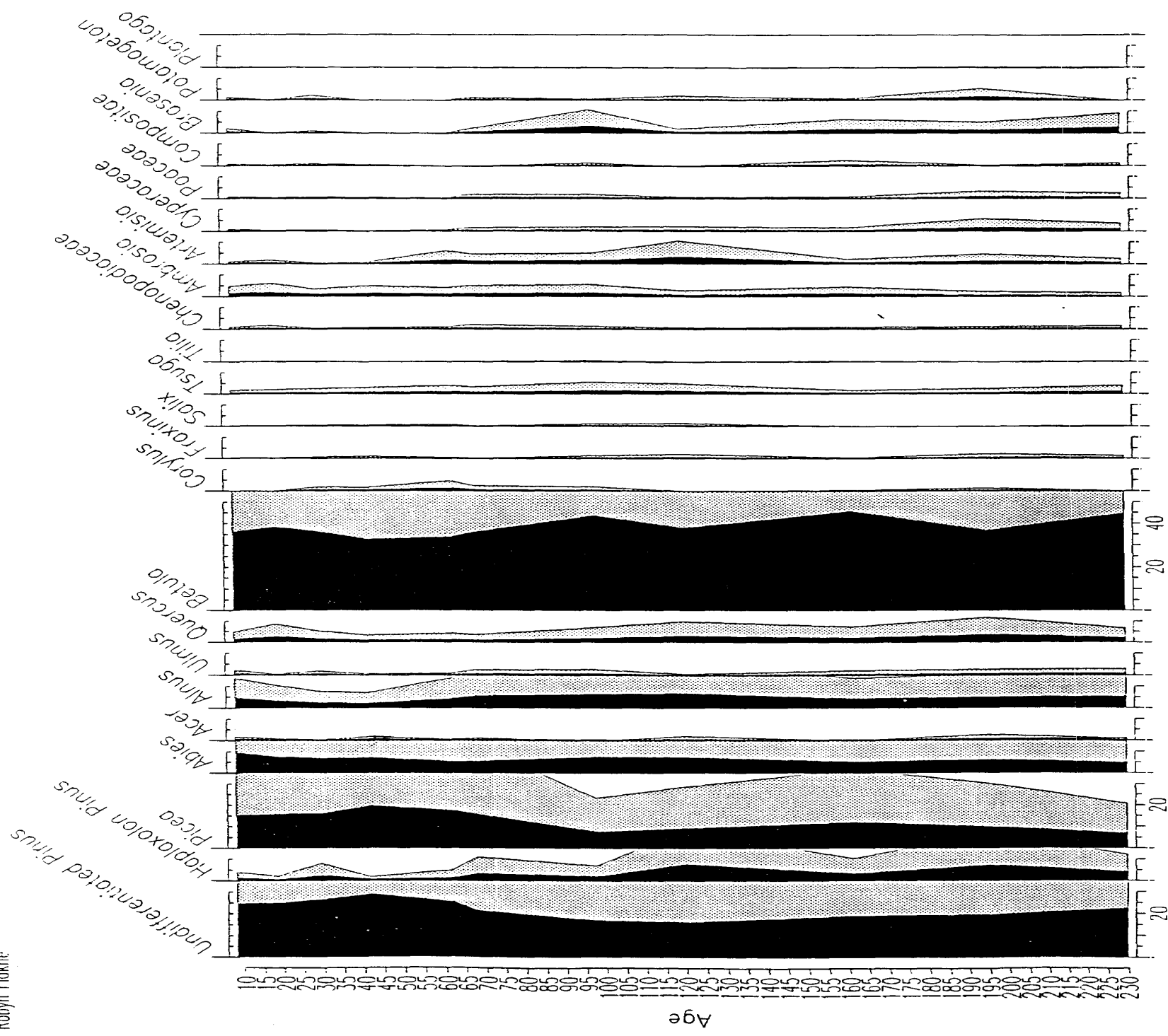


Figure 11: Lake Ojibway short core pollen diagram.

Exaggeration = 3X

Wallace Lake Short Core

2/22/96
Robyn Fane

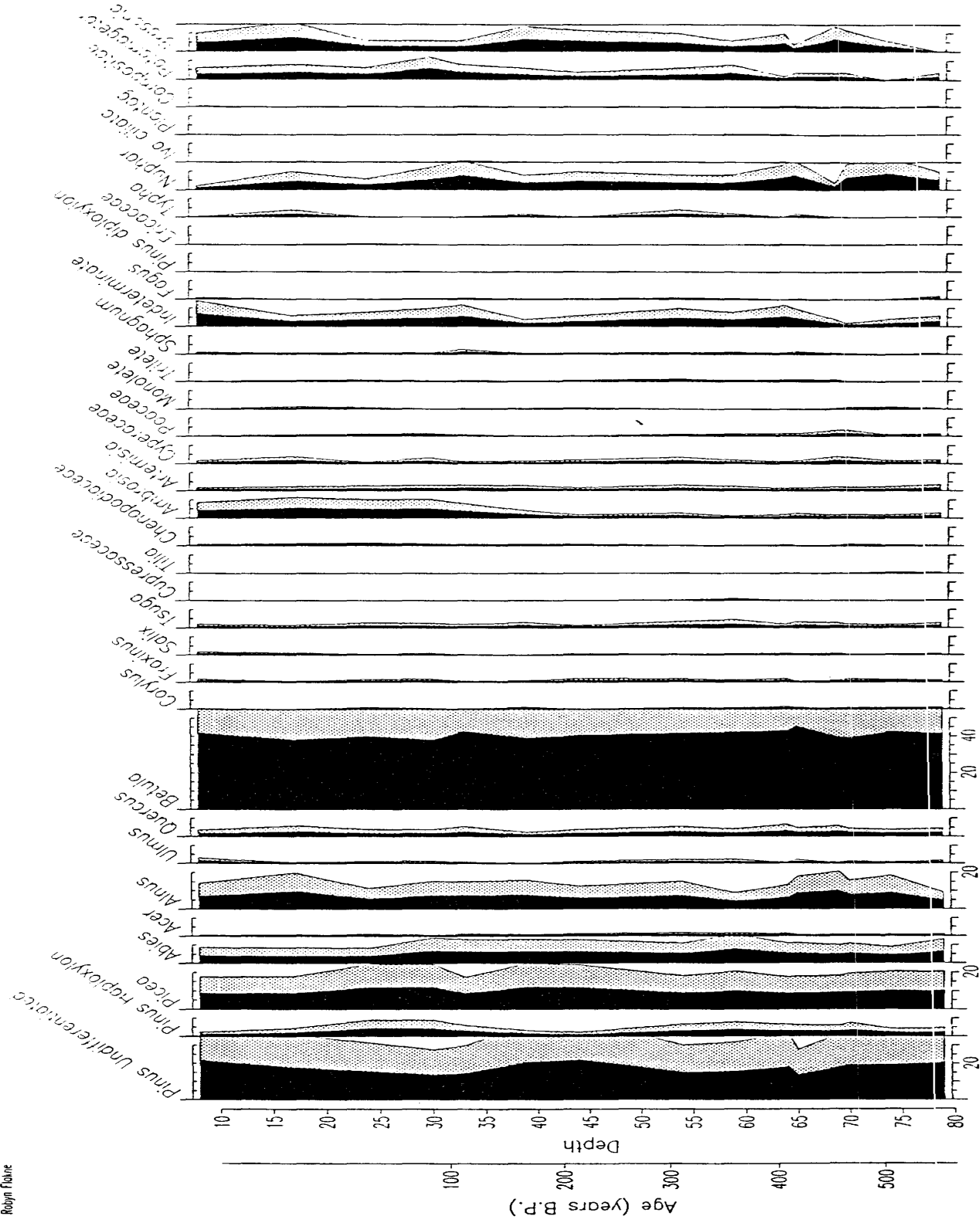


Figure 12: Wallace Lake short core pollen diagram.

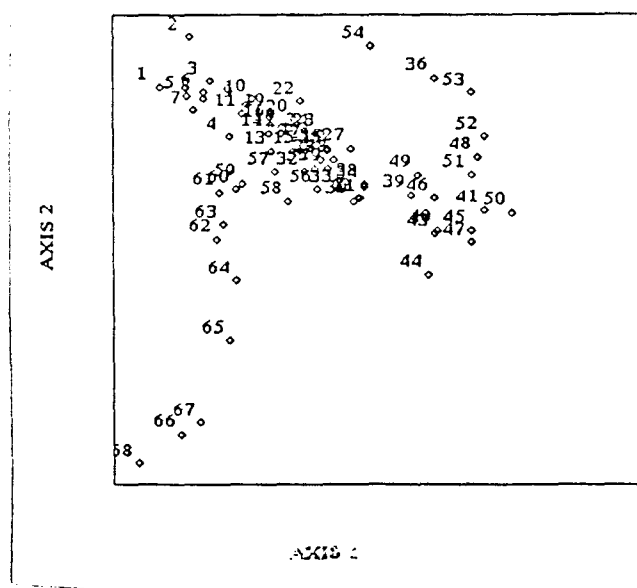


Figure 13: Lily Lake detrended correspondence analysis ordination.

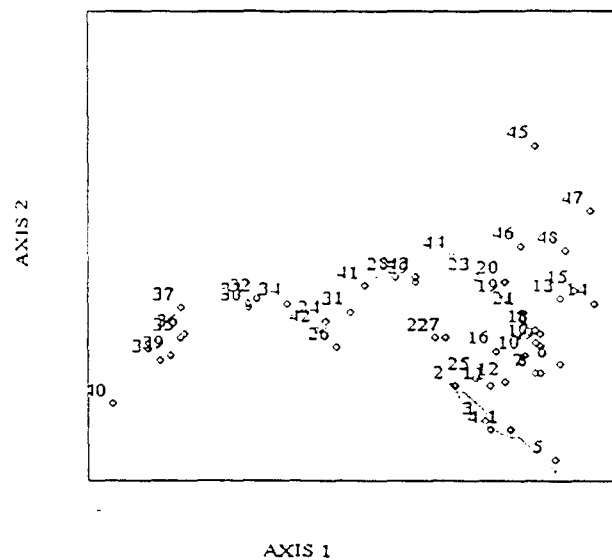


Figure 14: Lake Ojibway detrended correspondence analysis ordination.

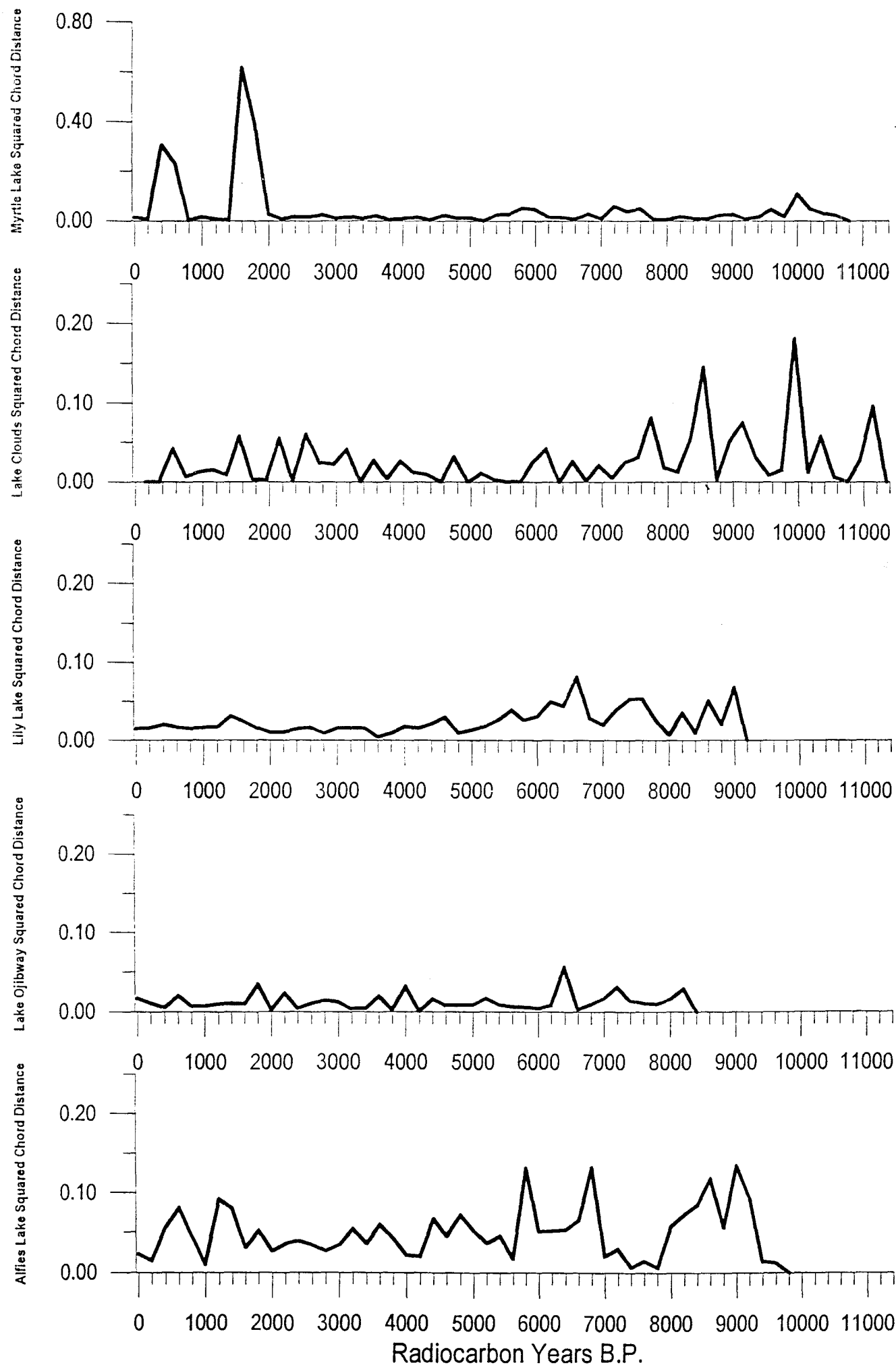


Figure 15: Holocene rates of vegetation change at five Great Lakes-region sites.

151000' 9200

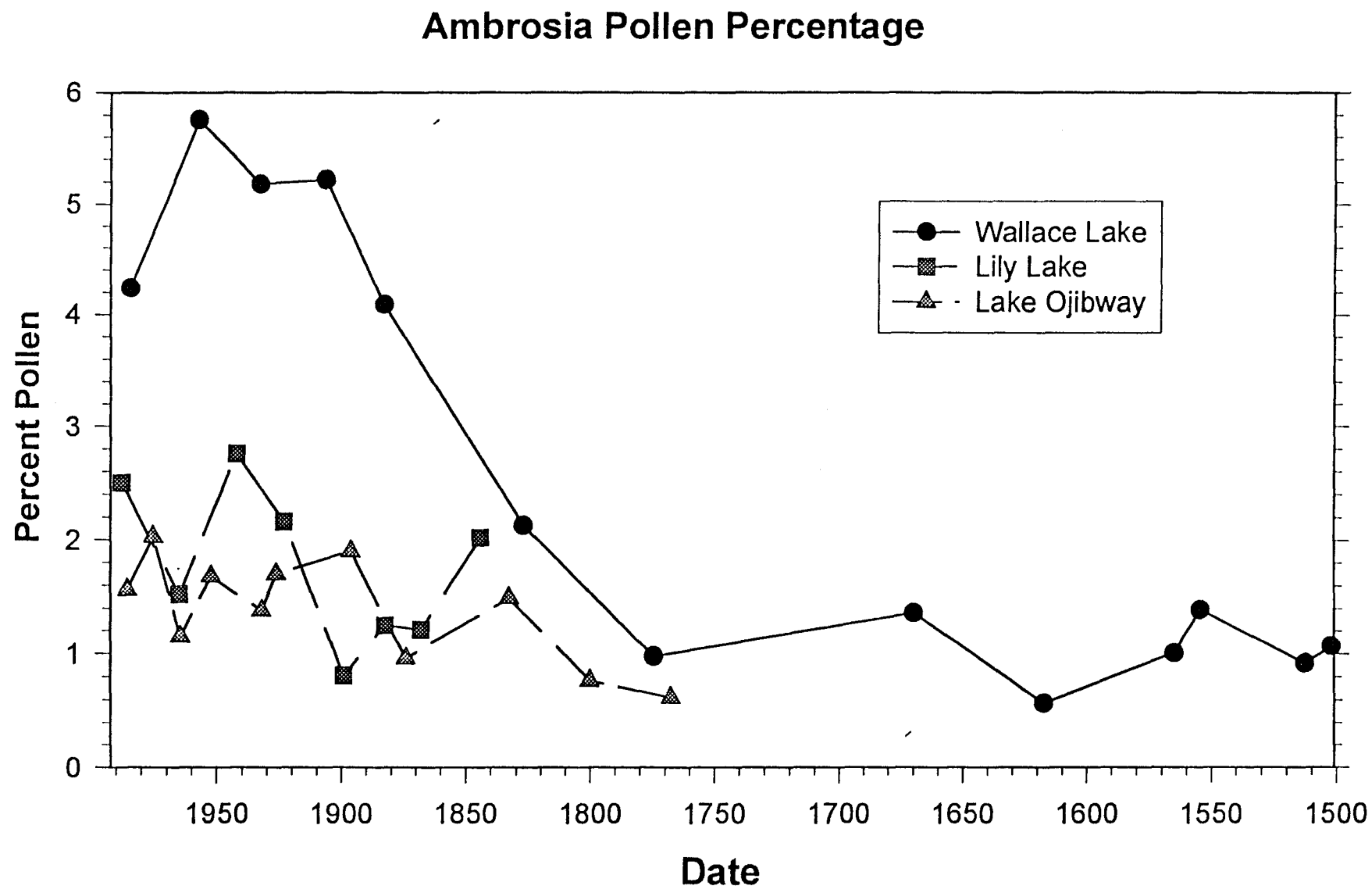


Figure 16: Ragweed (*Ambrosia*) pollen percentages in the short cores of Lily Lake, Lake Ojibway, and Wallace Lake.

