

THE LATE-HOLOCENE DEVELOPMENT OF JACK PINE FORESTS
ON OUTWASH PLAINS, NORTH-CENTRAL MINNESOTA

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ABSTRACT

Pollen diagrams from six study sites on outwash plains in north-central Minnesota are interpreted as records of similar vegetational change since ca. 5,000 yr B.P. All of these sites have undergone a shift from prairie to an aspen-oak community, followed by the jack pine forest that now occupies these sites.

The timing of these vegetational shifts is asynchronous among the study sites, with aspen and oak brush invading prairie at some sites as early as 4,500 yr B.P. and other sites as late as 2,800 yr B.P. Likewise, jack pine forests developed on some patches of outwash as early as 2,000 yr B.P. and at others as late as 500 yr B.P.

Locally varying factors determined where and when these vegetational shifts occurred. The flooding of depressions appears to be the event that allowed aspen to invade prairie locally. The rate at which afforestation proceeded appears to be related to local variability in the distribution of wet depressions that serve as firebreaks. Where peat-filled channels and chains of lakes occur, afforestation occurred first and was relatively rapid. Where lakes and peatlands are scattered, afforestation occurred later and required more time.

In these jack pine forests, the understory vegetation and the amounts of soil organic matter (SOM) are correlated with the length of time that jack pine has occupied the site. Where jack pine has been

established for less than 1,000 years, the shrub layer is tall and dense, and the soils have more than 2% SOM. Where jack pine has been established for more than 1,000 years, the shrubs are scattered and the soils have less than 2% SOM. The presence of "prairie indicator species" is a poor predictor of former occupation by prairie.

Land-survey records for 88 townships were analyzed to determine how jack pine trees are distributed and how they are associated with other tree species at the tension zone. Within its range, jack pine trees account for nearly 70% of the bearing trees occurring at upland corners on outwash. The only tree positively associated with jack pine is red pine. In contrast, the deciduous trees show an abundance of positive associations and can occur in almost any combination along the tension zone.

PREFACE

Large outwash plains are a common landscape feature of north-central Minnesota. Only a few tree species are abundant on the outwash, with jack pine, red pine, aspen, and oak accounting for nearly 90% of the forest cover. Of these taxa, jack pine is by far the most abundant, and it often forms pure stands. During my first few field trips to these jack pine stands, I was impressed by the remarkable heterogeneity of the understory vegetation -- in spite of the monotonous canopy of jack pine. The early settlers of the region were well aware of these vegetational differences, as they commonly distinguished jack pine communities as either barrens or true forest. Jack pine barrens were the preferred sites for farming and the understory of these areas is best described as a tall, nearly impenetrable thicket of aspen, oak grubs, and mesic deciduous shrubs. Because of the dense subcanopy of shrubs, the ground cover is sparse and contains several shade-tolerant herbs that also occur in mesic deciduous forests. The soils of barrens are prairie soils, so it is clear that jack pine has not long occupied these sites. In contrast, closed-canopy forests of jack pine occur on forest soils. These stands typically have a poorly developed subcanopy of shrubs, and the ground is carpeted with mosses, broadleaf evergreens, and numerous herb species. Other areas of jack pine are of an intermediate nature with regard to both the vegetation and soils.

These initial observations strongly suggested that the jack pine communities of north-central Minnesota became established in areas formerly occupied by prairie and that the present differences in vegetation and soils among stands might be the result of long-term forest succession and gradual degradation of the prairie soils caused by the acidic pine litter. The purpose of this thesis was to examine that possibility.

The first task was to describe and contrast the present vegetation and soils of jack pine barrens versus jack pine forest. This is the topic of Chapter 3. Relevés of 20 x 20 m vegetation plots, soil organic matter determinations, and soils maps provided the data for Chapter 3.

If the present spatial patterns of vegetation and soils are the result of long-term forest succession, then all patches of outwash should have experienced a similar sequence of vegetational change, but at different times. In simpler terms, the differences between jack pine barrens and jack pine forest should be related most to the length of time that forest (especially jack pine forest) has occupied different sites. Alternatively, they might have resulted from fairly synchronous but different afforestation sequences leading to the establishment of jack pine. Testing these hypotheses is the topic of Chapter 2. Six pollen diagrams provide the data to determine the vegetational history of the outwash plains. Preliminary results from Chapter 3 were used to locate the six study sites along a

vegetation/soils gradient, with jack pine barrens and jack pine forests serving as the two extremes.

Interpreting the pollen diagrams of Chapter 2 proved to be a difficult task. The complicating factor is that large areas of till surround the outwash plains, and the vegetational histories of these areas are different from those on the adjacent outwash. In order to reconstruct the vegetational history of outwash plains, it became important to understand how the major pollen-producing taxa are distributed with regard to outwash versus till. This is the topic of Chapter 1. To do this I analyzed the land-survey records for 88 townships in the study area. From this I identified the taxa that are essentially restricted to till, the species that can grow on outwash, and the circumstances under which jack pine tends to co-occur with other species that are common on outwash.

The three chapters are presented as individual papers, each with its own set of references. Chapter interrelationships are apparent only by internal citation (e.g. see Chapter X).

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CHAPTER 1: THE DISTRIBUTION AND ASSOCIATION OF MID-NINETEENTH
CENTURY TREES IN AN ECOTONAL REGION, NORTH-CENTRAL MINNESOTA

INTRODUCTION

In northern Minnesota prairie, deciduous forest, and coniferous forest come together in a narrow ecotone (Fig. 1.1). From the mid-Holocene to the present, the region has served as a transition between prairie and deciduous forest (McAndrews 1966), and the migration of pine into the region about 2,500 years ago (Jacobson 1979, and Chapter 2) has added to the vegetational complexity since that time. The north-south ecotone owes its stability, narrowness, and complexity to pronounced east-west changes in physiography. To the west, within the Red River drainage system, prairie has occupied flat ground moraine and the lacustrine deposits of Glacial Lake Agassiz. To the east, mixed conifer-hardwood forests have occupied the more rugged terrain drained by the Mississippi River. Prairie and conifer-hardwood forest are separated by a narrow band of deciduous forest that occurs on the western flank and highlands of the continental divide, which is located on a complex of north-south-trending end moraines rising 200 to 300 m above the Glacial Lake Agassiz plain.

Associated with the moraine complex and the Mississippi headwaters region are outwash plains, till plains, and drumlin fields composed of drift from three different ice lobes and deposited as a complicated mosaic of discrete physiographic units (Hobbs and Goebel 1982). The moraine itself is probably sufficiently high to trigger orographic precipitation and produce some adiabatic heating, as

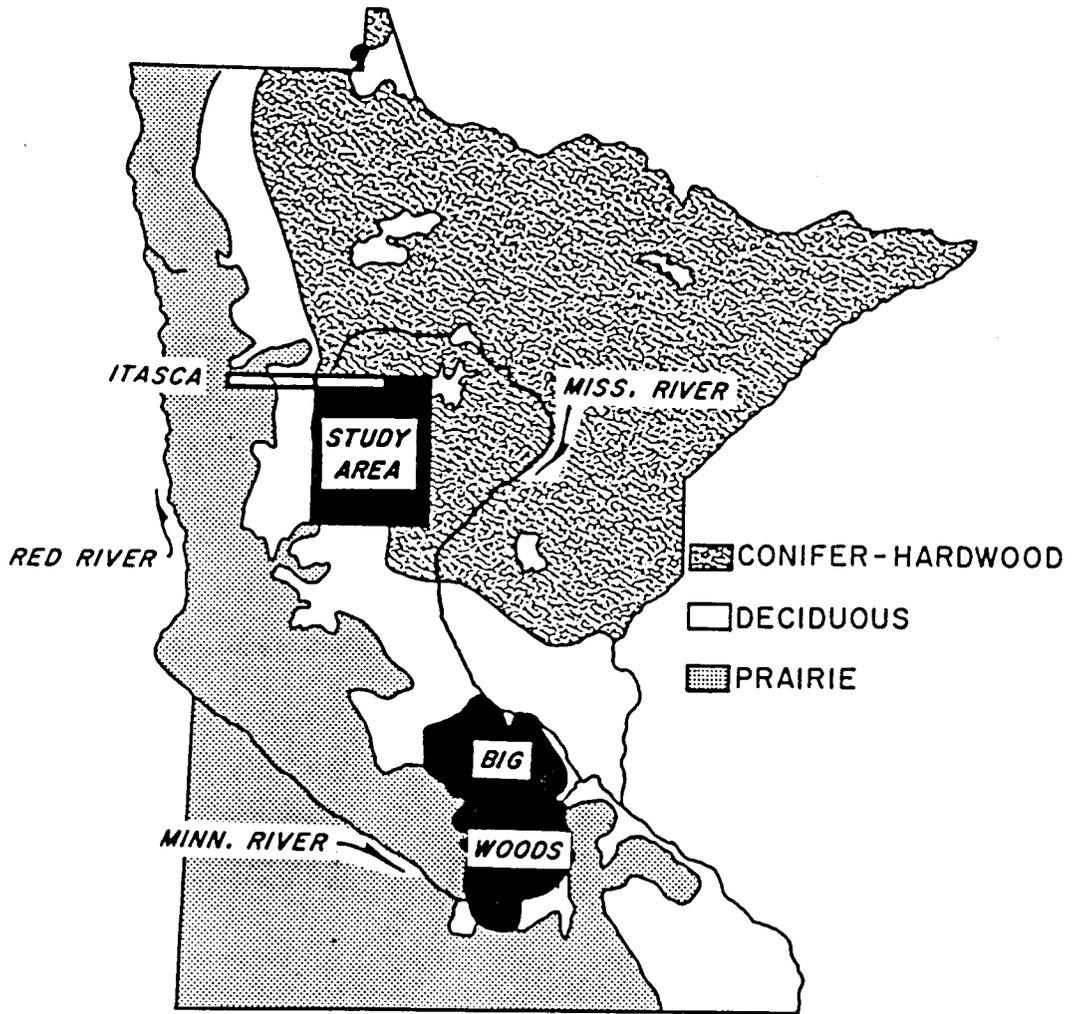


Fig. 1.1. The distribution of prairie, deciduous forest, and mixed conifer-hardwood forest in Minnesota, ca. AD 1850. The study area, the Itasca transect (McAndrews 1966), and the Big Woods (Grimm 1984, Daubenmire 1936) are areas discussed in the text. (Redrawn and modified from Rosendahl and Butters 1918)