Appendix A: Pollen counts from Lily Lake

11/20/1 WKL - Counts

Depth	Pinus U	Pin Hap	Picea	Abies	Acer sa	Acer ru	Alnus	Ulmus	Quercus
1.5	69	5	40	34	5	0	9	3	8
1.7	67	0	16	32	4	0	13	1	2
1.8	57	2	16	22	5	0	11	1	6
1.95	111	7	26	29	9	1	20	2	12
2.1	180	6	55	45	6	0	15	3	14
2.2	83	4	33	31	4	0	16	1	9
2.3	128	11	60	41	5	0	12	6	18
2.4	147	15	57	43	8	5	14	4	25
2.5	129	13	42	28	6	1	8	6	16
2.6	314	46	72	35	13	0	34	5	33
2.7	283	62	75	47	6	2	27	8	37
2.8	236	40	66	54	8	0	0	10	38
2.9	256	52	46	56	2	0	4	8	26
3	312	30	51	76	9	3	2	6	30
3.1	279	48	61	50	0	0	1	7	25
3.2	306	51	46	55	6	1	3	3	32
3.3	296	54	51	50	16	3	18	9	25
3.35	258	47	31	34	7	0	10	3	20
3.45	212	37	27	46	4	0	10	6	22
3.55	262	57	42	14	12	2	21	9	27
3.65	224	51	23	26	6	5	19	2	18
3.75	237	82	45	34	5	0	20	5	11
3.85	252	62	21	38	4	0	3	4	15
3.95	300	95	42	35	10	1	13	9	33
4.05	130	0	1	2	0	0	5	1	8
4.15	255	55	29	25	1	3	16	4	19
4.25	307	30	17	45	3	2	14	3	12
4.3	361	73	18	46	6	0	15	3	8
4.4	299	51	20	43	11	1	11	6	17
4.5	303	66	33	72	2	2	10	3	28
4.6	359	22	24	34	3	3	3	2	22
4.7	352	45	18	55	5	3	7	5	23
4.8	228	20	24	47	2	0	5	3	15
4.9	236	27	20	39	6	0	4	6	7
5	444	79	32	63	10	0	6	10	28
5.1	445	56	32	63	4	0	10	0	16
5.2	313	35	19	23	2	0	12	3	13
5.3	220	214	19	9	4	0	22	0	24
5.4	307	22	19	44	0	0	5	1	16
5.5	500	53	24	46	0	0	4	2	11
5.6	557	105	28	30	4	2	1	6	14
5.7	547	129	13	26	1	0	16	3	17
5.8	624	19	7	16	6	0	17	5	15
5.9	459	54	14	11	0	0	1	5	14
6	328	97	17	8	2	0	6	3	13
6.1	375	30	13	22	2	0	4	2	19
6.2	462	118	67	34	1	1	4	4	11
6.3	401	35	30	27	0	0	2	4	8
6.4	496	78	10	5	0	0	8	9	6
6.5	507	113	12	23	2	0	15	9	22
6.6	411	57	2	8	2	0	0	2	11
6.7	394	318	62	15	2	0	13	11	39
6.8	267	139	41	24	2	0	8	11	9
6.9	462	147	2	6	0	0	2	13	12
7	594	280	19	30	9	0	22	6	22
7.1	217	150	9	16	0	0	2	3	10
7.2	209	277	28	33	3	0	28	3	13
7.3	39	101	11	13	1	0	23	3	13
7.4	183	16	5	25	2	0	6	5	11
7.5	294	24	26	44	4	0	14	4	8
7.6	257	14	21	53	1	0	18	10	5
7.7	415	28	59	71	1	0	18	16	7
7.8	237	14	36	71	1	0	26	4	14

7.9	258	5	55	30	3	1	52	5	12
8	63	0	0	4	1	0	33	6	4
8.1	231	7	70	37	1	0	25	9	7
8.2	249	22	78	61	4	0	23	20	10
8.3	289	0	117	89	4	0	12	13	7
8.4	253	8	108	53	1	0	12	12	11
8.5	365	4	110	30	1	0	11	13	32
8.6	343	2	128	51	5	0	3	12	35
8.7	209	2	128	22	0	1	6	23	19
8.8	313	3	149	22	5	0	6	12	49
8.87	162	0	76	1	4	0	4	11	29

Betula	Corylus	Ostrya	Fraxinu	Juglans	Juglans	Salix	Tsuga	Cupress	Tilia
302	5	0	3	0	0	1	9	0	2
386	12	1	0	0	0	0	7	0	0
305	0	0	0	1	0	0	6	0	0
356	0	0	1	1	0	3	5	0	0
337	0	0	2	0	0	0	8	0	0
307	0	0	2	1	0	1	3	0	1
462	0	0	0	1	0	0	6	0	0
497	9	0	6	2	0	1	8	0	0
426	0	23	3	0	3	1	4	5	0
720	7	0	7	0	6	0	15	0	0
713	0	0	9	1	2	0	11	1	0
621	5	5	7	0	2	2	7	6	0
452	0	0	0	0	0	0	6	0	0
460	0	1	7	1	0	0	7	0	0
509	4	0	2	0	0	0	9	0	2
415	3	0	5	0	0	0	2	0	0
526	3	0	6	0	2	0	9	0	1
317	0	0	2	0	5	0	10	3	0
330	0	11	3	0	0	1	9	8	0
537	12	2	7	0	4	0	4	1	1
340	5	1	4	0	1	0	12	0	0
311	8	0	3	0	0	2	8	0	0
479	7	1	5	0	2	1	3	11	1
451	8	3	5	0	0	1	5	3	0
171	0	0	0	0	0	0	0	0	0
313	4	0	1	0	0	5	0	0	0
328	2	0	2	0	0	2	1	0	0
370	0	0	3	0	0	0	4	0	0
308	0	0	1	0	0	0	0	0	1
315	3	7	6	0	1	2	0	0	0
256	0	0	2	0	1	0	0	0	0
232	0	0	1	0	0	0	0	0	0
245	3	2	5	0	1	0	0	4	0
194	0	0	0	0	0	0	0	0	0
337	1	3	3	0	0	0	0	0	0
303	2	6	2	0	0	1	6	0	1
365	1	0	3	0	0	1	1	3	0
343	0	10	1	0	0	0	0	0	1
345	0	0	5	0	0	0	0	0	0
399	0	0	2	0	0	0	0	0	0
337	2	0	1	0	1	0	1	0	1
319	7	3	1	0	0	0	6	1	0
222	7	3	3	0	0	0	7	0	0
191	0	0	2	0	0	0	0	0	0
116	2	0	0	0	0	0	0	0	0
275	2	0	4	0	0	0	1	0	0
161	1	5	0	0	0	0	0	0	0
102	2	4	1	0	0	0	0	1	0
174	0	0	0	0	0	0	0	1	0
263	0	0	5	0	0	0	0	0	0
124	0	0	1	0	0	0	0	0	1
260	0	0	7	0	0	0	0	0	0
195	18	0	10	0	0	0	0	0	0
141	4	0	1	0	0	0	0	3	0
305	5	0	1	0	1	0	0	0	0
160	0	0	2	0	0	0	1	0	0
263	12	3	1	0	0	0	0	0	0
188	7	0	0	0	0	0	0	0	0
199	8	0	3	0	0	1	1	0	0
263	6	0	4	1	0	1	1	0	0
318	2	0	5	0	0	1	0	0	0
413	7	0	9	1	0	1	0	0	0
321	12	0	1	0	0	0	0	2	1

318	0	5	4	0	2	0	0	0	0
315	19	11	3	0	0	1	0	7	0
329	14	0	1	0	0	4	0	0	0
398	0	0	0	2	2	6	0	0	0
301	10	0	2	0	1	3	0	0	0
315	9	0	3	0	2	1	0	0	0
299	1	0	14	0	3	11	0	0	0
150	4	3	4	0	1	5	0	0	0
35	2	0	6	0	1	4	0	0	1
49	12	2	17	0	0	8	0	0	1
31	7	2	14	0	2	6	0	0	0

Taxus	Chenopo	Ambrosi	Artemis	Lycopod	Cyper	Poaceae	Larix	Carya	Polygon
0	2	11	6	31	3	0	0	0	0
0	0	4	3	113	0	0	1	0	2
0	1	5	1	89	4	0	0	0	0
0	0	8	4	14	0	1	0	0	0
0	0	2	7	28	3	0	0	0	0
0	1	13	2	27	4	1	0	0	0
0	4	2	2	123	0	0	2	0	0
0	5	27	9	136	2	1	1	3	0
0	2	19	4	98	2	2	2	1	2
0	3	4	8	236	0	2	4	0	0
0	3	8	0	217	0	0	5	0	0
0	2	6	14	199	1	0	3	1	0
0	5	4	12	197	0	1	0	0	0
0	0	6	11	103	0	0	0	0	0
0	3	3	8	174	1	0	0	0	0
0	4	2	3	135	2	0	4	0	0
0	3	7	7	90	0	4	0	0	0
0	1	2	7	160	0	1	4	0	0
0	4	4	6	108	1	1	2	0	0
0	0	4	11	164	0	1	0	1	0
0	2	11	3	144	0	0	5	0	0
0	0	5	17	97	0	0	0	0	0
0	3	4	4	106	0	0	4	1	0
0	2	8	5	172	1	3	0	0	0
0	0	0	2	74	0	0	0	0	0
0	0	4	6	117	0	0	0	0	0
0	0	4	4	66	0	0	0	0	0
0	1	5	6	142	0	0	2	0	0
0	1	11	8	173	0	0	0	0	0
0	5	9	9	140	1	3	0	0	0
0	4	0	4	65	0	1	0	0	0
0	2	7	5	37	2	1	4	0	0
0	1	6	5	69	0	2	0	0	0
0	0	7	6	48	0	0	0	0	0
0	1	8	9	62	0	0	0	0	0
0	1	1	2	73	0	2	1	2	0
0	0	3	5	95	1	1	0	2	0
0	0	5	6	76	0	3	0	0	0
0	2	3	6	120	0	0	2	0	0
0	1	6	11	49	0	1	0	0	0
0	2	4	9	56	0	0	1	0	0
0	3	6	7	72	1	4	1	1	0
0	4	2	6	97	1	3	2	0	0
0	2	2	2	62	0	0	0	0	0
0	0	3	0	17	0	3	0	0	0
0	7	12	8	107	0	0	1	0	0
0	1	3	1	57	3	1	0	0	0
0	0	3	4	59	0	1	1	0	0
0	0	2	3	54	0	2	0	0	0
0	3	4	8	91	10	1	0	0	0
0	2	7	1	44	2	0	0	0	0
0	7	14	12	93	0	3	0	0	0
0	3	3	3	49	8	0	0	0	0
0	3	4	12	69	5	0	0	0	0
0	5	18	22	67	0	2	3	0	0
0	2	7	4	50	0	1	0	0	0
0	5	7	14	91	0	3	0	0	0
0	1	9	8	66	5	0	0	0	0
0	8	1	1	52	0	0	0	0	0
2	1	14	10	56	0	0	0	0	0
0	9	20	9	105	7	0	0	3	0
0	6	13	14	82	1	4	0	0	0
0	1	9	16	75	2	4	3	1	0

0	4	9	12	41	0	1	0	1	0
0	1	5	1	61	2	1	5	0	0
0	4	10	18	78	1	0	0	0	0
0	12	24	22	83	0	0	0	0	0
0	16	19	11	86	1	0	4	0	0
0	7	16	18	63	0	1	0	0	0
0	7	31	34	80	0	3	0	0	0
0	13	27	39	107	5	2	0	3	0
0	6	16	19	69	0	1	0	0	0
0	8	20	32	106	1	1	0	1	0
0	14	16	37	193	5	1	0	5	0

Rosacea Mono	Trilete	Sphagnum	Indeter	Cornus	Fagus	Pinus d	Ericace	Typha
0	0	0	0	0	0	1	0	0
1	2	1	0	7	0	0	0	0
0	0	0	0	2	0	0	0	2
0	0	0	0	4	0	1	0	0
1	0	0	1	4	0	0	0	0
0	0	2	1	5	0	0	0	0
1	0	0	1	19	0	0	0	1
0	0	0	2	38	0	2	0	0
2	7	3	3	42	0	0	0	0
0	0	1	9	40	0	0	0	1
0	2	0	8	40	0	2	0	0
0	1	0	5	47	2	2	33	0
0	1	2	0	32	0	1	0	0
0	2	0	4	74	0	0	0	2
0	0	1	2	32	0	0	0	2
1	5	2	1	36	0	0	0	1
0	2	1	10	29	0	2	0	0
1	0	0	3	31	0	0	0	0
1	3	1	3	37	0	0	0	1
2	0	0	13	41	0	0	0	0
3	0	0	7	23	0	0	0	1
0	0	0	3	22	0	2	0	0
0	0	0	2	29	0	1	6	0
0	7	2	8	34	0	0	7	2
0	0	0	1	13	0	0	0	0
0	0	0	3	20	0	0	0	0
1	1	0	2	14	1	0	0	3
4	0	0	9	31	0	0	0	0
0	0	0	1	31	0	0	0	1
1	3	0	0	38	0	0	0	0
0	0	0	0	48	0	0	0	0
1	0	0	5	49	0	0	0	0
0	3	1	1	54	0	1	5	0
0	1	0	2	36	0	1	0	1
2	0	0	0	42	0	0	0	0
0	1	1	0	39	0	0	0	0
1	1	0	1	51	0	0	0	0
0	3	1	0	41	0	0	0	0
1	1	0	0	47	0	0	0	0
0	0	0	0	36	0	0	0	0
0	0	0	2	61	0	0	0	0
2	0	0	1	59	0	0	0	0
2	4	0	3	88	0	0	0	0
0	0	0	0	92	0	0	0	0
0	1	0	0	37	0	0	0	0
0	2	0	2	41	0	0	0	0
0	2	0	0	67	0	0	2	0
0	0	0	0	54	0	0	0	0
0	0	0	0	81	0	0	1	0
0	5	1	0	61	0	0	0	0
0	0	0	0	74	0	0	0	0
0	4	0	0	74	0	0	0	0
0	2	0	0	29	0	0	0	0
0	2	0	0	41	0	0	0	0
2	8	0	13	51	0	0	12	0
1	0	0	3	43	0	0	0	0
0	1	0	0	69	0	0	0	0
0	6	0	0	97	0	0	7	0
0	0	0	4	27	0	0	0	1
0	0	3	0	43	0	0	21	0
2	0	0	0	47	0	0	0	0
0	0	3	0	52	0	1	0	0
1	2	1	3	53	1	0	0	0

0	0	4	3	51	3	1	0	0	0
2	2	1	2	54	1	0	0	0	0
0	0	0	3	48	0	1	0	0	0
0	0	2	0	36	0	4	0	0	0
0	0	1	0	32	0	2	0	0	0
0	4	0	2	36	0	0	0	1	0
0	8	3	3	30	0	0	0	2	0
0	4	3	4	28	0	0	0	3	0
0	1	7	3	14	0	0	0	1	0
4	2	11	10	23	2	2	3	0	1
3	0	9	7	17	4	0	0	0	0

[illegible]

0	0	0	0
0	0	0	0
0	0	0	1
0	0	0	3
0	0	0	0
0	0	0	1
0	0	0	2
0	0	0	0
0	0	0	4
0	0	0	0
0	0	0	3