evidenced by the local steepening and convolution of map isolines for the duration of snow cover, annual precipitation, and growing-degree-days (Kuenast et al. 1982, and unpublished data provided by E.L. Kuenast). The net effect of the locally varying climate interacting with the complex surficial geology is to produce a wide variety of plant habitats over short distances. Thus on a local scale the transition from prairie to conifer-hardwood forest is not a smooth one; rather it is a complex mosaic of diverse vegetational units correlated with local physiography. Beginning in the study area (Fig. 1.1), an ecologist could in a single day visit study sites in tallgrass prairie (Buell and Facey 1960), aspen parkland (Svedarsky and Buckley 1975, Ewing 1924), oak savanna (McAndrews 1966), "climax" sugar maple forest (Buell and Cantlon 1951), pineries (Frissell 1973, and Chapter 3), spruce-fir forests (Buell and Gordon 1945), or patterned peatlands similar to those of boreal regions (Glaser et al. 1981).

The study area is situated on the contact between the deciduous and conifer-hardwood forests (Fig. 1.1), where prairies occur locally. The vegetation is complex. Of the 16 vegetation types recognized by Marschner (1974) in Minnesota, 14 occur in the small, 88-township study area. With the exception of a few trees limited to the southeastern corner of the state (e.g. Juglans, Carya, Celtis), the study area includes nearly all of Minnesota's forest trees. Thus the study area provides the opportunity to determine how individual tree

taxa are distributed in several habitats (physiographic units), and to see how the taxa are associated where so many tree taxa are present.

Land-survey records (ca. AD 1855-1880) provide data on the distributions of individual taxa and their associations. Actual descriptions of the vegetation by surveyors and early explorers provide some details of the composition and physiognomy of the vegetation.

METHODS

The data for this study are the surveyor's notes from the original survey of Minnesota's public lands. The contracts and instructions (standardized in AD 1855) for these surveys were controlled by the United States General Land Office (Dodds et al. 1943, Stewart 1935). The 88-township study area was surveyed between 1855 and 1880 and completed in two stages. First, the six-mile square township exteriors were established from a coarser grid of standard parallels and principal meridians. In forested areas, corner posts were set at half-mile intervals and "witnessed" by either two or four trees. Second, the townships were subdivided into 36 one-mile square sections. Posts were set at each section corner and witnessed by four trees, one in each of the contiguous sections. Midway between each section corner, quarter-section posts were set and witnessed by two trees on opposite sides of the survey line. For each corner, the nearest suitable tree in each quadrant was selected as a "bearing

tree." Bearing trees were distinguished by scribing their respective township, range, and section numbers within a blaze and by notching the side facing the corner post. For each bearing tree, the surveyors recorded its common name, diameter (inches, one inch = 2.54 cm), compass bearing from the corner (degrees), and distance from the corner (links, one link = 0.20 m).

The study area contains 9,650 corners and 21,587 bearing trees. The more common taxa recorded and their Linnaean equivalents are given in Table 1.1. The botanical nomenclature follows Gleason and Cronquist (1963). The use of land-survey records to reconstruct vegetation is described by Bourdo (1956) and reviewed by Grimm (1981).

Four physiographic characteristics were determined for each corner by plotting the corners on soils maps (Minnesota Soil Atlas 1969, 1980) and by referring to the survey notes. Outwash plains, moraine, till plains, and drumlin fields occur in 14 separate portions of the study area (Fig. 1.2). The texture of the upland soils near the corner was recorded as sandy, loamy, or mixed. The presence or absence of a mollic epipedon was recorded. The corners were classified as upland, lowland, or wetland. Corners on well-drained soil-mapping units were designated as upland. Alluvium and poorly drained mineral-soil units define the lowland class. The survey notes alone were used to determine wetland corners, defined as those falling in lakes, streams, marshes, or swamps. The assignment of physiographic classes to each corner permits the comparison of

Table 1.1. Numbers, percentages, and species equivalents of bearing-tree taxa in the study area.

TAXON	SPECIES	NUMBER	PERCENT
Fir	<u>Abies balsamea</u>	184	0.85
Sugar maple ¹	<u>Acer saccharum</u>	350	1.62
Paper birch	<u>Betula papyrifera</u>	879	4.07
Black ash	<u>Fraxinus nigra</u>	94	0.44
Ash ²	<u>Fraxinus pennsylvanica</u> some <u>F. nigra</u>	165	0.76
Tamarack	<u>Larix laricina</u>	3053	14.14
Ironwood	<u>Ostrya virginiana</u>	67	0.31
Spruce	<u>Picea glauca</u>	606	2.81
Pine ³	<u>Pinus strobus</u> some <u>P. resinosa</u> or some <u>P. banksiana</u>	394	1.83
Jack pine	<u>Pinus banksiana</u>	4962	22.99
Red pine	<u>Pinus resinosa</u>	2724	12.62
White pine	<u>Pinus strobus</u>	1024	4.74
Aspen	<u>Populus tremuloides</u> some <u>P. grandidentata</u>	3933	18.22
Balsam poplar	<u>Populus balsamifera</u>	170	0.79
Oak ⁴	<u>Quercus macrocarpa</u> some <u>Q. borealis</u>	1159	5.37
Red oak	<u>Quercus borealis</u>	318	1.47
Bur oak	<u>Quercus macrocarpa</u>	689	3.19
Basswood	<u>Tilia americana</u>	241	1.12
Elm	<u>Ulmus americana</u> some <u>U. rubra</u>	495	2.29
Rare ⁵	see footnote	80	0.37
TOTAL		21587	100.00

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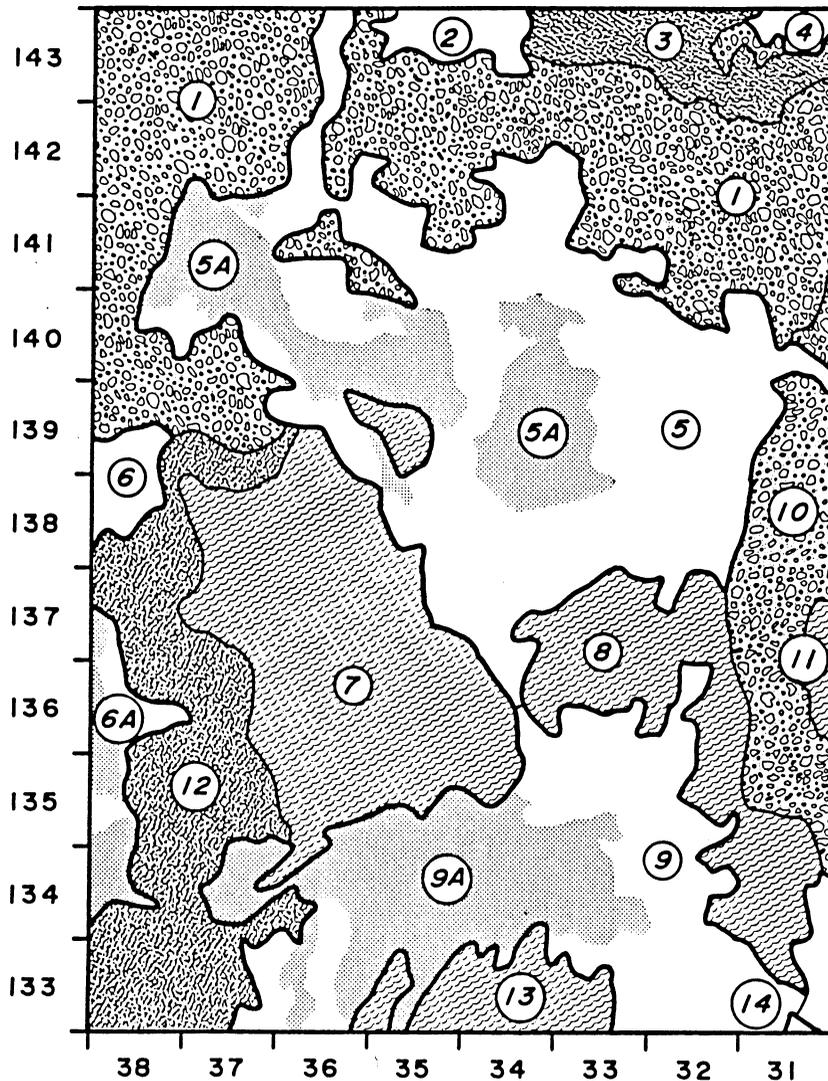