Appendix B: Pollen counts from Lake Ojibway

Depth	Pinus un	Pinus ha	Picea	Abies	Acer sac	Acer rub	Alnus	Ulmus
3.5	372	22	147	52	2	1	41	3
3.6	367	47	86	38	1	1	46	3
3.7	421	43	128	67	6	2	43	7
3.8	320	55	123	59	2	6	31	1
3.9	276	39	139	89	1	2	24	6
4	118	24	47	33	0	1	25	4
4.1	231	29	83	63	11	4	28	4
4.2	243	47	95	62	4	1	48	3
4.3	204	33	60	43	14	1	42	4
4.4	233	34	58	50	3	1	31	2
4.5	271	36	77	60	4	0	20	0
4.6	254	52	99	40	2	1	34	2
4.7	147	22	30	30	3	0	22	3
4.8	116	34	62	31	5	3	62	7
4.9	142	27	42	31	4	0	30	5
5	236	58	62	47	4	2	38	7
5.1	241	38	78	45	10	0	46	5
5.2	151	61	69	37	6	4	44	5
5.3	108	28	28	18	2	0	29	2
5.4	155	71	49	45	1	2	63	3
5.5	239	26	58	41	3	0	53	1
5.6	292	95	67	48	6	4	53	3
5.65	212	43	33	52	2	1	34	5
5.7	223	38	29	19	4	0	38	3
5.75	347	95	56	69	0	5	34	6
5.8	367	147	29	32	3	1	37	8
5.85	317	87	56	90	3	2	37	3
5.9	261	81	109	56	2	0	57	6
6	360	144	65	30	3	0	38	5
6.1	293	69	81	47	6	0	67	7
6.15	343	109	30	47	1	0	34	4
6.2	305	113	44	25	4	1	70	11
6.25	367	51	24	43	2	0	40	4
6.3	292	85	39	33	3	1	62	4
6.35	386	77	17	39	3	3	15	3
6.4	535	171	15	18	4	0	56	2
6.5	344	89	35	36	7	0	54	3
6.6	421	188	13	16	3	3	47	6
6.65	286	122	9	18	5	1	35	3
6.7	478	184	25	27	5	0	60	14
6.75	302	133	9	28	3	2	62	6
6.8	368	183	24	15	5	2	45	7
6.9	538	220	24	23	4	0	43	9
7	796	278	28	9	1	7	42	14
7.1	506	242	17	26	2	0	58	10
7.2	871	291	41	35	1	6	51	1
7.3	481	125	22	19	1	0	27	7
7.4	774	281	49	34	2	1	9	8
7.5	384	100	20	53	4	0	40	12

OJIBPOL

7.6	685	75	33	61	2	1	51	12
7.7	358	72	23	53	1	0	45	14
7.8	290	47	36	23	0	0	64	8
7.9	234	28	27	37	4	0	146	7
8	228	20	37	35	0	0	68	2
8.1	180	8	44	61	0	0	94	8
8.2	212	12	59	29	4	0	72	4
8.3	316	10	115	60	2	0	44	13
8.4	265	7	158	18	0	0	13	22
8.46	314	7	138	9	0	0	7	24

OJIBPOL

Quercus	Betula	Tsuga	Salix	Fraxinus	Corylus	Larix	Fagus	Ostrya
14	301	8	4	0	0	0	0	0
12	292	13	1	2	2	0	0	0
30	311	18	2	1	0	0	2	0
17	301	4	0	2	4	2	1	1
13	293	13	1	5	4	6	0	2
11	179	12	0	4	9	0	0	2
22	340	2	2	3	4	0	3	1
20	335	12	0	1	4	0	0	6
18	319	12	1	4	9	0	2	0
15	316	15	2	4	3	0	1	0
6	306	3	0	6	0	0	1	1
17	320	7	1	4	0	0	0	3
11	202	6	3	6	0	5	0	3
16	295	12	3	2	2	0	2	4
22	275	0	1	1	2	5	1	5
18	324	13	0	5	2	0	0	1
18	291	12	3	4	3	0	0	0
15	323	5	4	1	5	0	2	1
10	140	5	1	1	2	1	1	1
10	313	4	1	6	0	0	4	6
9	299	5	0	3	0	0	1	2
5	346	6	0	2	0	0	6	0
19	362	7	0	5	9	0	0	4
14	328	4	0	6	1	0	2	4
14	269	7	1	0	2	0	0	6
14	320	6	0	5	6	0	2	2
14	269	6	3	5	6	0	0	0
17	270	3	0	3	5	0	0	2
14	303	2	3	4	6	0	0	2
22	244	0	0	3	4	0	2	3
24	321	1	0	5	4	0	0	0
25	345	1	2	9	12	0	5	2
23	302	0	3	1	8	0	0	1
22	305	2	3	6	5	0	0	1
15	298	0	0	2	1	0	3	3
19	295	2	0	3	10	0	0	2
10	237	1	3	10	6	0	0	1
7	308	3	1	3	3	1	0	1
12	154	1	0	8	3	0	0	5
11	258	0	4	4	9	0	1	5
16	258	4	4	8	3	0	1	5
12	320	10	1	8	0	0	7	4
23	182	2	0	9	5	0	0	5
17	313	0	0	12	4	0	2	1
21	203	0	0	5	2	0	0	16
19	237	0	5	3	7	0	1	2
15	116	0	0	9	4	0	1	3
15	139	1	4	6	1	0	1	3
21	320	1	1	9	4	0	1	5

OJIBPOL

22	300	0	1	4	2	2	3	0
10	329	0	2	3	3	3	0	2
13	342	0	3	4	5	0	0	0
16	307	0	10	5	5	0	3	1
16	345	0	3	2	1	0	0	0
14	292	0	3	3	7	1	0	0
15	335	0	6	0	0	3	1	0
16	243	0	9	7	12	4	0	0
29	230	0	7	22	5	0	2	12
42	64	0	5	15	0	0	0	8

OJIBPOL

Juglans	Tilia	Cupress	Composit	Cyperace	Chenopod	Ericacea	Artemisi	Ambrosia
0	0	0	1	10	6	2	4	19
0	0	0	0	12	2	0	6	22
0	0	0	2	13	9	0	8	24
0	0	0	0	17	1	1	9	17
1	0	0	2	4	0	0	10	6
0	0	0	3	1	0	0	11	4
0	1	0	2	5	2	0	8	3
0	0	0	2	15	0	0	11	5
0	1	0	0	7	3	0	14	4
0	1	1	0	4	1	0	12	7
1	0	0	2	7	1	0	5	10
0	0	0	3	12	4	1	9	22
1	0	8	0	29	3	0	12	10
0	1	0	3	11	3	0	9	12
0	0	0	1	17	3	0	6	19
0	1	0	0	9	2	0	12	14
0	0	3	1	8	5	0	12	17
0	1	0	5	3	1	0	14	10
0	0	0	1	4	1	0	6	1
0	0	0	1	8	4	0	8	5
0	0	0	1	7	0	0	6	7
0	1	0	2	7	2	0	13	2
1	1	0	1	2	1	0	6	2
0	0	2	2	9	0	0	7	3
0	1	0	1	5	3	0	6	1
0	1	2	1	7	3	0	8	6
3	1	0	1	8	2	0	6	1
1	0	1	0	7	0	1	13	3
0	0	0	2	3	1	0	12	3
0	0	0	4	5	2	1	10	6
0	0	0	1	2	3	0	2	5
0	1	0	3	8	3	0	15	7
0	0	1	0	1	1	0	4	5
1	0	0	2	8	4	1	16	8
0	0	0	0	2	2	0	4	1
1	0	0	4	3	3	0	11	11
0	0	2	1	11	2	0	6	6
0	1	0	1	6	5	1	8	4
0	0	2	0	0	2	0	0	0
0	0	1	3	7	6	0	9	5
0	1	1	2	9	4	0	7	4
2	0	0	0	4	5	1	10	6
0	0	0	1	7	3	0	17	9
1	0	0	3	7	7	0	19	12
0	1	0	3	3	3	0	11	7
1	0	0	0	3	7	1	11	8
0	0	0	2	2	2	0	5	7
0	0	1	2	1	1	0	6	7
2	0	0	3	7	13	0	13	12

OJIBPOL

0	0	0	4	4	8	0	16	23
0	0	4	1	8	8	0	15	18
0	0	0	3	0	8	0	19	15
0	0	6	4	14	9	1	15	6
2	0	0	0	0	7	0	20	7
1	0	0	3	2	5	0	20	5
3	0	2	2	1	12	0	22	18
0	0	13	3	3	15	0	36	17
3	1	14	5	25	14	0	33	16
0	3	3	2	13	11	0	27	28

OJIBPOL

Poaceae	Trilete	Monolete	Sphagnum	Lycopodi	Iva	Nuphar	Brasenia	Carya
3	1	1	3	153	0	0	0	0
6	8	0	1	104	1	4	12	0
7	4	0	1	121	1	7	13	0
6	0	0	0	139	0	6	9	0
1	8	1	1	206	0	10	13	3
0	8	3	4	106	0	1	6	3
0	1	1	0	88	0	2	14	0
7	3	0	4	90	0	8	34	0
4	2	0	3	64	0	7	19	1
2	4	0	4	45	0	4	33	1
4	0	0	0	41	1	3	26	0
4	0	0	1	119	0	3	14	0
5	0	0	4	72	0	4	0	0
1	0	0	3	178	0	7	15	0
5	7	1	9	308	0	4	13	1
7	0	0	0	161	1	7	12	0
4	2	0	11	123	1	9	15	0
1	3	0	0	105	0	3	19	0
3	3	2	2	136	2	3	19	1
4	3	0	3	102	0	7	24	0
4	4	0	10	106	0	5	20	1
0	0	0	0	170	0	2	10	0
0	4	0	0	55	1	5	9	1
2	0	0	1	82	0	3	16	0
5	3	0	0	53	0	2	14	0
3	5	1	0	116	0	4	13	0
6	3	2	0	55	0	2	10	0
5	5	0	3	172	0	3	8	0
2	0	0	0	122	0	0	4	0
4	8	1	5	183	0	3	9	0
2	1	4	0	81	0	0	8	0
4	0	0	1	110	0	1	10	1
0	1	0	0	50	1	1	3	0
7	5	0	2	204	2	2	11	0
1	5	0	0	52	0	0	1	1
5	0	0	0	145	0	7	10	0
2	1	0	1	195	0	0	1	0
2	2	2	0	152	1	3	5	2
0	4	1	0	38	0	2	4	0
1	4	2	1	171	0	4	3	0
2	1	1	0	45	1	0	3	0
2	0	1	1	73	1	0	3	1
0	4	1	0	168	0	0	1	0
5	1	4	2	107	2	0	3	0
1	4	2	5	220	1	1	1	0
3	0	0	4	30	0	0	4	0
0	0	2	2	87	0	0	6	0
1	0	0	0	20	1	1	1	0
4	3	4	6	126	1	1	0	0

OJIBPOL

3	0	8	4	36	3	1	0	0
13	0	3	6	191	1	0	5	1
1	0	0	3	53	1	0	1	2
7	2	3	14	154	0	0	6	2
2	5	0	0	66	0	0	2	1
9	10	8	12	122	2	0	5	0
2	0	1	2	59	0	0	0	2
4	9	4	3	287	1	1	7	0
9	9	1	0	58	1	0	1	0
5	15	3	0	39	0	0	0	2

OJIBPOL

Potomoge	Equisetu	Typha	Rosaceae	Rumex	Diervill	Epilobiu	Total
0	0	0	0	0	0	0	1170
0	0	0	0	0	0	0	1089
0	0	0	0	0	0	0	1291
0	0	0	0	0	0	0	1134
3	0	0	0	0	0	0	1182
0	1	0	0	0	0	0	620
4	0	0	0	0	0	0	961
4	0	2	3	0	0	0	1069
2	0	0	2	0	0	0	899
1	0	1	0	0	0	0	889
19	0	27	0	0	0	0	938
7	0	0	3	0	0	0	1038
4	1	0	0	0	3	0	649
4	0	0	3	2	0	0	908
7	1	0	0	1	0	0	996
0	0	0	0	0	0	0	1043
4	1	0	0	1	2	0	1013
3	0	0	0	0	0	0	901
5	0	0	1	2	0	0	569
3	0	0	1	0	0	0	906
2	0	0	0	0	0	0	913
0	0	2	0	0	0	0	1144
0	0	0	0	0	0	0	877
4	0	0	0	0	0	0	844
2	0	1	1	0	0	0	1009
5	0	0	1	0	0	0	1155
2	0	1	3	1	0	0	1005
2	0	0	2	0	0	0	1098
0	1	1	0	0	0	0	1130
3	0	0	1	0	0	0	1093
0	0	0	0	0	0	0	1032
7	0	0	0	0	0	0	1145
1	0	0	1	0	0	0	939
2	0	0	0	0	0	0	1138
0	0	0	0	0	0	0	934
5	0	0	3	0	0	0	1340
0	0	0	0	0	0	0	1064
4	0	1	0	0	0	0	1224
1	0	0	0	0	0	0	716
5	0	0	1	0	0	20	1328
0	0	0	0	0	0	0	925
2	0	0	1	0	0	0	1124
1	0	0	0	0	0	0	1299
0	4	0	2	1	0	0	1704
2	0	0	0	0	0	0	1373
0	0	0	1	0	0	0	1644
1	0	0	0	0	0	0	946
0	0	1	3	0	0	0	1374
1	0	1	0	0	0	0	1172

OJIBPOL

7	0	0	1	1	0	0	1373
4	0	0	1	0	0	0	1197
1	0	0	0	0	0	0	942
2	0	0	0	0	0	0	1075
0	0	0	1	0	0	0	870
5	0	0	0	0	0	0	924
0	0	1	0	1	0	0	880
6	0	1	1	0	0	0	1262
4	0	3	4	0	0	1	992
2	0	2	1	0	0	0	789

Appendix C: Application of Quantitative Analysis to the Vegetation History of Isle Royale

Application of Quantitative Analysis to the Vegetation History of Isle Royale

Isle Royale is located in western Lake Superior, about 24 km south of the Canadian shore. The island is 72 x 14 km, composed of parallel ridges and valleys of Precambrian basaltic lava interbedded with sandstone and conglomerates (Huber 1975). The valleys contain numerous lakes, swamps, and streams. Unlike the northeastern end of the island, the southwestern end has a mantle of glacial till; this difference in substrate may have influenced the development of two broad forest types on the two ends of the island. The southwestern end supports a deciduous, northern hardwoods forest, especially at higher elevations, while the northeastern end and much of the periphery of the island support a more coniferous, boreal forest. Because Isle Royale is relatively inaccessible and, since 1940, incorporated into the National Park system, it is likely less disturbed than much of the mainland. To date, little paleoecological research has been conducted at Isle Royale (but see Potzger 1954 and Raymond et al. 1975).

Using pollen preserved in lake sediments as a proxy for past vegetation, I will reconstruct the history of the forests surrounding Lily Lake on the southwestern end and Lake Ojibway on the northeastern end of Isle Royale since deglaciation. Quantitative treatment of the pollen percentage data will include an ordination analysis that will describe the direction of changes in vegetation composition and an analysis of the rates of vegetation change that will address the following hypotheses:

1) The vegetation surrounding Lily Lake, because of its clayey till substrate, will initially change faster than that surrounding Lake Ojibway, without the thicker till soils. After vegetation is established, however, the vegetation on Lake Ojibway's shallow soil will be more sensitive to disturbance, so changes at Lake Ojibway will occur at a faster rate.

2) The climate-modifying effect of Lake Superior will be reflected in slower rates of vegetation change on Isle Royale than on mainland sites.

This paper examines the utility of various techniques for assessing rates of change and ordinating pollen data obtained from Lily Lake and Lake Ojibway. Both full and reduced (containing 24 pollen types) data sets were analyzed. To date, only data useful in addressing the first hypothesis have been analyzed.

METHODS

Two long sediment cores (dating to 9240 $\pm$ 90 yr B.P. and 8790 $\pm$ 40 yr B.P., respectively) were obtained from Lily Lake and Lake Ojibway. The cores were sampled for pollen analysis at 10-cm intervals. Pollen was extracted with standard techniques (Faegri and Iversen 1975) and a minimum of 500 arboreal grains was counted at each level. Using five radiocarbon dates from each core and percentage data from the pollen counts, pollen diagrams were constructed for Lily Lake and Lake Ojibway (Figures 1 and 2).

Rates of Change Analysis

My analysis of the rates of vegetation change is based on methods developed by Jacobson et al. (1987). They determined rates of change by calculating chord distances between pollen percentage data points representing 200-year intervals. Chord distance is a measure of the dissimilarity of pollen spectra, calculated using the formula $D_{ij} = \sum_k (p_{ik}^2 - p_{jk}^2)$, in which D_{ij} is the distance between sample i and sample j , and p_{ik} and p_{jk} are the proportions of pollen type k in samples i and j , respectively. It is a signal-to-noise distance measure that somewhat upweights rare taxa. Because counted pollen samples were spaced unequally in time, Jacobson and Grimm (1987) smoothed the data with five-sample averages, then by interpolating 200-year intervals chose points along the smoothed curve and calculated the chord distances between these composite pollen spectra.

I chose a somewhat different approach to estimate pollen spectra representing equally spaced, 200-year time intervals. First, I estimated a date for each sampled level of the long cores by linear interpolation between radiocarbon dates. The interpolated dates were generally less than 200 years apart. Next, I entered the pollen percentage data and the interpolated date from each sampled level into the Eseq-p program written by S. Sugita. This program uses the rectangular integration method to create equal-space time series in which composite pollen spectra are created to represent each interval of a user-defined time (in this case, 200 years) along the core. Rectangular integration is an appropriate interpolation method when observations exceed estimates (e.g., when data points less than 200 years apart are used to estimate pollen percentages spaced 200 years apart) (Davis 1986). The method assumes that a variable measured at one sampling point (in this case, a pollen percentage at one dated level in a core) remains constant until the next sampling point, where it changes stepwise. Graphically, the series of values for a variable (pollen percentage) changing stepwise at the sampling points forms a series of rectangles. To determine values for the pollen percentage at equally spaced time intervals, another series of rectangles is generated. These rectangles have equal lengths (equal time intervals), and the total area under them is equal to the total area under the original rectangles. The area under the curve from one equally spaced point to the next equals the area under the curve covered by that time span in the original data. Thus, the pollen percentage observations used to estimate a point are weighted proportionally to the length of the time interval that they represent.