Fig. 1.2. The physiographic units of the 88-township (77 x 106 km) study area. The units are (1) Itasca moraine, (2) Lake George outwash plain, (3) Guthrie till plain, (4) Bemidji sand plain, (5) & (5A) Park Rapids outwash plain, with forest soils and relict prairie soils respectively, (6) & (6A) Detroit Lakes outwash, with forest soils and relict prairie soils respectively, (7) Wadena drumlin field, (8) Cass drumlin field, (9) & (9A) Staples outwash plain, with forest soils and relict prairie soils respectively, (10) St. Croix moraine, (11) Pine River drumlin field, (12) Henning till plain, (13) Todd drumlin field, and (14) Crow Wing outwash plain. (Redrawn and modified from the Minnesota Soil Atlas 1969, 1980)

bearing-tree abundances, distances, and diameters by physiographic region.

A FORTRAN computer program BTPLOT written by E.C. Grimm was used to plot maps of bearing trees at the scale of 1:250,000. A solid square, representing a single bearing tree, was plotted in the appropriate quadrant relative to the corner at which it was recorded. These maps provide a visual assessment of how each bearing-tree taxon is distributed among the major physiographic regions. Comparing maps of the various taxa allows for qualitative estimates of associations among the taxa.

The strength of pairwise associations between bearing-tree taxa was measured with Cole's Coefficient (**C** hereafter; Cole 1949). In this analysis, corners are treated as very small plots that can hold but four individuals. A 2 x 2 contingency table was constructed from the presence and absence of all pairs of bearing-tree taxa. From these tables, it is possible to calculate **C** (range -1.0 to +1.0) and make a X^2 test of independence (Pielou 1969). Because only four individuals can occur at a corner, the presence of any one taxon significantly lowers the probability that another taxon will occur at that corner. This negatively biases the values of both X^2 and **C** (Grimm 1981). Thus the X^2 tests are conservative, and positive values of **C** represent strong positive association. Because of this bias, the analysis of association was restricted to upland corners having all four bearing trees.

To provide a visual interpretation of associated taxa, the 16 most abundant taxa were ordinated by a non-metric multidimensional scaling of their Cole's Coefficients. A version of KYST-2 (Kruskal et al. 1977) available at the University of Minnesota Computer Center was used to perform the scaling. The option to rotate the final configuration to its principal axes was selected.

RESULTS AND DISCUSSION

Analysis of Association

Groups of associated taxa.- The abundance of positive associations among the deciduous taxa is indicated on the scaling of Cole's Coefficients (Fig. 1.3). For convenience the deciduous taxa (and white pine) are divided into two groups on the basis of their first-axis scores and ecology. One group consists of fire-sensitive taxa, which have the highest first-axis scores and typically occur on fine-textured soils developed on till. Although these taxa represent a terminal or "climax" cover-type for the region (Buell and Gordon 1945), they are rare in the study area. Elm, sugar maple, basswood, ash (Fraxinus pennsylvanica ?), black ash, and ironwood collectively represent just 6.5% of the bearing trees.

White pine, aspen, paper birch, bur oak, red oak, and balsam poplar constitute the second group (fire-tolerant) and have lower first-axis scores. The deciduous trees of the fire-tolerant group

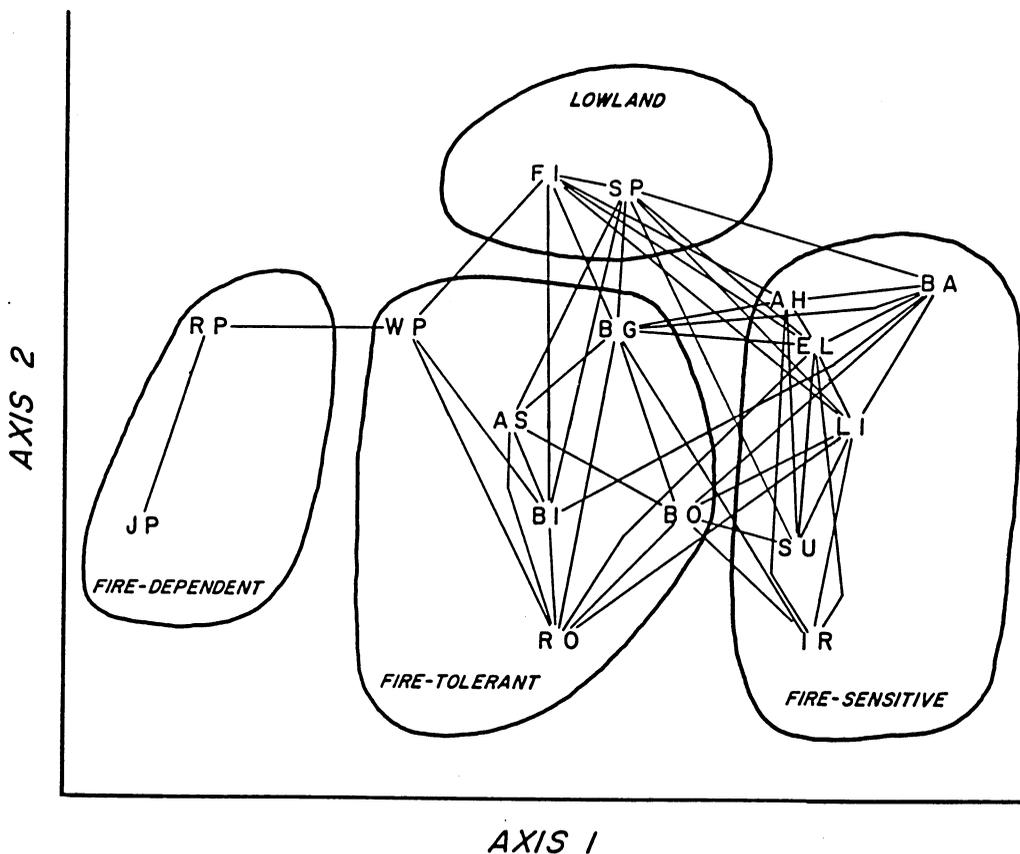


Fig. 1.3. Ordination of the bearing-tree taxa by nonmetric multidimensional scaling of their Cole's Coefficients. The lines connecting the two-letter taxon codes indicate a positive association among those taxa. The taxa codes are: (JP) jack pine, (RP) red pine, (WP) white pine, (AS) aspen, (BI) paper birch, (RO) red oak, (BO) bur oak, (BG) balsam poplar, (FI) balsam fir, (SP) white spruce, (AH) ash, (BA) black ash, (EL) elm, (LI) basswood, (SU) sugar maple, and (IR) ironwood.

generally produce more vigorous post-fire sprouts than the fire-sensitive hardwoods (except basswood; Perala 1974 a,b). The fire-tolerant taxa provide the bulk of the forest cover on till, where they collectively represent 56% of the bearing trees. However, with the exception of white pine and birch, these taxa also dominate in regions of outwash outside the range of jack pine.

In contrast to the deciduous taxa, the pines have few positive associations. The association of white pine with red oak and paper birch provides the only tie between the pines and deciduous taxa. White pine is thus included with the fire-tolerant hardwoods, whereas red and jack pine constitute the group of fire-dependent taxa, which have the lowest first-axis scores in Figure 1.3.

Both red and jack pine have strong negative associations with all of the deciduous taxa (Appendix 1.A, Table 1.A.1). This result is related to the ability of jack pine and to a lesser extent red pine to grow in pure stands on sandy soils, particularly outwash plains. Because land-survey data impart a negative bias on the values of C, taxa tending to grow in monospecific stands, even if only under special circumstances, are likely to have few positive associations with other taxa. Thus the strong negative associations between red or jack pine and the deciduous taxa are somewhat exaggerated, and the relationships of the pines to the other taxa should be evaluated with the X^2 test of independence. In this case, the probability that red or jack pine is distributed independently of any deciduous taxon is

less than 0.05 for all of the pairwise comparisons. Thus red and jack pine are clearly growing apart from the deciduous taxa.

Spruce (Picea glauca ?) and fir constitute the fourth group in Figure 1.3. In boreal forests white spruce and fir occur over a wide range of soil-moisture and light conditions (Curtis 1959). In the study area, however, these taxa are most abundant on poorly drained mineral soils. Spruce and fir account for 7.2% of the bearing trees on poorly drained soils versus 3.0% on well drained soils. Also, both taxa are associated with tamarack, which was recorded occasionally as a bearing tree on poorly drained mineral soils. Both taxa can tolerate a thin veneer of organic soils but not deeper peats, which in the study area tend to be open or forested with tamarack. Black spruce (Picea mariana) does occur on deeper peat, but it is rare in the study area.

Comparison with the Big Woods.- By design, the methods used in this study are the same as those used by Grimm (1981, 1984) in his study of the Big Woods in southern Minnesota (Fig 1.1). The methodological similarity allows a comparison of the Big Woods, a large expanse of fire-sensitive taxa bordered by fire-tolerant types, with the study area, which is characterized by small patches of fire-sensitive taxa in a matrix of fire-tolerant types. In general, the values of *C* in this study are 0.2-0.4 units higher for the pairwise comparisons of the eight taxa growing in both regions. Consequently, positive associations among the deciduous taxa in this study are more

numerous.

In the Big Woods aspen, bur oak, and red oak (two positive associations) are included in a group of fire-tolerant taxa separate from a group of fire-sensitive taxa that include elm, basswood, ash, ironwood, and sugar maple (seven positive associations). The distributions of bearing trees were sufficiently distinct geographically to map them as vegetation units larger than ca. 15 townships. In this study the same eight taxa form a single group with 20 positive associations. Although there is some distinction between fire-sensitive and fire-tolerant taxa in Figure 1.3, there are only a few places in the study area where plots of these bearing trees exhibit sufficient pattern for mapping on a scale similar to Grimm's study. Specifically, most patches of fire-sensitive trees tend to be no larger than a township or two in size.

There are both methodological and environmental reasons for the abundance of positive associations among the deciduous taxa studied here. Because the number of individuals per sample is small (4 at a survey corner), C is somewhat sensitive to the number of taxa included in the analysis. By including more taxa, 16 here versus 12 in Grimm's study, the number of joint absences increases for taxa that commonly grow in mixed stands. Large joint absence values cause high, positive values of C . For this study, the large number of corners falling in monotypic pine stands resulted in high joint absence values for the deciduous taxa. However, when corners having pine bearing trees were

eliminated from the analysis, the values of *C* are still 0.1-0.2 units higher than those obtained by Grimm. This indicates that the deciduous taxa of the study area probably do grow in more mixed stands than the deciduous taxa of the Big Woods.

The most obvious environmental difference between the two study areas is that sandy soils, loamy soils, and mixed sandy-loamy soils are equally represented in the study area (Minnesota Soil Atlas 1969, 1980), in contrast to the dominance of loamy soils in the Big Woods (Grimm 1984). Curtis and McIntosh (1951) demonstrated that in Wisconsin the same taxa form a vegetational continuum along a gradient of xeric to mesic habitats. Apparently the bearing trees of this study occur in mixtures because the complete range of xeric to mesic soils is available and equitably represented.

Interpretation of the ordination.- The concurrent influence of a single or few factors on the distributions of several species results in their association (Grieg-Smith 1983). If the association of bearing trees is the result of similar responses to the environment, then it is sensible to construct hypothetical environmental gradients to correspond with the ordination axes (Fig. 1.3). Studies of the same taxa in Wisconsin and Minnesota have led to considerably different conceptual models of vegetation dynamics and the interpretation of ordination axes. In Wisconsin, Curtis and his colleagues (Curtis 1959, Bray and Curtis 1957, Curtis and McIntosh 1951) used data from detailed (high resolution) descriptions of

vegetation to rank the upland tree species along a continuum of pioneer to climax species consistent with a gradient of xeric to mesic habitats (essentially soil-moisture). Although this successional model may apply in the absence of disturbance, studies of the vegetation using low-resolution, systematic sampling such as land-survey records (Grimm 1984, Canham and Loucks 1984) have emphasized the role of disturbance as the more proximal cause of vegetation pattern and dynamics. In such disturbance models, vegetation change is brought about by changes in the frequency, severity, and predictability of disturbance, and the state of the soils is more a result than a cause of vegetation patterns or history - as evidenced by the biosequence of Big Woods soils described by Grimm (1984) and a chronosequence of soils under the jack pine stands of the present study (see Chapter 3). Vegetation types, whether defined as climax or successional, may persist for long periods of time and over broad ranges of climate because the vegetation itself largely determines the probability of disturbance, e.g. windthrow, disease, and fire.

The Wisconsin model of a vegetational-continuum fails to account for several observations in this study. First, as evidenced by the abundance of positive associations among all deciduous taxa (Fig. 1.3), nearly any combination of deciduous trees may occur in the study area. That is, stands of deciduous trees need not be composed of nearest neighbors on the vegetational continuum. The most obvious departure is the association of bur oak with sugar maple, basswood,

and ironwood. Second, the pioneer species jack pine, aspen, and bur oak occur on all soil units in the study area and are not restricted to xeric sites. While sugar maple, basswood, ironwood, and elm reach their peak abundances on till plains characterized by fine-textured upland soils, these till plains were dominated by aspen, with bur oak and jack pine as the second and third most abundant taxa respectively (Table 1.2). Third, taxa near the sugar-maple end of the continuum are expected to occur on well-drained soils. In the study area, however, sugar maple, basswood, ironwood, and elm are (essentially) twice as abundant on poorly drained soils and alluvium, where they grow because they are protected from fires, regardless of soil conditions.

The overwhelming abundance of successional taxa in the study area (jack pine, aspen, and bur oak account for 44% of the bearing trees) indicates that disturbance, especially fire, is the major proximal factor controlling the distribution and association of bearing trees. This was not unknown to the proponents of the continuum model, as Bray and Curtis (1957) noted:

"The coincidence that Quercus macrocarpa is both the most initial and fire resistant species, and that Acer saccharum is the most terminal and fire susceptible species, suggests that the ultimate explanation for the composition of a forest stand in upland Wisconsin is largely an historic one."

Unlike soil properties, disturbance factors are not easily measured because of their historical nature. Determining the frequency and predictability of fire or other disturbances requires

Table 1.2. Bearing-tree percentages for upland (U) and lowland (L) corners as they occur on outwash plains, end moraine, drumlin fields, and till plains. The taxa are grouped by their peak relative abundance on one of the four geomorphic units. Note the similarity of the taxon groups with the groups in the ordination (Fig. 1.3). Lowland corners are those falling on poorly drained soils or alluvium. Dashes indicate percentages less than 0.1%.

TAXON	OUTWASH		MORAINE		DRUMLINS		TILL	
	U	L	U	L	U	L	U	L
Jack pine	53.0	16.0	17.5	----	8.9	4.6	6.4	----
Red pine	17.4	13.4	21.5	2.9	7.1	1.9	4.8	----
White pine	1.1	6.4	12.0	5.7	3.1	2.0	6.4	8.8
Paper birch	1.3	3.0	8.6	8.6	5.1	3.9	5.5	5.5
Red oak	0.6	0.7	2.9	5.7	2.0	0.6	2.5	----
Aspen	9.1	14.1	22.4	34.3	35.2	40.4	28.4	44.0
White spruce	1.1	4.3	1.7	11.4	3.5	6.3	2.2	2.2
Bur oak	4.3	2.3	1.4	----	4.7	4.7	7.6	6.6
Ash	0.1	2.6	0.7	----	1.3	1.5	0.6	1.1
Balsam fir	0.1	1.1	1.0	----	1.2	2.2	0.6	1.1
Balsam poplar	0.5	0.3	1.1	----	1.2	0.7	1.6	----
Black ash	0.1	2.1	0.1	----	0.6	0.6	0.6	2.2
Elm	0.8	6.9	1.1	5.7	3.8	6.9	5.7	8.8
Basswood	0.2	1.5	0.7	2.9	3.3	2.0	3.8	1.1
Sugar maple	0.2	2.3	0.6	2.9	4.3	5.9	4.3	1.1
Ironwood	0.1	0.7	0.2	----	0.8	1.1	1.0	----
TOTAL CORNERS	2534	320	2009	12	1052	218	786	40
TOTAL TREES	6067	724	5111	35	2631	539	1794	91

either long-term observation or adequate historical methods. The analysis of fire-scar data and stand-origin maps (Frissell 1973, Heinselman 1973) have led to some insights, as have charcoal concentrations in laminated lake sediments (Swain 1973, 1978). Although the ranking of bearing-tree data on the first axis of Figure 1.3 appears consistent with their fire ecology, demonstration of a causal relationship between fire and the distribution or association of bearing trees is problematic because of a lack of historical information.

The Distribution of Bearing-tree Taxa

The distributions of bearing trees are best correlated with physiography because the factors that distinguish physiographic units also provide the abiotic settings that strongly influence the behavior of fires and soil properties (Grimm 1984). Regardless of a bias towards a model of bearing-tree taxa sorted out in successional order along a gradient of soil-moisture (Curtis 1959, Bray and Curtis 1957, Curtis and McIntosh 1951) or a bias towards the influence of fire on vegetation (Grimm 1984, Heinselman 1973, 1981), the distributions of bearing trees would be expected to correlate with physiography. The physiographic factors that appear to be most influential and that are emphasized below are (1) soil drainage, (2) soil texture, (3) the distribution of wetland firebreaks, (4) topography, and (5) the size of the physiographic unit (Fig. 1.4).

Because the physiographic units are large, relatively homogeneous, and typically have sharp boundaries, patterns of trees sampled at half-mile intervals can be apparent. Where boundaries are diffuse, the bearing-tree distributions appear mixed.