I calculated squared chord distances between successive 200-year composite pollen spectra from Lily Lake and Lake Ojibway. I then plotted the squared chord distances against time. This was done using a complete data set (Fig. 3) and using only 24 common pollen types at each lake (Fig. 4).

Ordination Analyses

To describe relationships among the pollen spectra from the cores, I ordinated the data. Ordination is an attempt to organize multivariate raw data into a simplified, more comprehensible low-dimensional format that highlights the main directions of variation. Units of information (in this case pollen types according to the samples in which they appear or samples according to the pollen types they comprise) are ordered along a number of axes representing a number of dimensions. Two axes at a time can then be projected into a two-dimensional illustration of the

ordering of information along the selected axes. The goal is to summarize relationships by depicting similar entities (e.g., samples) near one another and dissimilar entities far apart (Gauch 1982). Thus, implicit or explicit in ordination is some calculation of how "distant" entities are from one another. This distance, or dissimilarity (in, for example, the species composition of samples) is presumed to reflect differences in how the entities respond to some underlying variable(s) represented by the axis. In most ordinations, the variable represented by the axis is not certain. Interpretation of the axes (in ecology, usually believed to be environmental gradients) is often difficult and subjective. Because reducing multidimensional data to only a few dimensions inevitably results in loss or distortion of information, it is important that the axes chosen to summarize the data are the major axes of variation.

Beals (1984) discusses two features of community ecological data that cause problems in ordinations. First, species have a nonlinear relationship to the environment and overlapping (to various degrees, or not at all) relationships with one another. Species' relationship to the environment is conceptualized as involving optimal levels of various resources, such as light, nutrients, and water. Species abundance responds to gradients of each of these resources by building to a peak as the level of resource approaches the optimum, then tapering off as the level of the resource departs from the optimum. Given the large number of resources to which species respond and the complications of competition, species assortments in any environment are complex. Nonlinear species-environment relationships can be modeled in many forms; a bell-shaped species response curve is referred to as the Gaussian model.

The second problematic feature of ecological data is that species abundance does not fall below zero as environments become ever more unfavorable for those species. Beals (1984) notes that the severity of both the nonlinearity and the zero truncation problems is a function of the beta diversity of the data (i.e., the degree of difference among the samples). Different ordination techniques, using different standardizations and distance measures on data sets having different beta diversities, will cope with these problems with different levels of success.

Ordinations can be performed on many types of data. In community ecology, most ordinated data are sets of samples, each composed of a number of species (or, particularly with pollen data, higher taxonomic levels). The samples can be ordinated in species space or the species can be ordinated in sample space, or both ordinations can be carried out simultaneously. In the examples to follow, I illustrate sample ordinations, and I will hereafter refer primarily to sample ordination.

Innumerable ordination techniques are available. Some are considered more objective than others, because they depend only on the data and not on the investigator's initial assessment of the samples or species. Yet, as Gauch (1982) points out, the objective methods merely "defer the subjectivity" to the interpretation stage of the analysis. To cover a representative breadth of commonly used ordination techniques, I investigated the Bray-Curtis, principle components analysis, detrended correspondence analysis, and nonmetric multidimensional scaling techniques to determine their efficiency and clarity in describing my data. Analyses were performed using PC-ORD (McCune 1995).

Bray-Curtis

For sample ordination with the Bray-Curtis (or polar ordination) technique, first a samples-by-samples dissimilarity (distance) matrix is calculated from the original species-by-samples matrix. Two samples are then selected as endpoints of an axis, along which the rest of the samples are ordinated. Several methods exist for selecting the endpoints. The PC-ORD package offers the Bray-Curtis (also known as maximum range), variance-regression, minimum deviation (a.k.a. minimum residual distance), and subjective (a.k.a. extreme environment) methods.

Beals (1984) considers all of the above methods and, among them, recommends the variance-regression method. He criticizes the Bray-Curtis method because, in choosing endpoints having the greatest distances from other samples and from one another, the method is highly sensitive to outliers. If outliers are excluded to correct this problem, then defining which samples are outliers is left to the investigator's subjective judgment. Beals describes the usual interpretation of the minimum deviation method and criticizes it as an approximate method, inferior to principal components analysis. He then offers an alternative, exact method using unsquared (as opposed to squared in the more traditional method) sums of residual distances in calculating the departure of the data from the model. PC-ORD adopts this alternative method, but notes that it is time-consuming (McCune 1995). Beals (1984) criticizes the subjective method for requiring investigator assumptions about "what the important environmental [or other] factors are." He notes that even if the first ordination axis could be confidently constructed based on the most important environmental factor, it is unlikely that environmental factors underlying secondary axes could be known.

Thus, for low sensitivity to outliers, ease, and objectivity, I chose the variance-regression method. In this method, the variance of the distances for each sample is calculated, and "the first endpoint has the greatest variance in distances" (McCune 1995) from other samples. Next, "distances between each point and the first endpoint are then regressed against distances between each point and trial endpoints. The trial endpoint with the lowest regression coefficient is chosen as the second endpoint." (McCune 1995). Thus, the method finds the longest linear axis. Outliers--samples that "fall at the edge of the axis of major variation defined by the other samples" (Beals 1984)--are automatically, objectively, excluded. Beals (1984) concludes that "this method tends to analyze complex-shaped clusters of data points . . . one linear axis at a time, and does not become muddled by combining unrelated axes". Endpoints for subsequent axes are samples that are separated by large interpoint distances but have small projected distances on previous axes (Bray and Curtis 1957, Gauch 1982).

The distances are derived from the samples-by-samples distance matrix, which is generated using one of several distance measures (PC-ORD offers Euclidean, Sorensen, Jaccard, and Correlation). I used the Euclidean and Sorensen (referred to as percentage dissimilarity, or PD, by Gauch 1982) measures. In the Euclidean measure, distances are calculated using the formula $D_{ij} = \sqrt{\sum_k [(x_{ik} - x_{jk})^2]}$, where D_{ij} is the distance between samples i and j , and x_{ik} and x_{jk} are the values of species k in samples i and j , respectively. The Euclidean distance measure is implicit in principal components analysis, and so was chosen to enhance comparability of the results of the Bray-Curtis and principal components analyses. Euclidean distance can exaggerate the relative significance of dominant taxa, because it squares differences in abundance values (Gauch 1982,

Overpeck et al. 1985, Prentice 1980) Beals (1984) criticizes Euclidean distance on these grounds and also on the grounds that it can emphasize narrow-amplitude species over broad-amplitude species (again by squaring abundance differences between samples), with the result that distances "rise more sharply at smaller environmental distances and level off more dramatically as environmental distance increases." This produces excessive curvature in the line between identical samples and samples having no species in common. Beals (1984) strongly recommends the Sorensen measure (which uses the formula $D_{ij} = \sum_k |x_{ik} - x_{jk}| / (\sum_k x_{ik} + \sum_k x_{jk})$) because of its superior theoretical and empirical performance in producing less curvature in that line (see Beals 1984, Fig. 2). Bray and Curtis (1957) used essentially the Sorensen measure in developing their ordination technique. The Sorensen measure gives equal weight to common and rare taxa (see Prentice 1980a, who calls the above formula the Canberra metric).

Principal Components Analysis

Principal components analysis (PCA) is an eigenanalysis technique that seeks to discover independent, fundamental variables (components) that are linear functions of measured statistical variables, which are often correlated. Its apparent advantages over Bray-Curtis ordination are that it does not require endpoint selection and that it simultaneously ordinales species and samples; results for one may be used to calculate results for the other (Gauch 1982). Its disadvantages are that it assumes that the components have normal distributions and are uncorrelated.

These assumptions are seldom met by ecological data, and even when they can be loosely adhered to (i.e., when the analysis is performed strictly for descriptive purposes), Beals (1984) objects to PCA on empirical and theoretical grounds. His theoretical objections arise first from PCA's reliance on Euclidean distance (his arguments against this have been documented above) and second from the way in which PCA derives its component axes, which will be discussed below.

As with other ordination techniques, PCA generates a secondary matrix from the original samples-by-taxa data matrix. This matrix can be calculated as correlation coefficients or variances and covariances. PCA uses matrix algebra computations to extract the eigenvalues and eigenvectors from this matrix. The eigenvectors yield the orientations of the principal axes and the eigenvalues represent their lengths (Davis 1986). Beals (1984) comments, "the use of correlation and covariance implies distances which emphasize ecologically less meaningful information, such as joint absences, and differences in rare species compared to differences in common species."

PCA centers its axes by selecting the point located at the average for each species in all of the samples (the centroid) as the origin of the PCA axes. Beals (1984) objects to this as a distortion, noting "no environment exists that would allow all species to coexist, except in very homogeneous data sets."

Finally, PCA chooses its first principal component axis by rotating the centered axes rigidly around the centroid until an axis is found that captures the greatest variance possible along the ordination axis (in matrix algebra terms, the axis with the highest eigenvalue). Subsequent axes have descending eigenvalues and are orthogonal to the preceding axes. Beals (1984) saves his

harshest criticism for the variance-maximizing strategy of PCA: "in maximizing variance PCA necessarily tries to make all species correlate or covary linearly with each successive principal component . . . PCA finds axes that do their best to make species peak at one end or the other . . . Since along any extended vegetational or environmental gradient, many or even most species peak between the ends, PCA makes an unacceptable assumption about the ecological data and will distort whatever gradients occur in the data set." Though Beals (1984) envisions some community data sets that PCA could satisfactorily analyze (particularly those covering only short environmental gradients and having low beta diversity), he does not find it appropriate for most samples-by-species data.

The gradient distortion is often attributed to PCA's inability to cope with the Gaussian species response curve along the gradient (Beals 1984, Gauch 1982), though Minchin (1987) demonstrates that it also occurs in simulated data using other nonlinear response models. In attempting to use a linear model for species response to a single gradient, PCA can cause an ordination that should appear one-dimensional to instead appear to respond to two gradients. The distortion is in the form of an arched configuration of the sample points. Gauch (1982) comments, "The second PCA axis in this case does not convey meaningful or independent information; it is merely a quadratic distortion of the valid first PCA axis . . ."

Despite these difficulties, PCA is theoretically appropriate for some ecological data sets (Beals 1984, Jeffers 1978) and has been used often in paleoecology (e.g., Bennett 1992, Brubaker 1975; see Prentice 1980a). I therefore tested its applicability to my data. PC-ORD offers correlation, variance-covariance, and noncentered cross-products matrices; to standardize (which alleviates some of the problems of the Euclidean distance measure, but as Prentice 1980a points out, aggravates others, by upweighting narrow-amplitude species) and center my data (as recommended by McCune 1995 and Minchin 1987), I chose the correlation option.

Detrended Correspondence Analysis

Ecologists devised detrended correspondence analysis (DCA) to correct two problems with another ordination technique, known as reciprocal averaging or correspondence analysis (Hill and Gauch 1980). The parent technique is related to principal components analysis and the weighted averages technique (Gauch 1982, Hill 1973). For it, taxa are assigned arbitrary "scores" or "weights." Samples are then scored as averages of the scores of the taxa they comprise. Next, taxa are rescored as averages of the scores of the samples in which they occur. Several iterations of this process are run, until the scores stabilize and can thus be used for the ordination. The result is a first-axis ordination of samples "very comparable to what would have been obtained from principal components analysis; and to go with this will be a species ordination which is markedly more meaningful than the principal components species loadings" (Hill 1973). Subsequent axes, with descending eigenvalues, are extracted by the same iterative method, corrected for preceding axes (Gauch 1982, Hill 1973). The implicit distance measure is the chi-squared distance (Gauch 1982, Minchin 1987). Like chord distance, this is a signal-to-noise distance measure that somewhat upweights rare taxa (Overpeck et al. 1985, Prentice 1980a).

The two main problems with this technique are that, as in principal components analysis, subsequent axes can arch with the first, and that the first-axis ends are compressed relative to the

axis middle. Both of these problems arise from the ordination technique's failure to fully account for the Gaussian model of community structure (Beals 1984, Gauch 1982). Both of these problems can cause misleading results. The arch problem can occur because, while the calculations for the technique ensure that subsequent axes are uncorrelated with preceding axes, they do not ensure that the axes are independent (Beals 1984). As with PCA, the arch effect can lead an investigator to believe that the second axis carries information about an actual environmental gradient, when it is really just a mathematical artifact. The compression problem is most easily seen when samples contrived to be of equal compositional distance are plotted only on the first axis, without the arch (Gauch 1982). Compression of samples on the ends of the axis is bothersome because ideally the ordination would plot the samples in such a way that the distances between all of the sample points would reflect the actual compositional distances of the samples.

DCA addresses these problems by "detrending" and "rescaling" the ordination. To detrend is to eliminate any systematic relations of subsequent axes to the first. To do this, DCA segments the first axis, and the second axis scores are adjusted to have an average of zero within each segment (Gauch 1982, Hill and Gauch 1980). To rescale is to cause plotted intersample distances to reflect the magnitude of distance implied by the compositional dissimilarity of the samples. Based on the assumption that species appear and disappear at a constant rate along a given gradient, DCA rescales by equalizing "the mean within-sample dispersion of the species scores at all points along the gradient" (Hill and Gauch 1980). Furthermore, DCA adjusts the average species abundance profile to have a standard deviation of 1, thus scaling the axes such that if one ordination axis is longer than another, the first axis represents a longer community gradient than the second (Gauch 1982, Hill and Gauch 1980).

Beals (1984) criticizes DCA for its "intense manipulations" of data. He likens the detrending and rescaling processes to "taking a hammer to pound out an unwanted bulge." Furthermore, Beals (1984) and Minchin (1987) point out that detrending can destroy real trends in the data along with the artifact. Minchin (1987) found that DCA was not as robust as nonmetric multidimensional scaling to variations in the underlying species response model, beta diversity, and sampling pattern in simulated data. Nevertheless, other empirical studies have found DCA to be superior to other techniques, including nonmetric multidimensional scaling, in recovering data structure (Hill and Gauch 1980). It has been popular in ecology, including paleoecology (e.g., Foster and Zebryk 1993, Jacobson and Grimm 1986).

Nonmetric Multidimensional Scaling

For nonmetric multidimensional scaling (NMDS), once a dissimilarity matrix is generated the only information used in the ordination is the rank order of its entities. Thus, when the ordination is plotted in a specified number of dimensions, the distances between points should reflect the rank order of the compositional dissimilarity of the samples (Minchin 1987). NMDS assumes only a monotonic (not a linear, as in metric ordination techniques) relationship between ordination distance and compositional dissimilarity. The data need not adhere to the Gaussian species response model to be interpretable; "NMDS can accommodate any type of response function, provided that the resulting relationship between compositional dissimilarity . . . and sample separation in environment space remains approximately monotonic" (Minchin 1987).

Before the analysis begins, the investigator must determine the number of dimensions (axes) to be solved for, because the solution for any given axis will change if the total number of dimensions changes. This is because NMDS seeks iteratively to rank samples such that "stress" is minimized. Stress is defined as the departure from monotonicity in the relationship between the original, high-dimensional compositional dissimilarity and the ordination distance in the low-dimensional solution (McCune 1995).

PC-ORD uses Kruskal's (1964) "steepest descent" method to find minimum stress. One criticism of NMDS is that it is possible that stress will stabilize after a number of iterations, but that this stabilization will represent only a local minimization of stress (Beals 1984, Minchin 1987, Prentice 1977, 1980b). One consequence of this might be that the investigator chooses an inappropriate number of dimensions for the ordination, as PC-ORD suggests that the investigator choose "a number of dimensions beyond which additional dimensions provide only small reductions in stress" and for which the solution is stable (McCune 1995).

PC-ORD implements the "global" form of NMDS, which requires that the ordinated distances between every pair of sample points are in the same rank order as their compositional dissimilarity. Prentice (1977, 1980a, 1980b) and Minchin (1987) advocate the "local" form, in which the ordination distances from every sample point (as opposed to pairs of sample points) to every other sample point are in the same rank order as their compositional dissimilarities. The theoretical advantage is that the local form "allows for the possibility that the pattern of decline in compositional dissimilarity with increasing environmental separation may differ from point to point in environment space" (Minchin 1987). McCune (1995) states that "the consequences of the choice of local vs. global [NMDS] have not been fully explored in the literature."

For calculation of the NMDS distance matrix, PC-ORD offers Euclidean, Sorensen, Jaccard, or Correlation distance measures. Because Beals (1984) recommends it for ecological data, Minchin (1987) uses it in preparing his NMDS data, and it was useful in the Bray-Curtis ordination of my data, I chose the Sorensen measure. PC-ORD can generate the starting configuration for the NMDS procedure using either random numbers or the coordinates file from a previous ordination. Because using random starting coordinates offers no advantage and requires that the program be run several times (McCune 1995), I followed Minchin (1987) in using the coordinates file from the DCA ordination of my data. After initially running each analysis in six dimensions and checking for the degree to which additional axes reduced stress, which in every case was not great after the second axis, and after noting that most ordinations of these data were informative in two dimensions and heeding Prentice's (1980a) remark that "a good result from non-metric scaling cannot require more dimensions" than metric techniques, I ran the final analyses in two dimensions.