As will be demonstrated below, the bearing-tree distributions are influenced most by the complex pattern and the sharp boundaries between till and outwash. Thus the outwash/till boundary appears on all of the bearing-tree distribution maps (Figs. 1.5-1.17). The most striking vegetational difference between the two physiographic units is the dominance of just four taxa on outwash plains. Jack pine, red pine, oak, and aspen account for 90% of the bearing trees on outwash. None of these taxa, however, is restricted to outwash plains. Red pine, oak, and aspen are actually more abundant on till (Table 1.2). Although jack pine is the dominant taxon on outwash plains, it is a common bearing tree on any sandy soil regardless of topography. Thus the overall vegetation pattern is characterized most by the absence of many taxa on outwash plains. Only under rare circumstances, usually in association with poorly drained soils and peatlands, do mesic taxa occur on outwash plains.

Jack pine.- Dense patches of jack pine bearing trees occur on flat portions of outwash plains, where there are few water-related firebreaks (Figs. 1.4.B and 1.5; townships 141-37, 140-36, 140-35, 140-32, 139-32, 138-34, 138-33). Such areas, however, were occupied by two very different types of jack pine-dominated vegetation.

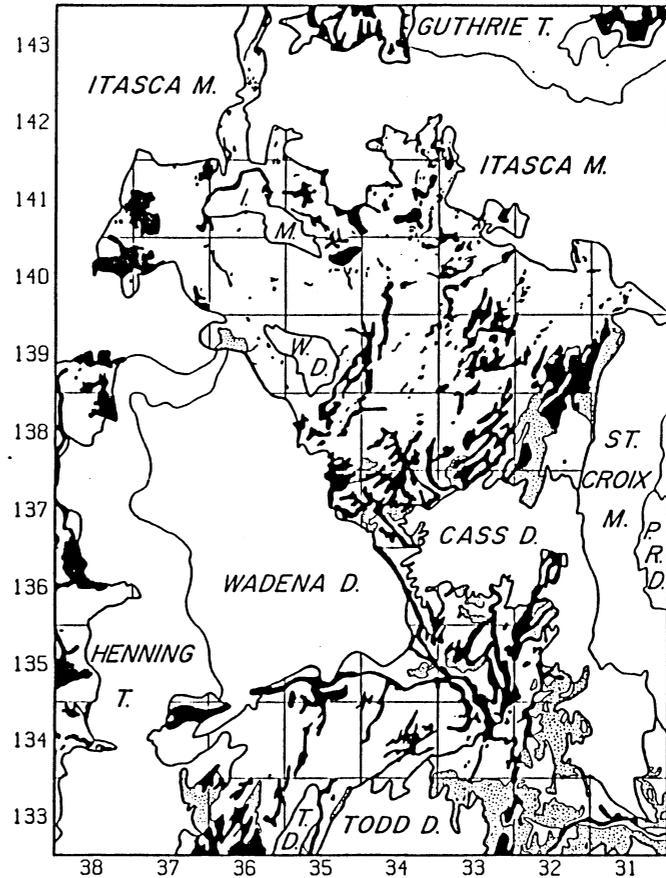
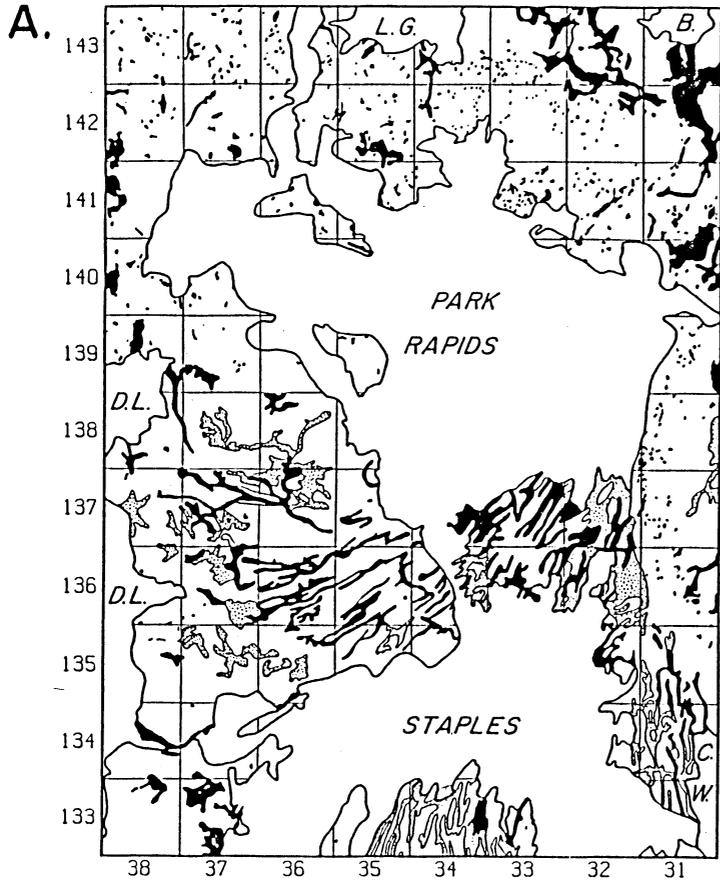


Fig. 1.4. The distribution of water-related firebreaks on till (A) and outwash (B). Lakes, peatlands, and alluvial soils (as they mark the wider streams) are shown in black. Poorly drained soils are indicated by stippling. The labeled physiographic regions of map A serve as the key to map B and vice versa. Abbreviations: (M) moraine, (T) till plain, (D) drumlin field, (D.L.) Detroit Lakes, (L.G.) Lake George, (B.) Bemidji, (C.W.) Crow Wing, and (P.R.) Pine River. Township (vertical) and range (horizontal) numbers are relative to the fifth principal meridian.

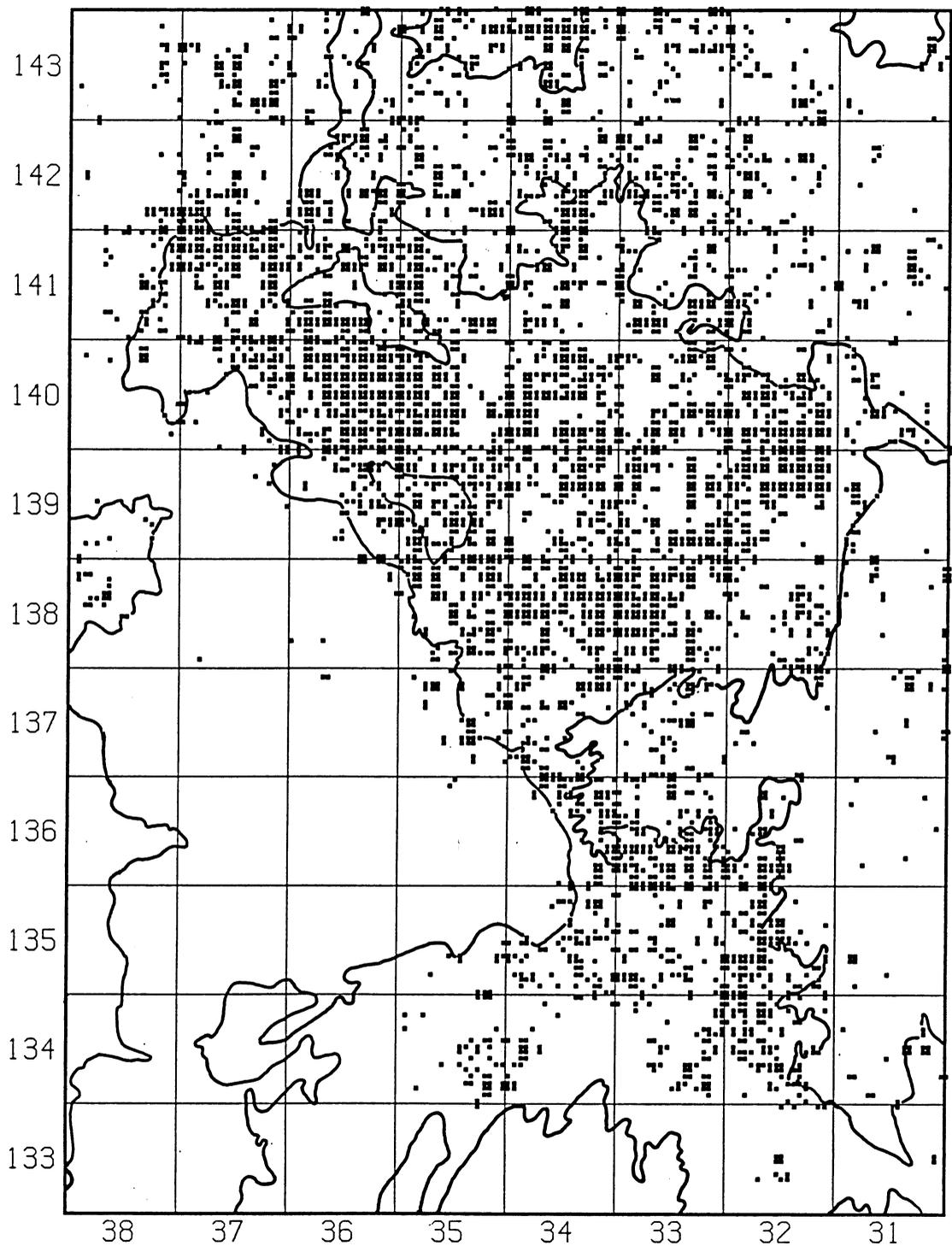


Fig. 1.5. The distribution of jack pine bearing trees, concentrated on the Park Rapids and Staples outwash plains (see Fig. 1.4).

Some of these flat, lakeless districts supported jack pine stands in which there is relatively little brush and where the ground is carpeted by mosses, low-growing ericaceous shrubs, and several species of broadleaf evergreens. The soils of these areas are light-colored forest soils (Entisols, Minnesota Soil Atlas 1969, 1980) and were described by surveyors as "third-rate" and of little agricultural value. This type of jack pine forest is probably more common today than it was naturally. Where the soil is slightly richer or where firebreaks occur (see below), the surveyors described brushy stands of jack and red pine. The intense selective logging of red pine and the destructive slash fires that followed have left nearly pure stands of jack pine in some of these areas (Bourgeois et al. 1974). Portions of the study area that most likely supported the natural pure stands of jack pine are in townships 140-32, 139-32, 138-34, and 138-33 (Fig. 1.5).

Other areas of outwash with few firebreaks supported a type of jack pine-dominated vegetation that was quite different from the above. Here the jack pines were widely spaced and the vegetation was described by the surveyors as jack pine "barrens" or "openings." In such areas (Figs. 1.4.B and 1.5; townships 141-37, 140-36, 140-35, 140-34, 139-34, and 134-35) the average distance from a survey corner to a jack pine bearing tree was 35.4 m in contrast to 14.3 m in the pure jack pine forests on outwash described above. In jack pine openings, the variance of bearing-tree distances is much higher (3,860

m²) than it is in jack pine forest (508 m²). The high variance suggests that the trees in jack pine openings occurred in scattered patches rather than in an orchard-like savanna. The explorer O.E. Garrison noted the "peculiar" nature of these jack pine openings (from Todd 1899).

"The characteristic tree is still the black (jack) pine but there are also many small burr-oaks with aspen, birch, and iron wood with small prairies and openings. These openings have a character peculiar to themselves. As throughout the west the prairie oak openings were considered choice locations by the early emigrants, so here the black pine openings with the small prairies are the choice places.

This peculiar tract of country commences near the west bank of the Crow wing river where it runs south through Ts. 139, 140-33, and extends northwest to the range of hills dividing the head of Otter Tail or Red river from the Shell." (essentially the dark-soil regions of the Park Rapids outwash plain, Fig. 1.2)

Garrison's observation that these black pine openings were similar to oak openings was quite perceptive. Pollen diagrams from these areas indicate that jack pine had invaded oak-dominated brush-prairie or openings only a few centuries before Garrison made his observation (see Chapter 2). Consequently the prairie soils (Fig. 1.2) and the luxuriant undergrowth of oak and aspen is a relict condition that is absent from regions with a longer record of jack pine occupation. Thus these jack pine openings are clearly a transitional state between oak openings and jack pine forest, and they are not analogous to the well-studied jack pine barrens of Wisconsin (Curtis 1959), which have probably persisted as barrens throughout the Holocene as indicated in the limited pollen record (Wilson 1938).

The jack pine openings of the study area are all but gone from the modern landscape. Most of the land is under cultivation, and many of the remaining woodlots have succeeded to oak forest after a century of fire suppression (see Chapter 3).

Much of the outwash-plain surface is undulating, particularly where drainage channels (of glacial origin) persist and where sand blankets former drumlin fields (Wright 1962). Many of these drainage channels and inter-drumlin swales now lie below the water table and are consequently filled with long lakes, chains of lakes, peat, or poorly drained soils (Fig. 1.4). These water-related firebreaks effectively isolated small patches of outwash from the frequent crown fires that characterize the large, continuous stands of jack pine on outwash. Jack pine is still a common bearing tree on these smaller patches of outwash, but here it is mixed with other taxa, particularly red pine. Townships 141-34, 140-33, 139-33, and 138-34 provide good examples of mixed red and jack pine (Figs. 1.5 and 1.6) in the lake and peatland district of the Park Rapids outwash plain (Fig. 1.4.B).

Jack pine is also common on moraine, where it accounts for 17.5% of the bearing trees (Table 1.2). Jack pine is one of the few species to be distributed differentially between the Itasca and St. Croix moraines (Figs. 1.2 and 1.4). Twenty percent of the bearing trees on the Itasca moraine are jack pine, as opposed to just 4.9% on the St. Croix moraine. One difference between the moraines is that the Itasca moraine contains sand and gravel deposits associated with tunnel-

valley systems and ice-contact features (Hobbs and Goebel 1982). Twelve percent of the Itasca moraine's survey corners fall on sand and gravel deposits, and there jack pine accounts for 29.5% of the bearing trees. However, jack pine accounts for 20.6% and 17.1% of the bearing trees respectively on mixed sandy-loamy soils and loamy soils of the Itasca moraine. These soils are as fine-textured as those of the St. Croix moraine, mapped as having mixed sandy-loamy soils (Minnesota Soil Atlas 1969, 1980). Thus comparing the abundance of jack pine bearing trees on morainic soils of different textures fails to provide an explanation for the paucity of jack pine on the St. Croix moraine or alternatively the abundance of jack pine on loamier soils of the Itasca moraine. The moraines do differ with regard to the calcareousness of the drift. The Itasca moraine is calcareous and the St. Croix moraine is not (Hobbs and Goebel 1982). That jack pine is most abundant in the Park Rapids outwash plain (Fig. 1.5) where the sands are noncalcareous or leached of their carbonates argues against the hypothesis that soil calcareousness is a factor controlling the distribution of jack pine.

Red pine.- Apart from the occurrence of red pine with jack pine on the Park Rapids outwash plain, the distribution of red pine is best described as transitional between sandy sites occupied by jack pine and loamy sites dominated by white pine. Thus it is difficult to relate the distribution of red pine to landforms or soil units because it is abundant along physiographic boundaries. This observation is

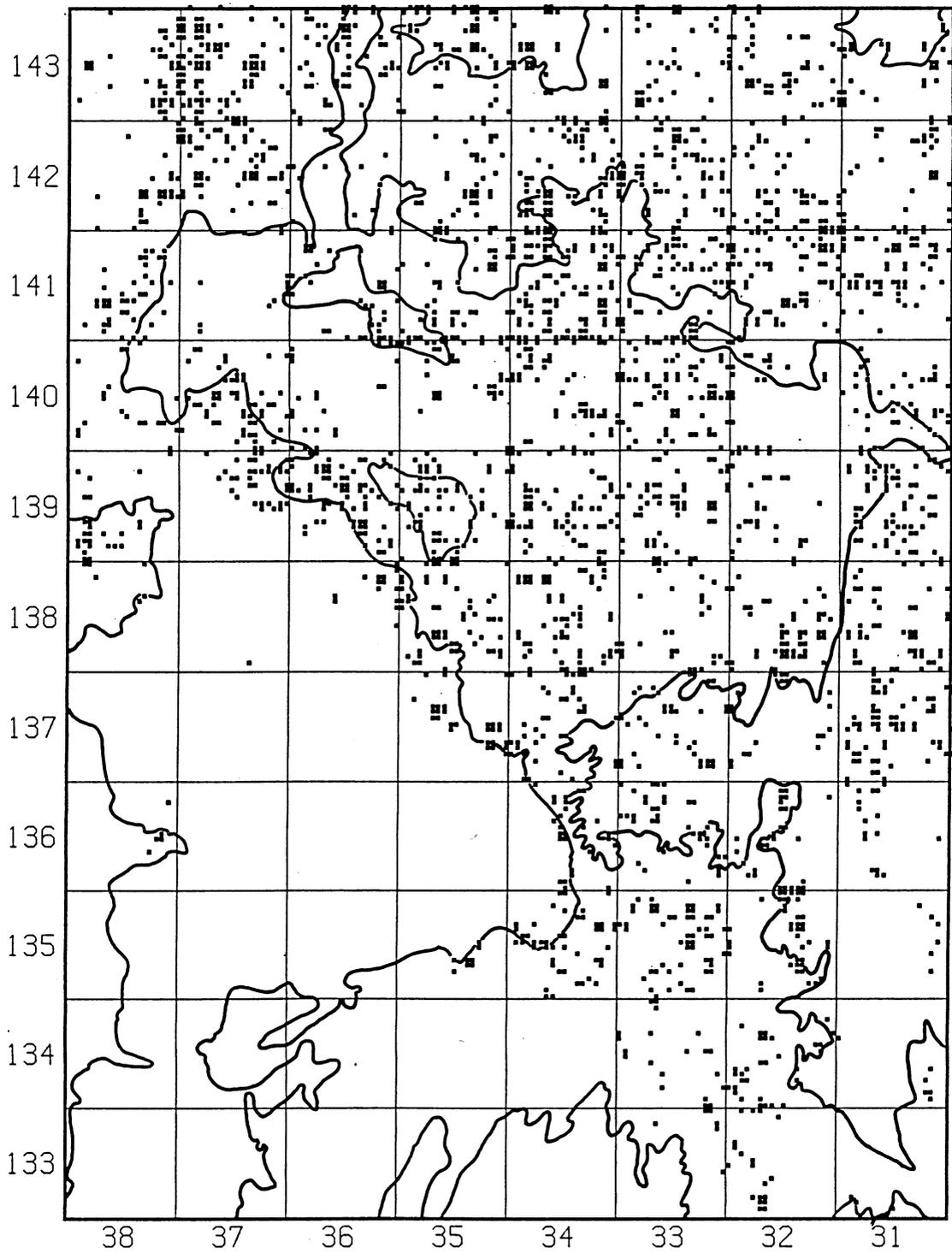


Fig. 1.6. The distribution of red pine bearing trees, occurring on both till and outwash (see Fig. 1.4).