RESULTS

When particular samples are mentioned in the following discussion, their approximate dates as derived from linear interpolation between radiocarbon dates are given in parentheses. Full data sets are all counted samples with their percentages of all counted pollen types except aquatic pollen. For the reduced data sets, pollen types that appeared in few samples, or at very low percentages in many samples, were eliminated, and some pollen types were combined (e.g.,

haploxylon, diploxylon, and undifferentiated pine) so that the resulting data sets contained 24 pollen types (the full data sets have 68 and 41 pollen types for Lily Lake and Lake Ojibway, respectively). Percentages were recalculated using only these pollen types for the pollen sum. In the ordination analyses, the third and higher axes usually offered no further separation of samples or other interpretable information. Therefore only the results of the first two axes are presented, except for the one case in which the third axis provided useful information.

Rates of Change Analysis

Full Data Set: The rate of change, as estimated by squared chord distance between samples, is relatively high in the early-Holocene, especially at Lily Lake. But it peaks during the early part of the mid-Holocene, again especially at Lily Lake. Near the end of the mid-Holocene, it drops at Lily Lake but increases at Lake Ojibway (Fig. 3).

Reduced Data Set: The rate of change in the reduced data set is always lower than the rate of change in the full data set (i.e., the squared chord distances are lower) (Fig. 4). The general pattern is similar to that of the full data set, but the appearance of higher mid-to-late-Holocene rates of change at Lake Ojibway compared to Lily Lake is less clear. Thus, the overall effect of reducing the data set was to dampen the calculated rates of change and to obscure late-Holocene differences in rates of change between the two lakes.

Ordination Analyses at Lily Lake

Bray-Curtis

Full Data Set, Euclidean Distance: PC-ORD selected samples 2 (416 yr BP) and 44 (5610 yr BP) as the first-axis endpoints (Fig. 5). For the second axis, samples 37 (4563 yr BP) and 53 (7407 yr BP) were chosen (Fig. 5), and for the third, 47 (6209 yr BP) and 66 (9318 yr BP) (Fig. 6). The first axis contrasts late-Holocene samples, containing high percentages of birch pollen, against mid-Holocene samples, containing high percentages of pine pollen. The second axis contrasts mid-Holocene samples in which haploxylon pine pollen percentages peak against those in which undifferentiated pine pollen is more dominant, and the third axis contrasts mid-Holocene high-pine-pollen samples against early-Holocene samples containing relatively high percentages of spruce pollen.

Reduced Data Set, Euclidean Distance: PC-ORD selected samples 2 (416 yr BP) and 50 (6808 yr BP) as the first-axis endpoints and samples 24 (3252 yr BP) and 66 (9318 yr BP) as the second-axis endpoints (Fig. 7). As with the full data set, the first axis contrasts late-Holocene, high-birch-pollen samples against mid-Holocene, high-pine-pollen samples. Unlike the second-axis ordination of the full data set, however, the second-axis ordination of the reduced data set contrasts mid-Holocene, moderate-pine-and-birch samples against early-Holocene samples containing a relatively high percentage of spruce pollen. Because all pine pollen has been lumped together in the reduced data set, the second axis does not contrast mid-Holocene samples differing in their emphasis on haploxylon and undifferentiated pine pollen, as does the second axis of the full data set ordination.

Full Data Set, Sorensen Distance: PC-ORD selected samples 2 (416 yr BP) and 50 (6808 yr BP) as the first-axis endpoints and samples 40 (5145 yr BP) and 68 (9504 yr BP) as the second-axis endpoints (Fig. 8). As with the Euclidean-distance Bray-Curtis ordinations, the first axis contrasts late-Holocene samples containing high percentages of birch pollen against mid-Holocene samples containing high percentages of pine pollen. The second axis contrasts mid-Holocene, high-pine-pollen samples against early-Holocene, high-spruce-pollen samples.

Reduced Data Set, Sorensen Distance: PC-ORD selected identical endpoints for the first two axes as in the full-data-set, Sorensen distance ordination (Fig. 9). These axes are interpreted as above. The overall effect of reducing the data set was to slightly enhance the separation of the sample groups.

Principal Components Analysis

Full Data Set: Jeffers (1978) states, "practical experience with the technique suggests that a valid interpretation may usually be expected for those components which account for a significant part of the total variation" but offers no guide as to how much explained variation is significant. McCune (1995) offers the broken-stick eigenvalue as a guide to which components "contain more information than expected by chance and should be considered for interpretation." From the species-by-species correlation matrix, PCA extracted at least ten components, the first four of which should be considered for interpretation according to the broken-stick eigenvalue. PC-ORD permits graphing of the first three axes, but since the third extracts relatively little additional variance (7.7%) and the third-axis graphs and coefficients did not offer further clarification of relationships among the samples, I limit my discussion to the first two. The variance extracted by the first two components was $1 = 21.8\%$ and $2 = 10.2\%$; cumulatively 32%. Table I presents the coefficients of the variables for the first two vectors (the "loadings"), which may be used "to interpret the ecological meaning of the components, using the sign and relative size of the coefficient as an indication of the weighting to be placed upon each variable" (Jeffers 1978). The first axis appears to be an index of species that have peaks, however small, in the early Holocene. Many of these species drop off somewhat and then peak again, though not as strongly, in the late Holocene. This could be why graphically the first axis separates a few of the late Holocene samples quite clearly, but the rest of the samples become jumbled together. The most dissimilar samples on this axis are samples 45 (5810 yr BP) and 68 (9504 yr BP) (Fig. 10). The second axis contrasts the two pine pollen types, which peak in the mid-Holocene, against the birch, hemlock, and *Juglans* pollen types, which peak in the mid-to-late Holocene. Graphically, it is a short axis that does not clearly separate the samples. The most dissimilar samples on this axis are samples 1 (0 yr BP) and 45 (5810 yr BP) (Fig. 10).

Reduced Data Set: From the species-by-species correlation matrix, PCA extracted at least ten axes, all of which should be considered for interpretation according to the broken-stick eigenvalue (McCune 1995). Again, I will limit my discussion to the first two. The variance extracted by the first two components was $1 = 26.3\%$, $2 = 14\%$; cumulatively 40.3%. Table II presents the coefficients of the variables for the first two vectors. The interpretation of the coefficients for the first two axes is the same as above; though the absolute values of the coefficients are generally higher, they accrue to the same pollen types, minus those that have been removed from the analysis. The overall effect of reducing the data set was to sharpen the analysis. The variance

extracted by each axis was enhanced, the absolute values of the coefficients were made greater, and the graphic separation of the samples was clarified. On the first axis, the most dissimilar samples were samples 24 (3251 yr BP) and 68 (9504 yr BP), and on the second axis they were samples 1 (0 yr BP) and 50 (6808 yr BP) (Fig. 11).

Detrended Correspondence Analysis

Full Data Set: The sample scores plotted for DCA are weighted mean species scores, and vice versa. The first axis separates mid-Holocene samples with large pine percentages from the others, particularly those with a relatively large percentage of weedy pollen types, which generally have peaks in the early Holocene and the late Holocene. The most dissimilar samples on this axis are samples 50 (6808 yr BP) and 68 (9504 yr BP) (Fig. 12). The second axis separates early-Holocene samples having high percentages of spruce and many of the weedy species from late-Holocene samples having high percentages of birch, other northern hardwoods trees and shrubs, and a few weeds. The most dissimilar samples on this axis are samples 2 (416.1 yr BP) and 68 (9504 yr BP) (Fig. 12).

Reduced Data Set: The first two DCA axes for the reduced data set are somewhat different from the first two axes for the full data set. The first axis separates late-Holocene samples with high percentages of pollen of northern hardwoods trees and shrubs from mid-Holocene samples with high percentages of pine pollen and early-Holocene samples with relatively high percentages of spruce and some weedy pollen types. The most dissimilar samples on this axis are samples 2 (416 yr BP) and 50 (6808 yr BP) (Fig. 13). The second axis separates early-Holocene samples having high percentages of spruce and some weeds from mid-Holocene samples having high percentages of pine. The most dissimilar samples on this axis are samples 47 (6209 yr BP) and 68 (9504 yr BP) (Fig. 13). The effect on the DCA analysis of reducing the data set was to change the emphasis of the axes and to isolate mid-, early-, and late-Holocene samples somewhat more clearly.

Nonmetric Multidimensional Scaling

Full Data Set: The two-dimensional results of the NMDS ordination were nearly identical to those of the first two DCA axes (Figs. 12 and 14). There was a somewhat greater separation of points on the second NMDS axis. Interpretation of the axes is the same as that for the full-data-set DCA.

Reduced Data Set: Again, the two-dimensional results of the NMDS ordination were nearly identical to those of the first two DCA axes (Figs. 13 and 15). In this case, there was somewhat less separation of points on the second NMDS axis. Interpretation of the axes is the same as that for the reduced-data-set DCA.

Ordination Analyses at Lake Ojibway

Bray-Curtis

Full Data Set, Euclidean Distance: PC-ORD selected samples 14 (1148 yr BP) and 40 (6642 yr

BP) as endpoints for the first axis and samples 34 (5457 yr BP) and 1 (181 yr BP) as endpoints for the second axis (Fig. 16). The first axis distinguishes mid-Holocene samples, with high pine pollen percentages, from early-and-mid-Holocene samples with less pine pollen. The second axis also separates early- and late-Holocene samples, with high birch and weed pollen percentages, from mid-Holocene samples with relatively less birch and weed pollen.

Reduced Data Set, Euclidean Distance: PC-ORD again selected samples 14 (1148 yr BP) and 40 (6642 yr BP) as endpoints for the first axis (Fig. 17). For the second axis, samples 32 (4842 yr BP) and 5 (471 yr BP) were chosen (Fig. 17). Interpretations for these axes are the same as above. In this case, reducing the data set had the effect of obscuring some of the sample point separation along the second axis.

Full Data Set, Sorensen Distance: PC-ORD again selected samples 14 (1148 yr BP) and 40 (6642 yr BP) as endpoints for the first axis (Fig. 18). For the second axis, samples 20 (1613 yr BP) and 49 (8475 yr BP) were chosen (Fig. 18). The axes are interpreted as above.

Reduced Data Set, Sorensen Distance: PC-ORD selected samples 14 (1148 yr BP) and 39 (6445 yr BP) as endpoints for the first axis and samples 38 (6247 yr BP) and 49 (8475 yr BP) as endpoints for the second axis (Fig. 19). The axes are interpreted as above. Reducing the data set had little effect on the first two axes.

Principal Components Analysis

Full Data Set: From the species-by-species correlation matrix, PCA extracted at least ten axes, of which the first six should be considered for interpretation according to the broken-stick eigenvalue (McCune 1995). Again, I will limit my discussion to the first two. The variances extracted by the first two eigenvalues were 1 = 17.7%, 2 = 11.9%; cumulatively 29.6%. Table III presents the coefficients of the variables for the first two vectors. The first axis contrasts the pine pollen types, which peak in the mid-Holocene, against pollen types like birch, alder, and fir, which have peaks in the early and late Holocene, but decline relative to pine pollen in the mid-Holocene. The most dissimilar samples on this axis are samples 40 (6642 yr BP) and 47 (8043 yr BP) (Fig. 20). The second axis contrasts the pine pollen types and a few others with small peaks in the early and late Holocene against pollen types such as spruce, birch, and maple, with high percentages in the late Holocene. The most dissimilar samples on this axis are samples 7 (616 yr BP) and 49 (8475 yr BP) (Fig. 20). The axis separates early- and late-Holocene samples.

Reduced Data Set: From the species-by-species correlation matrix, PCA extracted at least ten axes, the first seven of which should be considered for interpretation according to the broken-stick eigenvalue. Again, I will limit my discussion to the first two. The variances extracted by the first two eigenvalues were 1 = 19.6%, 2 = 13.6%; cumulatively 33.2%. Table IV presents the coefficients of the variables for the first two vectors. The interpretation of the coefficients for the first two axes is the same as above; though the absolute values of the coefficients are generally higher, they accrue to mostly the same pollen types, minus those that have been removed from the analysis. The overall effect of reducing the data set was to sharpen the analysis. The variance extracted by each axis was enhanced, the absolute values of the coefficients were made greater, and the graphic separation of the samples was clarified. On the first axis, the most dissimilar

samples were samples 15 (1226 yr BP) and 40 (6642 yr BP), and on the second axis they were samples 4 (399 yr BP) and 49 (8475 yr BP) (Fig. 21).

Detrended Correspondence Analysis

Full Data Set: The sample scores plotted for DCA are weighted mean species scores, and vice versa. The first axis separates samples with high pine pollen percentages from the other samples, particularly those high in pollen from spruce and from a variety of relatively uncommon taxa tending to peak in the late Holocene. The most dissimilar samples on this axis are samples 14 (1148 yr BP) and 40 (6642 yr BP) (Fig. 22). The second axis separates samples high in spruce, maple, and hemlock pollen (i.e., late-Holocene samples) from samples having high percentages of weedy or uncommon pollen types (early-to-mid-Holocene samples). The most dissimilar samples on this axis are samples 5 (471 yr BP) and 45 (7630 yr BP) (Fig. 22).

Reduced Data Set: The first two DCA axes for the reduced data set are quite similar to those for the full data set. For each axis, the most dissimilar samples are the same as those for the full data set (Fig. 23). The species scores contributing to the sample scores are also similar. Graphically, the first two axes of the full and the reduced data sets are nearly identical. On the first axis, the sample points are somewhat more separated in the full data set analysis, but on the second axis there is somewhat more sample point separation in the reduced data set analysis (Figs. 22 and 23). Overall, the effect on the DCA analysis of reducing the data set was minimal.

Nonmetric Multidimensional Scaling

Full Data Set: The two-dimensional results of the NMDS ordination were similar to those of the first two DCA axes (Figs. 22 and 24). NMDS provided somewhat greater sample point separation on the first axis; DCA provided somewhat greater sample point separation on the second axis. Interpretation of the NMDS axes is the same as for the DCA axes.

Reduced Data Set: The two-dimensional results of the NMDS ordination were similar to those of the first two DCA axes (Figs. 23 and 25). DCA provided somewhat greater sample point separation, particularly along the second axis. Interpretation of the NMDS axes is the same as for the DCA axes.

DISCUSSION

Rates of Change Analysis

In general, the rates of change calculated for the pollen spectra at Lakes Ojibway and Lily Lake support the hypothesis that rates of change would at first be higher at Lily Lake, and later be higher at Lake Ojibway. This pattern becomes less clear, however, when reduced data sets are used for the calculations. This suggests that uncommon pollen types influenced mid-to-late-Holocene rates of change at Lake Ojibway more than at Lily Lake. Reducing the data sets also dampened the rates of change calculated for both lakes. This is to be expected because fewer pollen types contributed to differences between the composite pollen spectra. Both full and reduced data sets indicate that vegetation change at both lakes was highest in the early mid-

Holocene.

Ordination Techniques

It is difficult to evaluate the performance of ordination techniques in summarizing data structure when, as in most real-world studies, the data structure is unknown. The choice of the "best" technique is informed by theoretical considerations and the results of ordinations of simulated and field data sets with known structure, but comes down to subjectively determining which technique gives the most interpretable results for a given data set.

Gauch (1982) remarks, "It is reassuring if the same general ordination pattern emerges from different ordination techniques." For both the full and reduced data sets, at both Lily Lake and Lake Ojibway, the first two axes of most, and the first three axes of all, of the ordinations broadly separate mid-Holocene samples from early- and late-Holocene samples and early- and late-Holocene samples from one another. Transitional samples (early-to-mid, then mid-to-late) clump in the middle. As the pollen diagrams from both lakes suggest (Figs. 1 and 2), the composition of many of the samples is similar; palynological change is gradual and not great (particularly at Lake Ojibway). Thus, to evaluate the ordination techniques, I focus on their clarity in separating the sample groups. For both sets of data at both lakes, DCA and NMDS provided the clearest separation of the sample groups, followed by Bray-Curtis (with the Sorensen distance measure or reduced data sets providing better separation than the Euclidean distance measure or full data sets), and finally PCA.

The differences in performance result from an interaction of the assumptions and methods of various techniques with the nature of these data. For instance, PCA performs best with relatively short gradients and low-beta-diversity data sets (Beals 1984, Gauch 1982, Minchin 1987); it was stronger at Lake Ojibway, where these conditions are better met (Fig. 2). At Lily Lake, the gradients and data were apparently not short and homogeneous enough for effective PCA. At both lakes, the first two PCA axes did not extract a great deal of the variation, but third axes were not easily interpretable.

Bray-Curtis separation of the groups was enhanced by either reducing the data set or using the Sorensen distance measure. This is because both options reduced the influence of "narrow-amplitude" (appearing in just one or a few samples) pollen types, which can contribute disproportionately to Euclidean distances and therefore obscure some patterns (Beals 1984). Similarly, reducing the data set enhanced separation of the groups by PCA, which used the standardized Euclidean distance measure. Reducing the data set had less effect on the DCA (which uses the chi-squared distance) and NMDS analyses (using the Sorensen distance). The Euclidean-distance Bray-Curtis ordination of the full Lily Lake data set was the only instance in which a third axis revealed additional interpretable information. This suggests that in this case the Bray-Curtis technique did not summarize the directions of variation as efficiently as did the other techniques.

The clarity of DCA complements the results of Hill and Gauch (1980), which found it to be a robust technique. Beals (1984) admits that "DCA can produce reasonable ordinations at times" and that in real-data studies it was "close behind" variance-regression Bray-Curtis ordination.