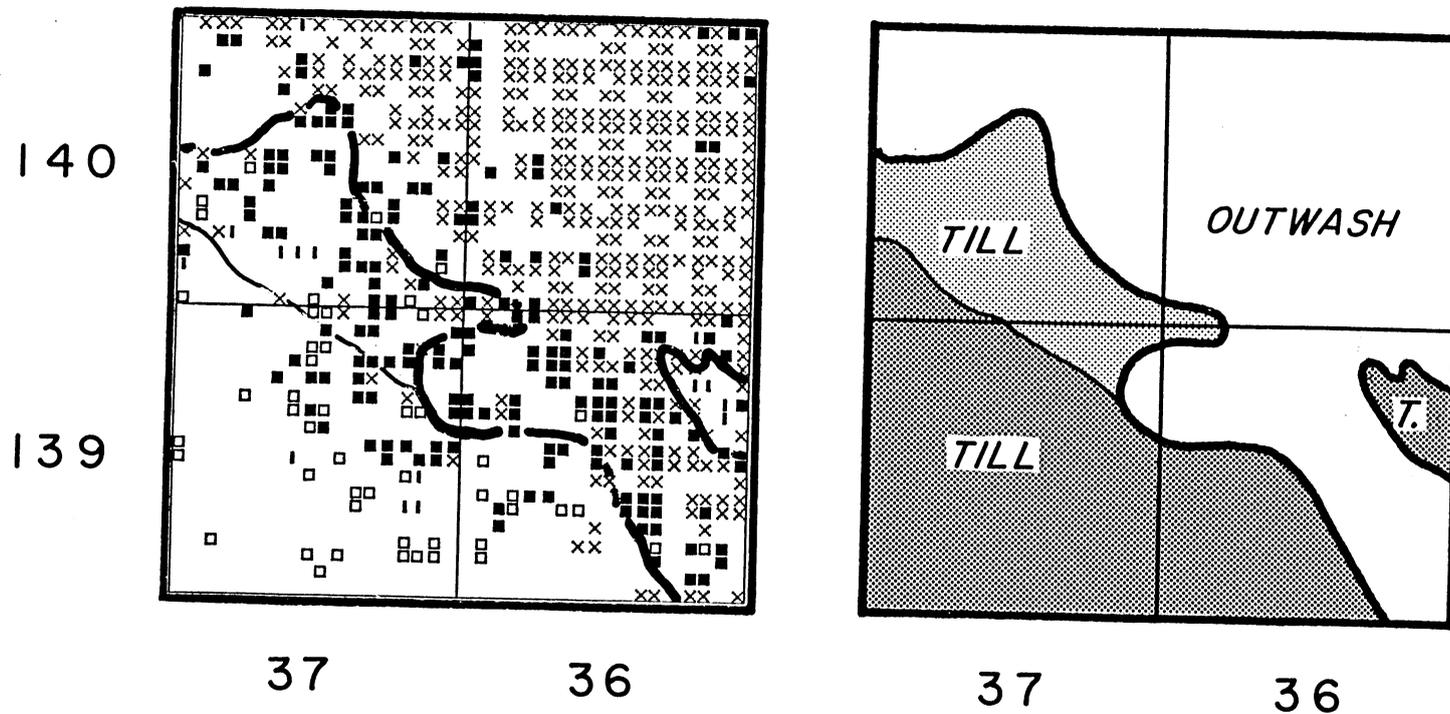


Fig. 1.7. The distribution of jack pine (X), red pine (solid squares), and white pine (open squares) bearing trees along a contact between outwash and till. The outwash soils are sandy, the lighter shaded area of till has mixed sandy-loamy soils, and the darker shaded area of till has loamy soils (Redrawn from the Minnesota Soil Atlas 1969).

supported by the analysis of association where red pine is positively associated with both jack pine and white pine (Fig. 1.3). Such transitional areas occur along the contact of sandy and loamy soils within the Itasca moraine and along the margins of outwash plains. In Figure 1.6, the large patch of red pine in townships 143-37 and 142-37 and the red pines along the southwest margin of the Park Rapids outwash plain (township 141-38 to 137-35) are sandwiched between jack pine to the northeast and white pine to the southwest. To demonstrate a jack-red-white pine transition, the pine bearing trees of townships 140-37, 140-36, 139-37, and 139-36 are plotted at a larger scale with the corresponding map of physiography in Fig. 1.7. Brubaker (1975) has similarly described the distribution of white, red, and jack pine along the margins of an outwash plain in upper-peninsula Michigan.

Oak.- The differentiation and distribution of the oak taxa are unfortunately correlated most with the blocks of townships contracted to particular surveyors. In completing the township subdivisions, many surveyors either listed all oaks as "oak" or identified one taxon but not the other. Quercus macrocarpa and Q. borealis complex -- hybrid swarms of Q. borealis X ellipsoidalis (Swain 1972) -- are the only two taxa abundant in the study area. The identification of one taxon and not the other is particularly annoying because the probable identity of the "oak" bearing trees cannot be inferred from adjacent subdivision lines where the oaks were occasionally identified. If a surveyor could only recognize bur oaks, then he might have honestly

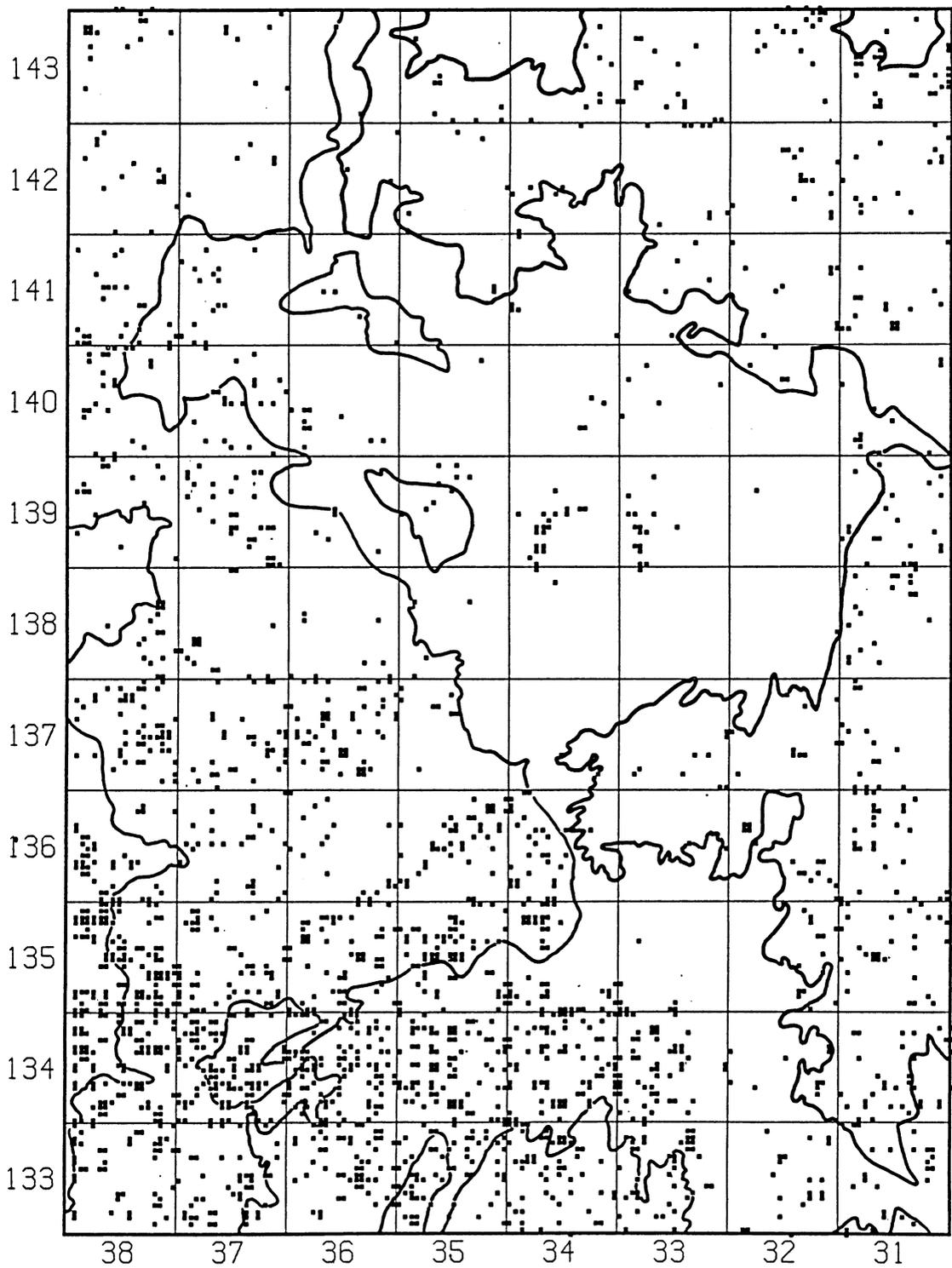


Fig. 1.8. The distribution of oak bearing trees, concentrated on areas of till and outwash with relict prairie soils (see Figs. 1.2 and 1.4).