The NMDS ordinations were similar to the DCA ordinations. Minchin (1987) found NMDS to be more robust than DCA to variations in underlying vegetation structure; apparently the underlying structures of these data are captured almost equally well by either technique. NMDS has theoretical advantages in its less strict assumption about the relationship between ordination distance and compositional dissimilarity (monotonic, but not necessarily linear), but in plant community ecology DCA is a more widely used, familiar technique.

Like the rates of change analysis, the ordination techniques highlight the unique character of the mid-Holocene at Isle Royale. Evidence for a mid-Holocene warm dry interval is persuasive at many Midwestern sites (e.g., Craig 1972, Fries 1962; see Webb et al. 1983, Winkler et al. 1986)), but weaker in the upper peninsula of Michigan (e.g., Brubaker 1975). The dominance of pine pollen during the mid-Holocene at Isle Royale argues for at least a dry mid-Holocene there.

CONCLUSIONS

The clearest, most interpretable ordinations of these data were provided by DCA and NMDS. Because these ordinations were nearly identical, the choice of technique becomes one of balancing the theoretical advantages of NMDS against the popularity advantages of DCA. To enhance communication of the results, I prefer the widely used DCA technique.

In the next stage of the analysis, I plan to calculate rates of change and perform ordinations on previously published pollen data from sites at the approximate latitude of Isle Royale differing in the degree to which their local climates are influenced by Lake Superior (likely candidates are Alfies Lake [Saarnisto 1975], Lake of the Clouds [Craig 1972], and Myrtle Lake [Janssen 1968]). My choice of ordination technique will doubtless be influenced by the empirical performance of the various techniques in summarizing these data.

REFERENCES

- Beals, E.W. 1984. Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. *Advances in Ecological Research* 14:1-55.
- Bennett, K.D. 1992. Holocene history of forest trees on the Bruce Peninsula, southern Ontario. *Canadian Journal of Botany* 70:6-18.
- Bray, J.R. and J.T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs* 27:325-349.
- Brubaker, L.B. 1975. Postglacial forest patterns associated with till and outwash in north central upper Michigan. *Quaternary Research* 5:499-528.
- Craig, A.J. 1972. Pollen influx to laminated sediments: A pollen diagram from northeastern Minnesota. *Ecology* 53:47-57.
- Davis, J.C. 1986. *Statistics and Data Analysis in Geology*, 2nd ed. John Wiley and Sons, New

York.

- Faegri, K. and J. Iversen. 1975. *Textbook of Pollen Analysis*. Hafner Press, New York.
- Foster, D.R. and T.M. Zebryk. 1993. Long-term vegetation dynamics and disturbance history of a Tsuga-dominated forest in New England. *Ecology* 74:982-998.
- Fries, M. 1962. Pollen profiles of late Pleistocene and recent sediment from Weber Lake, Minnesota. *Ecology* 43:295-308.
- Gauch, H.G., Jr. 1982. *Multivariate Analysis in Community Ecology*. Cambridge University Press, Cambridge.
- Hill, M.O. 1973. Reciprocal averaging: an eigenvector method of ordination. *Journal of Ecology* 65:157-174.
- Hill, M.O. and Gauch, H.G., Jr. 1980. Detrended correspondence analysis: an improved ordination technique. *Vegetatio* 42:47-58.
- Huber, N.K. 1975. *The Geologic Story of Isle Royale National Park*. Geological Survey, Washington, D.C.
- Jacobson, G.L. and E.C. Grimm. 1986. A numerical analysis of Holocene forest and prairie vegetation in central Minnesota. *Ecology* 67(4):958-966.
- Jacobson, G.L., T. Webb III, and E.C. Grimm. 1987. Patterns and rates of vegetation change during the deglaciation of eastern North America. In, W.F. Ruddiman and H.E. Wright, Jr., eds. *North America and Adjacent Oceans Since the Last Glaciation*. Geological Society of America, Inc., pp. 277-288.
- Janssen, C.R. 1968. Myrtle Lake: a late- and postglacial pollen diagram from northern Minnesota. *Canadian Journal of Botany* 46:1397-1408.
- Jeffers, J.N.R. 1978. *An Introduction to Systems Analysis With Ecological Applications*.
- Kruskal, J.B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29:1-27.
- Minchin, P.R. 1987. An evaluation of the relative robustness of techniques for ecological ordination. *Vegetatio* 69:89-107.
- McCune, B. and J. Mefford. 1995. *PC-ORD: Multivariate Analysis of Ecological Data*.
- Overpeck, J.T., T. Webb III, and I.C. Prentice. 1985. Quantitative interpretation of fossil pollen spectra: dissimilarity coefficients and the method of modern analogs. *Quaternary Research* 23:87-108.

- Potzger, J.E. 1954. Post-Algonquin and post-Nipissing forest history of Isle Royale, Michigan. *Butler University Botanical Studies* 9:200-209.
- Prentice, I.C. 1980a. Multidimensional scaling as a research tool in Quaternary palynology: a review of theory and methods. *Review of Paleobotany and Palynology* 31:71-104.
- Prentice, I.C. 1980b. Vegetation analysis and order invariant gradient models. *Vegetatio* 42:27-34.
- Prentice, I.C. 1977. Non-metric ordination methods in ecology. *Journal of Ecology* 65:85-94.
- Raymond, R.E., R.O. Kapp, and R.A. Janke. 1975. Postglacial and recent sediments of inland lakes of Isle Royale National Park, Michigan. *Michigan Academician* 7:453-465.
- Saarnisto, M. 1975. Stratigraphical studies on the shoreline displacement of Lake Superior. *Canadian Journal of Earth Science* 12:300-319.
- Webb, T. III, E.J. Cushing, and H.E. Wright. 1983. Holocene changes in the vegetation of the Midwest. In, Wright, H.E., ed. *Late Quaternary Environments of the United State. Vol. 2: The Holocene*. University of Minnesota Press, Minneapolis.
- Winkler, M.G., A.M. Swain, and J.E. Kutzbach. 1986. Middle Holocene dry period in the northern Midwestern United States: lake levels and pollen stratigraphy. *Quaternary Research* 25:235-250.

Lily Lake

Isle Royale National Park

Pollen analyst: Robyn Flakne

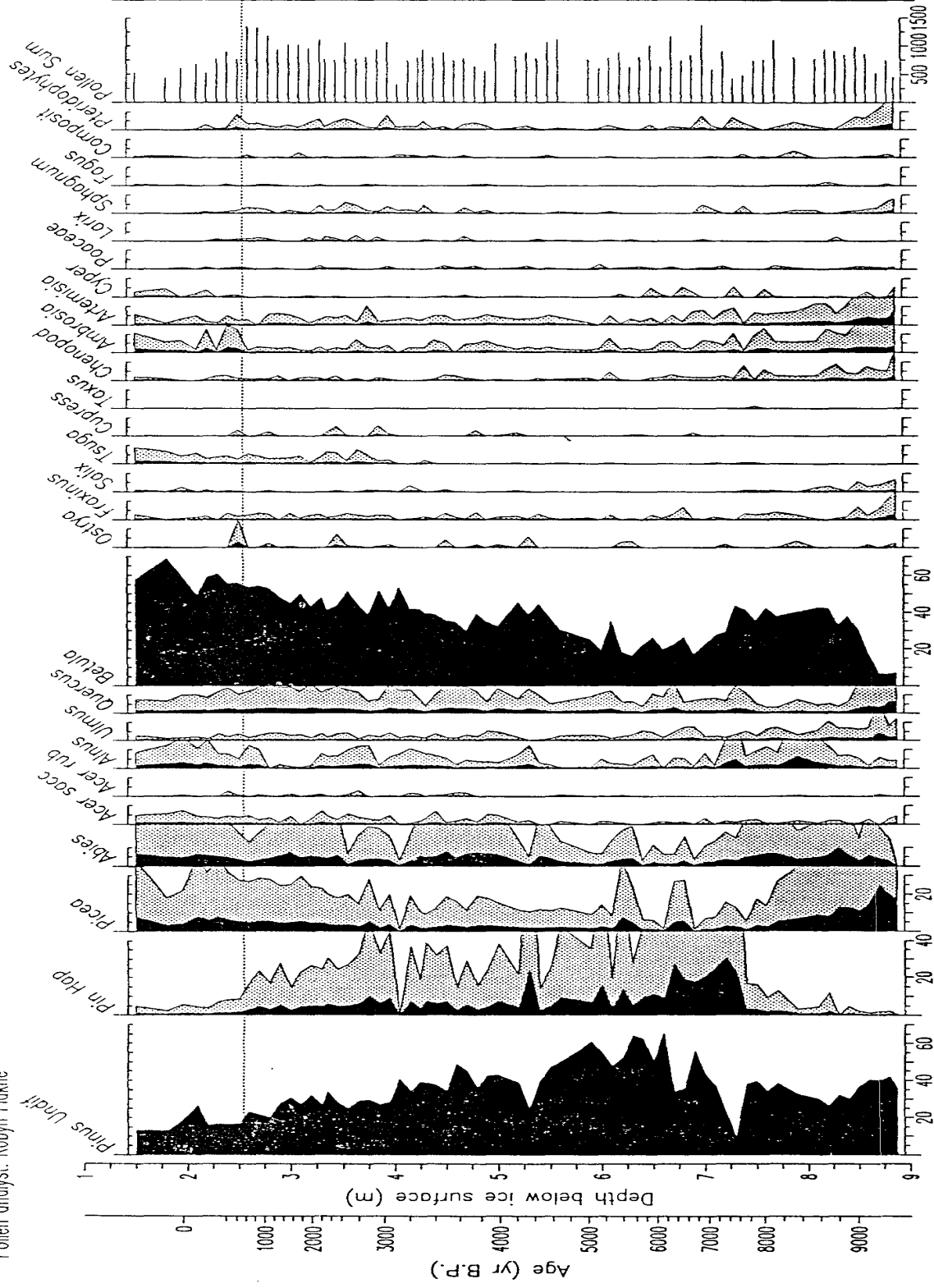


Fig. 1. Lily Lake pollen diagram

Exaggeration = 5X

Lake Ojibway, Isle Royale

4/17/97

Pollen analyst: Robyn Flakne

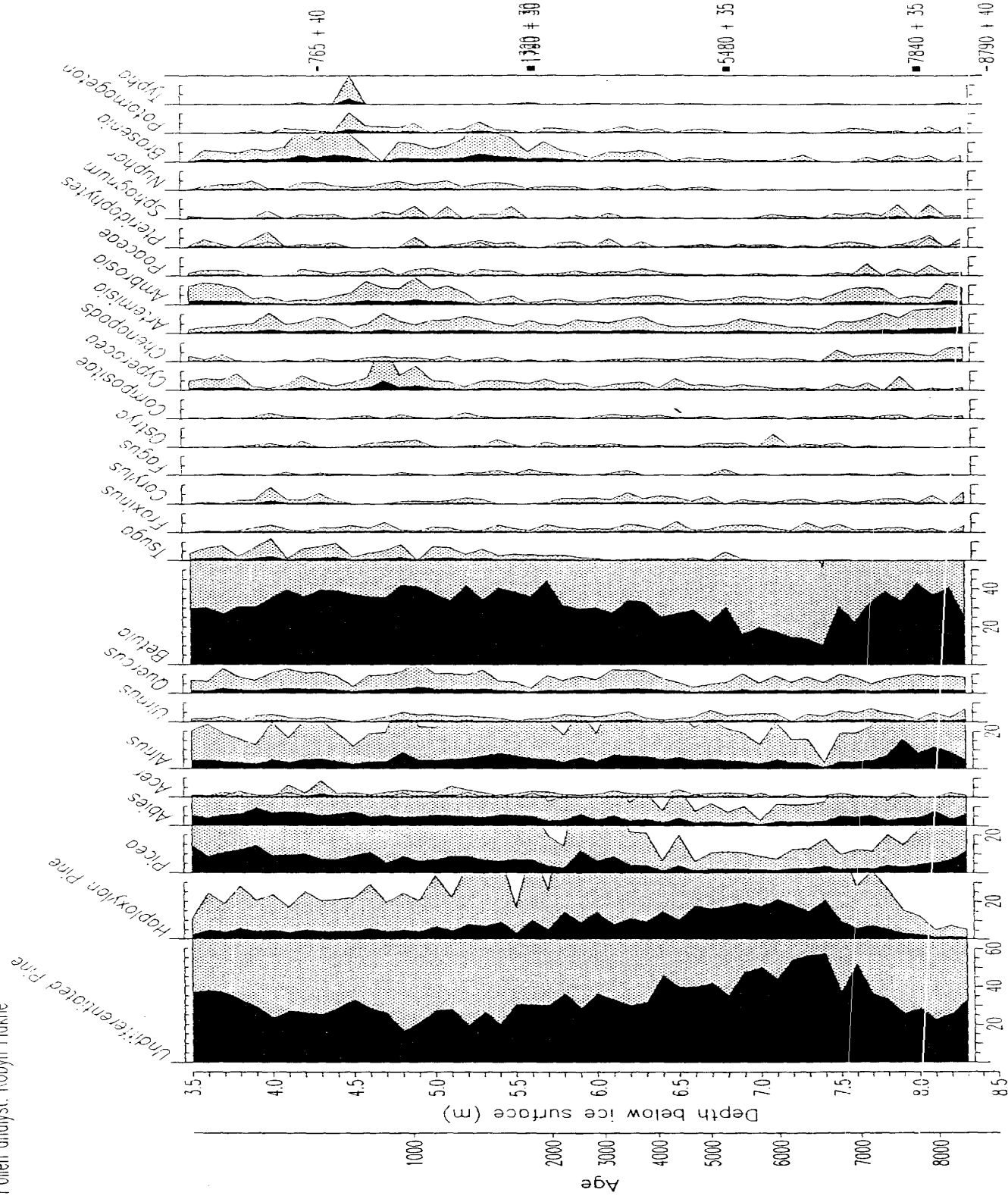


Fig. 2: Lake Ojibway pollen diagram

Exaggeration = 5x

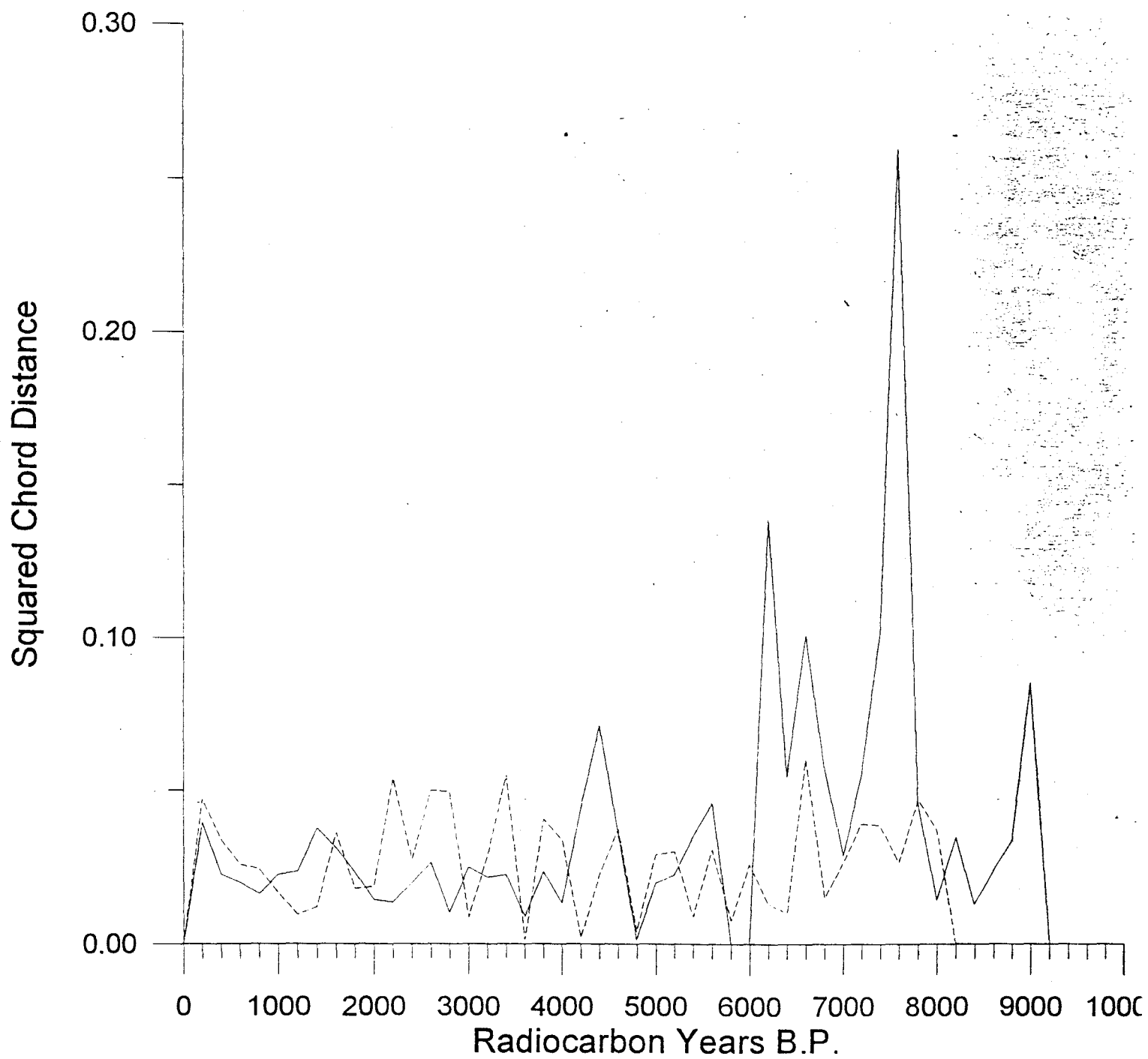


Fig. 3: Rates of change, full data set (solid line = Lily Lake; dashed line = Lake Ojibway)

Rates of Change--reduced data set

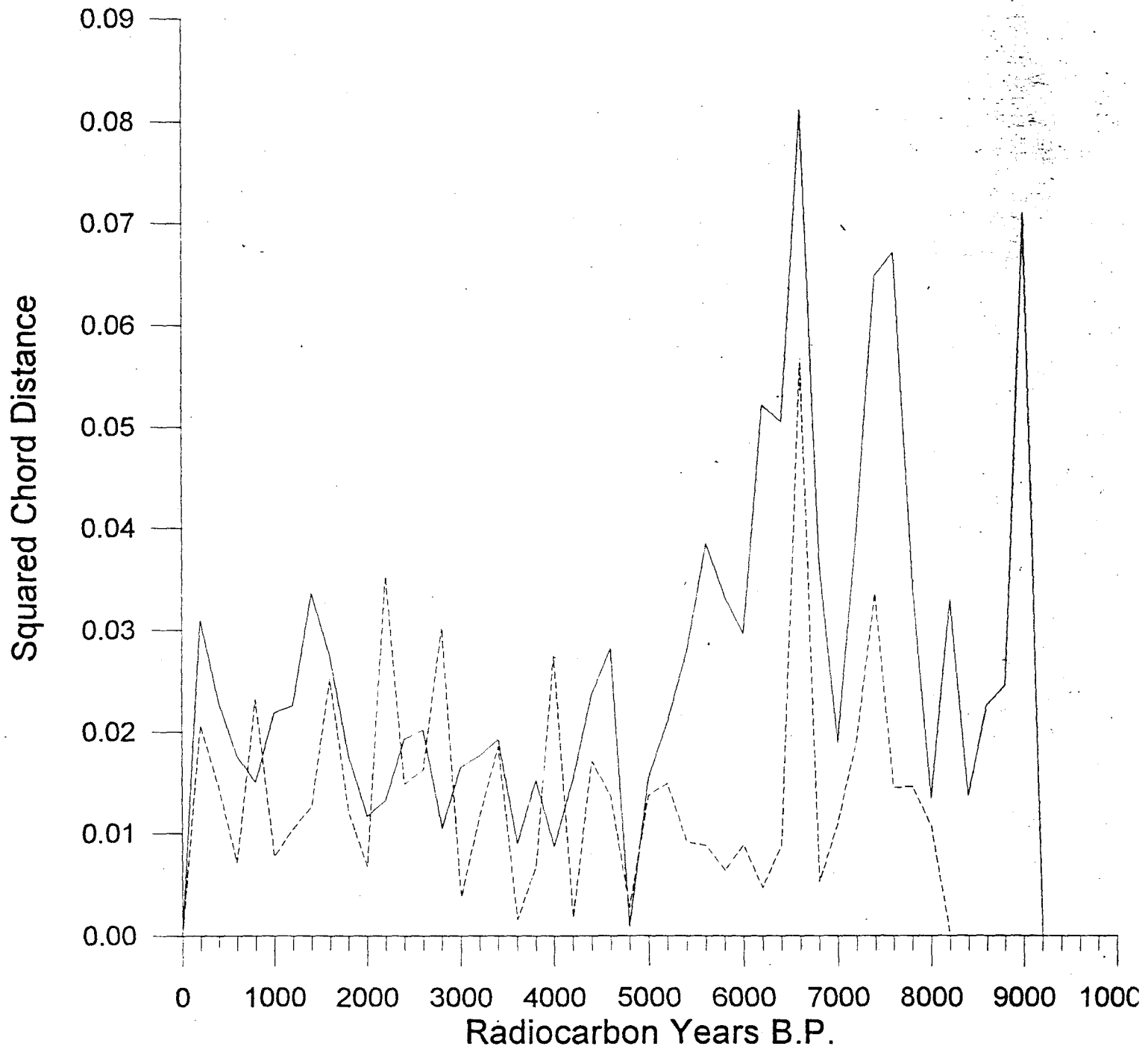


Fig. 4: Rates of change, reduced data set (solid line = Lily Lake; dashed line = Lake Ojibway)

Table I. Taxa coefficients for the first two PCA vectors of the full Lily Lake data set.

taxa	Vector 1	Vector 2
PINUND	.0267	-.3906
PINHAP	.0985	-.2464
PICEA	-.2633	.0560
Abies	.0306	.2189
ACESUG	-.0276	.3326
ACESIL	.0121	.1444
Alnus	-.0072	.1782
Ulmus	-.2315	-.0911
QUERC	-.2205	.0086
Betula	-.1386	.3924
CORYLU	-.1378	.0023
OSTRYA	-.0364	.0417
FRAXIN	-.2812	-.0038
JUGNIG	.0151	.2441
JUGCIN	-.1340	.1231
Salix	-.2795	.0088
Tsuga	.0502	.3792
CUPRES	.0284	.0594
Tilia	-.0449	.1221
Taxus	.0110	.0026
CHENOP	-.2650	-.0294
AMBROS	-.2362	.0846
ARTEMI	-.3058	-.0524
Cyper	-.1016	.0047
POA	-.0632	-.1219
Larix	.0406	.1624
Carya	-.2473	.0083
POLYGO	-.0151	.0783
ROSACE	-.1859	.0391
Mono	-.0380	-.0860
TRI	-.3058	-.0248
SPHAGN	-.1900	.0923
Cornus	-.2541	-.0099
Fagus	-.0559	.2024
PINDIP	.0072	-.0136
ERICAC	-.0564	.0007
POPULU	.0030	-.0258
SAGITT	.0339	-.1332
IVACIL	-.2333	.0037
PLANTA	-.0055	.1708
COMPOS	-.0826	.0787

Table II. Taxa coefficients for the first two PCA vectors of the reduced Lily Lake data set.

taxa	Vector 1	Vector 2
Pinus	.0590	-.4926
Picea	-.3299	.0852
Abies	.0099	.2579
Acer s	-.0023	.3509
Acer r	.0289	.1382
Alnus	-.0081	.2283
Ulmus	-.3068	-.0716
Quercu	-.2408	.0171
Betula	.1788	.4198
Corylu	-.1831	.0427
Ostrya	-.0132	.0339
Fraxin	-.3095	.0090
Salix	-.3387	.0345
Tsuga	.0848	.3998
Cupres	.0579	.0408
Chenop	-.3200	-.0114
Ambros	-.2983	.1124
Artemi	-.3572	-.0235
Cyper	-.1268	.0349
Poacea	-.0796	-.1262
Fagus	-.0810	.2368
Ericac	-.0838	.0213
Iva ci	-.2947	.0218
Planta	-.0109	.2117
Compos	-.0769	.0982

Table III. Taxa coefficients for the first two PCA vectors of the full Lake Ojibway data set.

taxa	Vector 1	Vector 2
Pinund	.3068	-.2350
Pinhap	.3324	-.1520
Picea	-.1703	.2914
Abies	-.2427	.1964
Acesug	-.0601	.2417
Acesil	.0795	.2520
Alnus	-.2143	-.0829
Ulmus	-.0837	-.2778
Quercu	-.1972	.0916
Betula	-.2502	.2498
Tsuga	-.1094	.2957
Salix	-.2092	-.1543
Fraxin	.0400	-.1483
Corylu	-.0984	-.1164
Larix	-.2062	-.0676
Fagus	.0353	.1379
Ostrya	.0421	-.0145
Jugni	-.0793	-.1142
Tilia	.0323	.2345
Cupres	-.1796	-.1604
Compos	-.1095	-.0862
Cypera	-.1444	.1272
Chenop	-.1630	-.2593
Ericac	.0299	.0482
Artemi	-.2692	-.1690
Ambros	-.1622	.0278
Poacea	-.2115	-.0266
Trilet	-.2105	-.0607
Monole	-.1548	-.2842
Sphagn	-.2559	-.1038
Iva	-.0748	-.1548
Carya	-.1609	-.0378
Equise	-.0786	-.0632
Rosace	.0112	.0916
Rumex	-.1244	.0280

Table IV. Taxa coefficients for the first two PCA vectors of the reduced Lake Ojibway data set.

species	Vector 1	Vector 2
Pinus	.4250	.1141
Picea	-.2592	-.2800
Abies	-.3032	-.1796
Acer s	-.1056	-.2421
Alnus	-.2192	.2327
Ulmus	-.0433	.3796
Quercu	-.2507	-.0121
Betula	-.3416	-.1328
Tsuga	-.1679	-.3093
Salix	-.2217	.2985
Fraxin	.0895	.1118
Corylu	-.0646	.2049
Larix	-.2176	.0388
Fagus	.0010	-.0677
Ostrya	.0603	-.0328
Compos	-.1006	.2104
Cypera	-.1974	-.1719
Chenop	-.1546	.3792
Ericac	.0159	-.0759
Artemi	-.2701	.3193
Ambros	-.2171	-.0058
Poacea	-.2408	.0336
Iva	-.0593	.1677
Rumex	-.1557	.0260

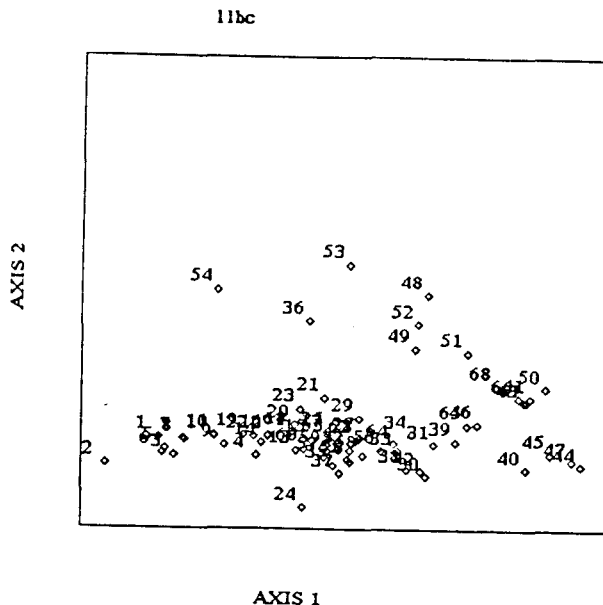


Fig. 5: Lily Lake Bray-Curtis ordination, Euclidean distance, full data set

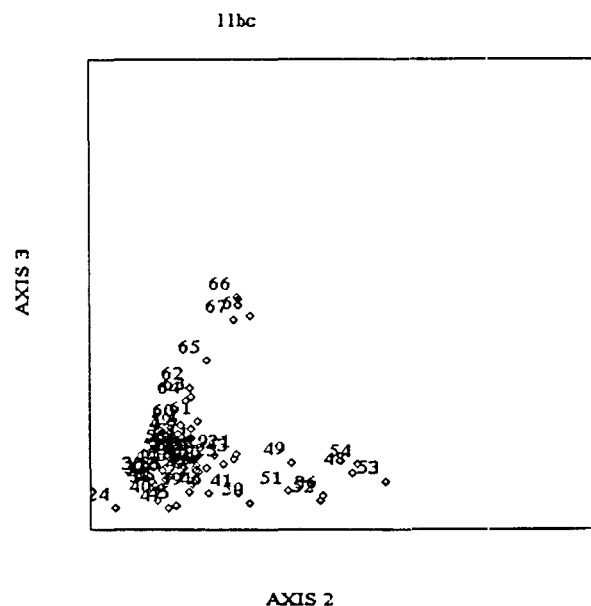


Fig. 6: Lily Lake Bray-Curtis ordination, Euclidean distance, full data set, third axis

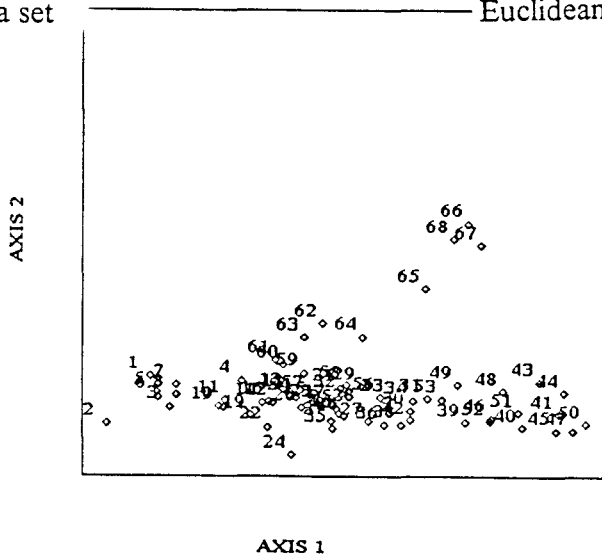


Fig. 7: Lily Lake Bray-Curtis ordination, Euclidean distance, reduced data set

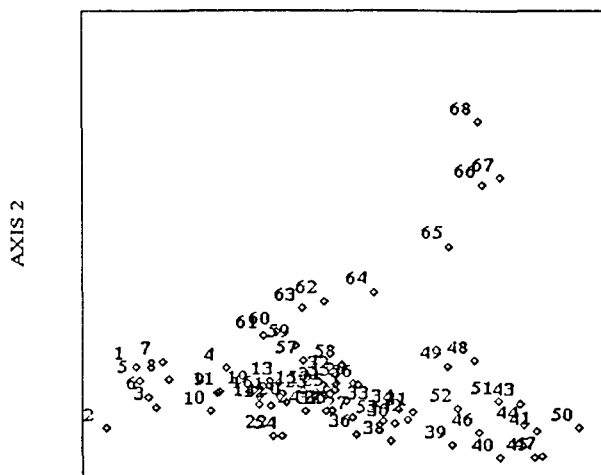


Fig. 8: Lily Lake Bray-Curtis ordination, Sorensen distance, full data set

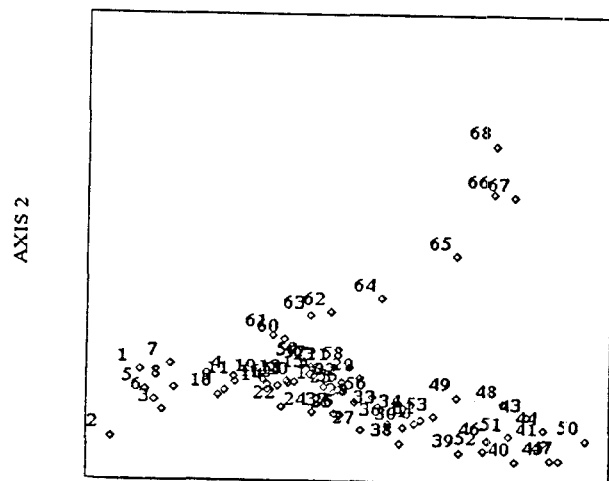


Fig. 9: Lily Lake Bray-Curtis ordination, Sorensen distance, reduced data set

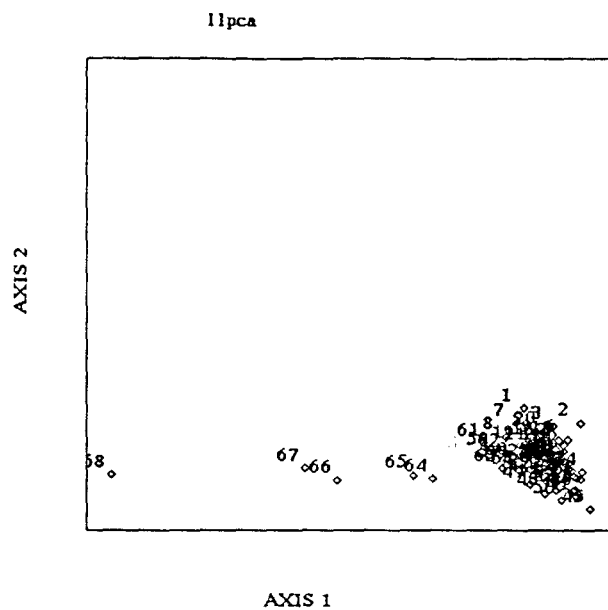


Fig. 10: Lily Lake PCA, full data set

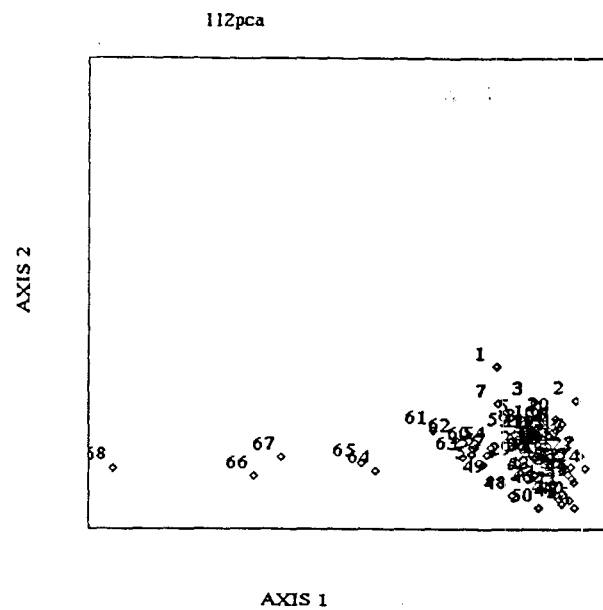


Fig. 11: Lily Lake PCA, reduced data set

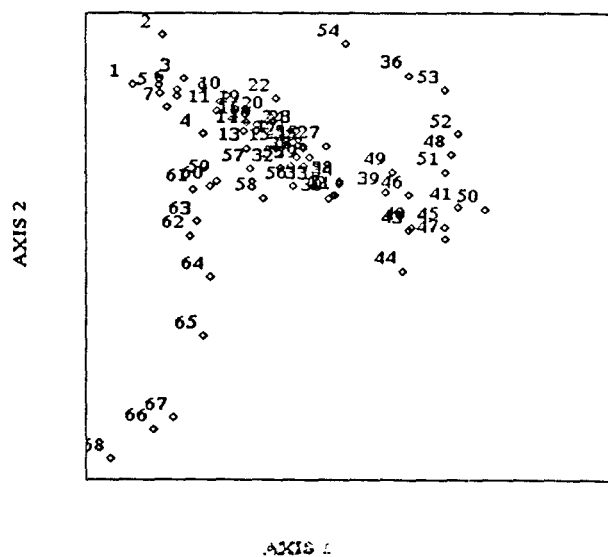


Fig. 12: Lily Lake DCA, full data set

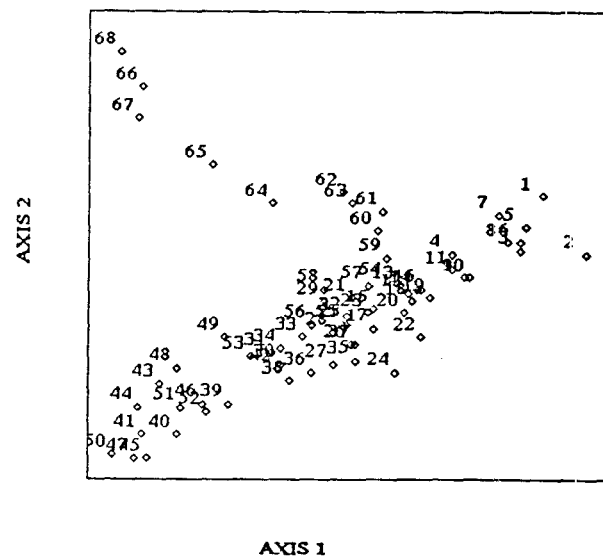


Fig. 13: Lily Lake DCA, reduced data set

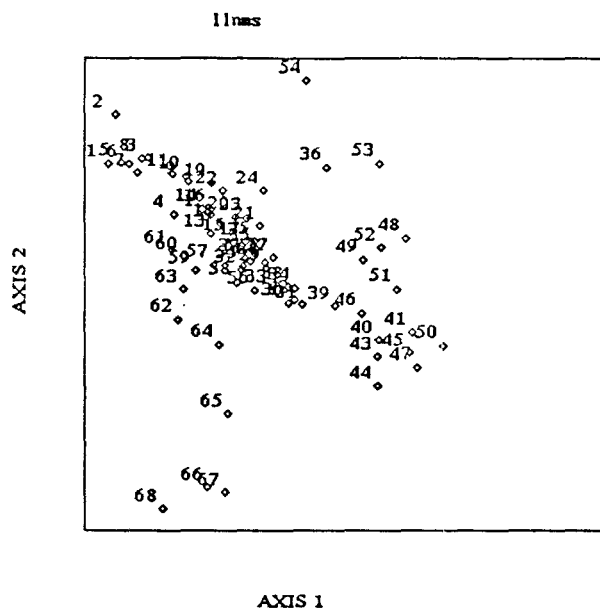


Fig. 14: Lily Lake NMDS, full data set

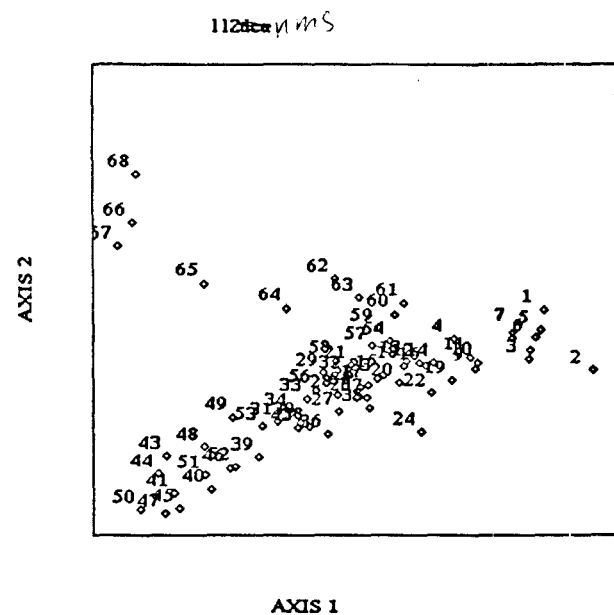


Fig. 15: Lily Lake NMDS, reduced data set

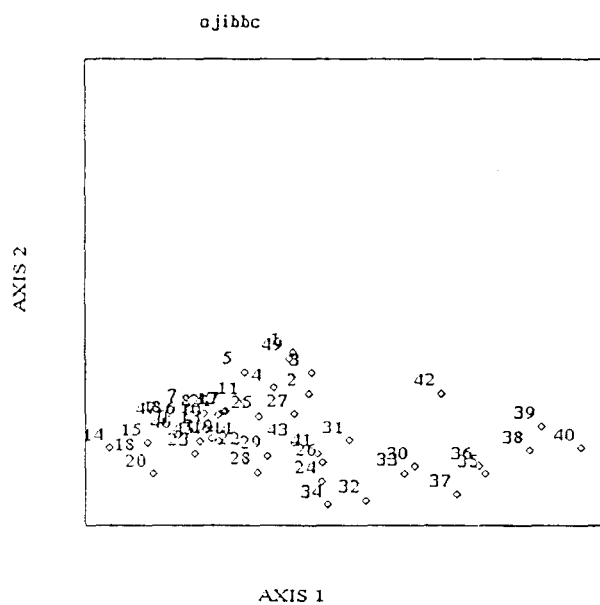


Fig. 16: Lake Ojibway Bray-Curtis ordination,
Euclidean distance, full data set

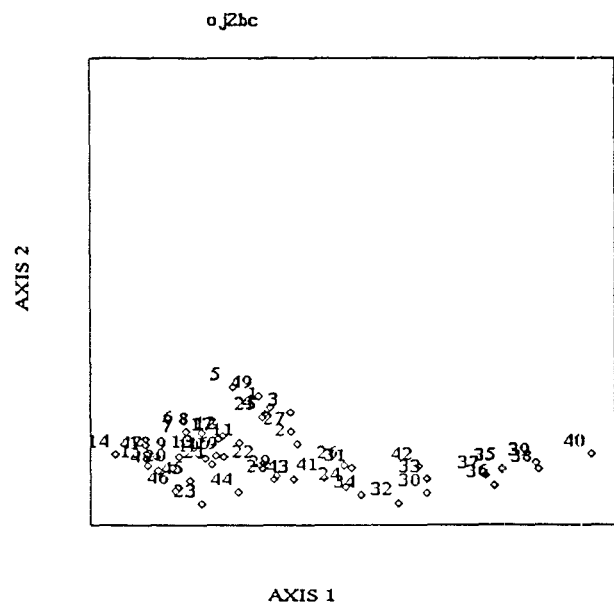


Fig. 17: Lake Ojibway Bray-Curtis ordination,
Euclidean distance, reduced data set

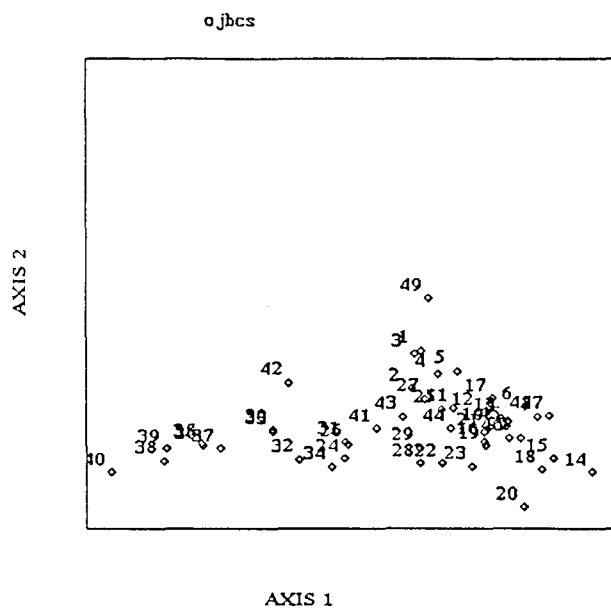


Fig. 18: Lake Ojibway Bray-Curtis ordination,
Sorensen distance, full data set

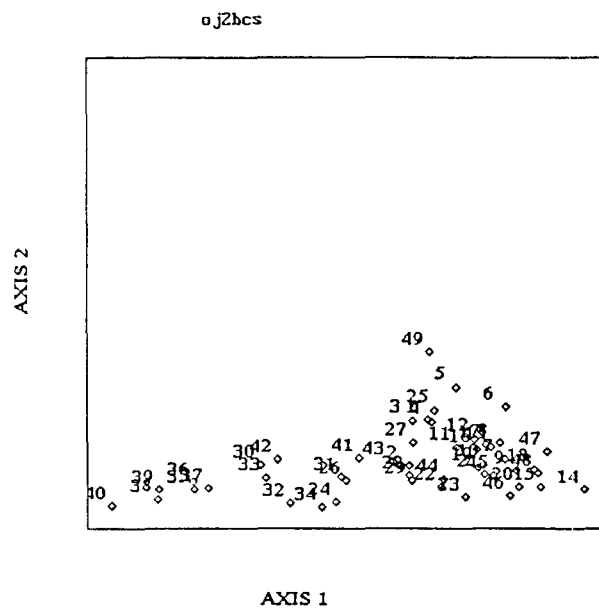


Fig. 19: Lake Ojibway Bray-Curtis ordination,
Sorensen distance, reduced data set

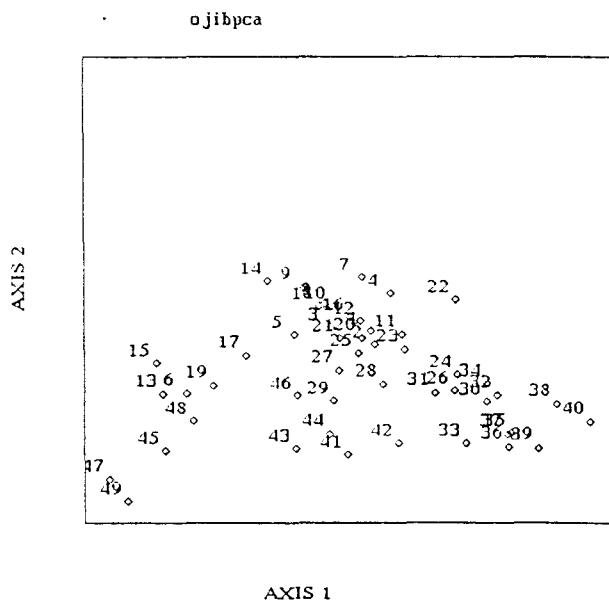


Fig. 20: Lake Ojibway PCA, full data set

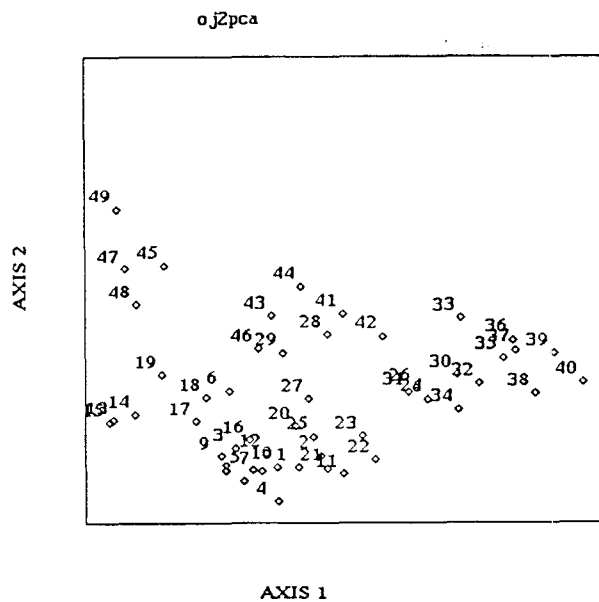
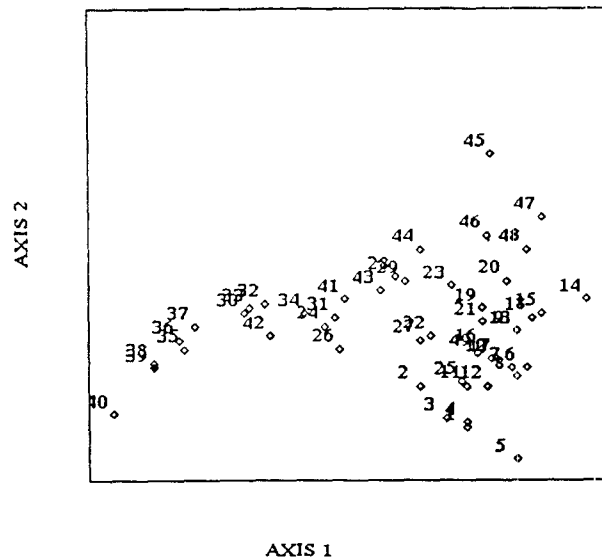
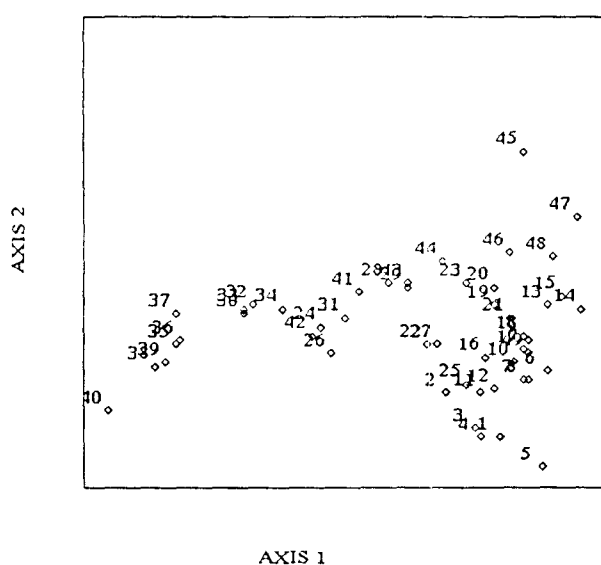


Fig. 21: Lake Ojibway PCA, reduced data set



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Fig. 22: Lake Ojibway DCA, full data set

Fig. 23: Lake Ojibway DCA, reduced data set

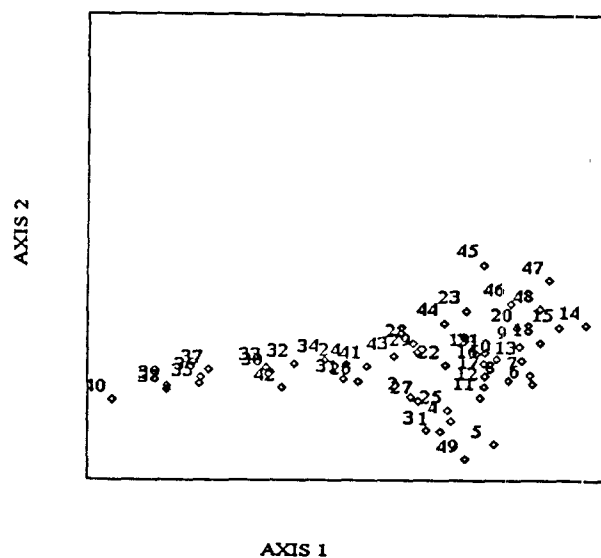
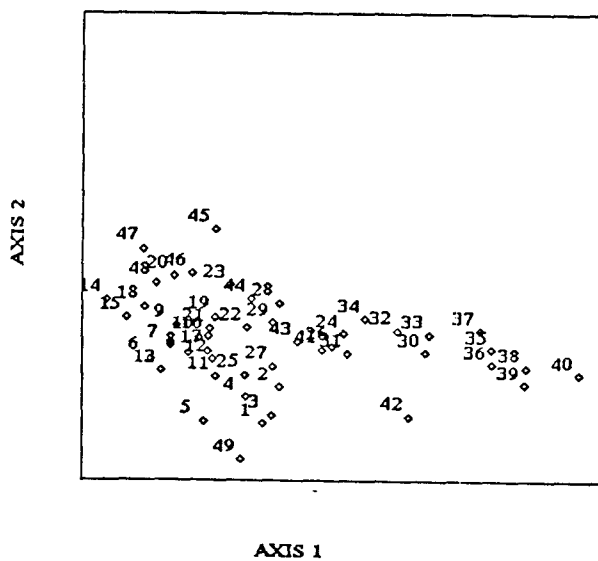


Fig. 24: Lake Ojibway NMDS, full data set

Fig. 25: Lake Ojibway NMDS, reduced data set