recorded red oaks or the less abundant pin oaks as "oak" because they were not bur oak or because he could not distinguish red and pin oaks. In such cases it would be reasonable to presume that bearing trees recorded as "oak" are red oaks (Q. borealis complex) if bur oaks were distinguished and vice versa. However, if the township was being subdivided by two different survey crews (a common practice) and one crew bothered to distinguish oaks and the other did not, the identity of the "oak" bearing trees is unknown. Thus the identity of over half of the oak bearing trees (54% as "oak") in the study area cannot be determined with certainty.

Oak bearing trees, however, were consistently distinguished by crews surveying the township exterior lines. This six-mile square gridwork of identified oaks represents just 17% of the oak bearing trees, and thus only general conclusions about the relative distributions of red and bur oak are justified. Typically, red oak occurs on till within the range of its associate, white pine (see next section, Figs. 1.9 and 1.11). There red oak accounted for more than 40% of the oak bearing trees. Southwest of the limit of white pine, where oak is the dominant taxon (Fig. 1.8), red oak accounts for approximately 10% of the oaks identified along township exteriors. Thus the dense patches of oak in the southwestern portion of the study area are presumed to be predominantly bur oak.

Southwest of the limit of jack pine (townships 135-34 and 134-33) oak dominates the vegetation of outwash plains and is highly

correlated with relict prairie soils (Figs. 1.2 and 1.8). The oak bearing trees are evenly distributed across this area (Fig. 1.8; townships 134-36, 134-35, 134-34, 134-33, and 133-36), but they do not reach the density of jack pine bearing trees on outwash (Fig. 1.5). There are two reasons for this. First, oak is mixed with some aspen on outwash, and some of the bearing trees are aspen (Fig. 1.12). Second, and more important, these regions were dominated by oak brush, and few tree-sized individuals were available to serve as bearing trees. Thomas Walker, the surveyor of township 134-36 noted:

"It (T. 134-36) is quite brushy and with but few trees. there once was a fair growth of timber but it has blown down and mostly decayed. The establishment of the corners was very tedious and at best unsatisfactory (presumably due to the lack of trees)...timber a scattering of large Oak trees - Poplar and Oak thickets"

The plat maps for this region of outwash (Staples, Fig. 1.4.b) show several small prairies, but they were probably not true tallgrass prairie, as pointed out above and by Upham (1899):

"Like most of the tracts called prairie in Wadena county, this is mainly covered with scattering hazels, dwarfed oaks and other shrubs, having little clear grassland"

The contact between outwash and till has a lesser effect on the distribution of oak than it does on the distribution of jack pine. In the southwestern portion of the study area the plot of oak bearing trees shows little change in density across outwash-plain/till boundaries. The uninterrupted band of oak across the Detroit Lakes outwash plain, the Henning till plain, and the Staples outwash plain is an excellent example of this (Figs. 1.4 and 1.8; townships 135-38,

134-38, 134-37, and 134-36). Presumably the outwash/till boundary has little impact on the distribution of bur oak, because bur oak occurs over a broad range of soil textures and fire frequency. Different soil textures and fire regimes influence the physiognomy of oak-dominated vegetation. On outwash plains, oak timber was scattered in a matrix of brush-prairie described above. The large average corner-distance to oak bearing trees (46.6 m) and the high variance (4,134 m²) suggests that on outwash the larger individuals occurred in scattered groves, much like the jack pine openings. In contrast, the average distance to an oak bearing tree on the Henning till plain was 19.3 m and the variance is 487 m². Such areas on till (e.g. townships 135-38 and 135-37) were clearly described by surveyors as oak forest with lesser amounts of elm, basswood, and sugar maple. Such oak forests were also common on drumlin crests in the southern half of the Wadena drumlin field, and the lines of oak bearing trees match the orientation of the drumlins (Figs. 1.4.A and 1.8).

White pine, paper birch, and red oak.- White pine, paper birch, and red oak form a group of associated taxa (Fig. 1.3) that are mostly restricted to till (Figs. 1.9 - 1.11). Together they account for 18.6% of the bearing trees on till versus just 3.0% on outwash. The distributions of these taxa are most concentrated on rugged moraine as opposed to any other unit of till (Table 1.2). White pine was a common bearing tree on both the Itasca and St. Croix moraines, where it constituted 11.0% and 16.2% of the bearing trees respectively. Red

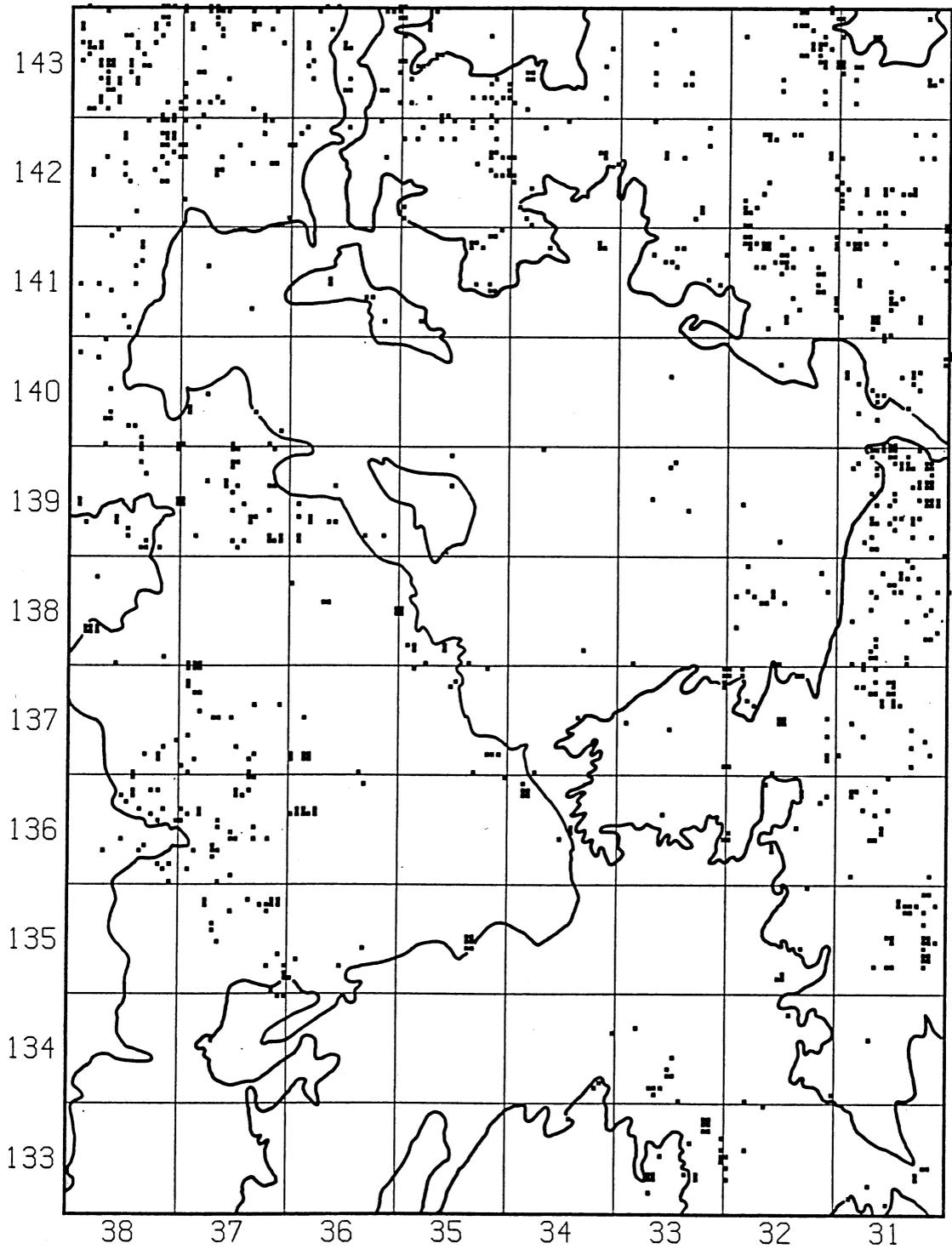


Fig. 1.9. The distribution of white pine bearing trees, concentrated on areas of till (see Fig. 1.4).

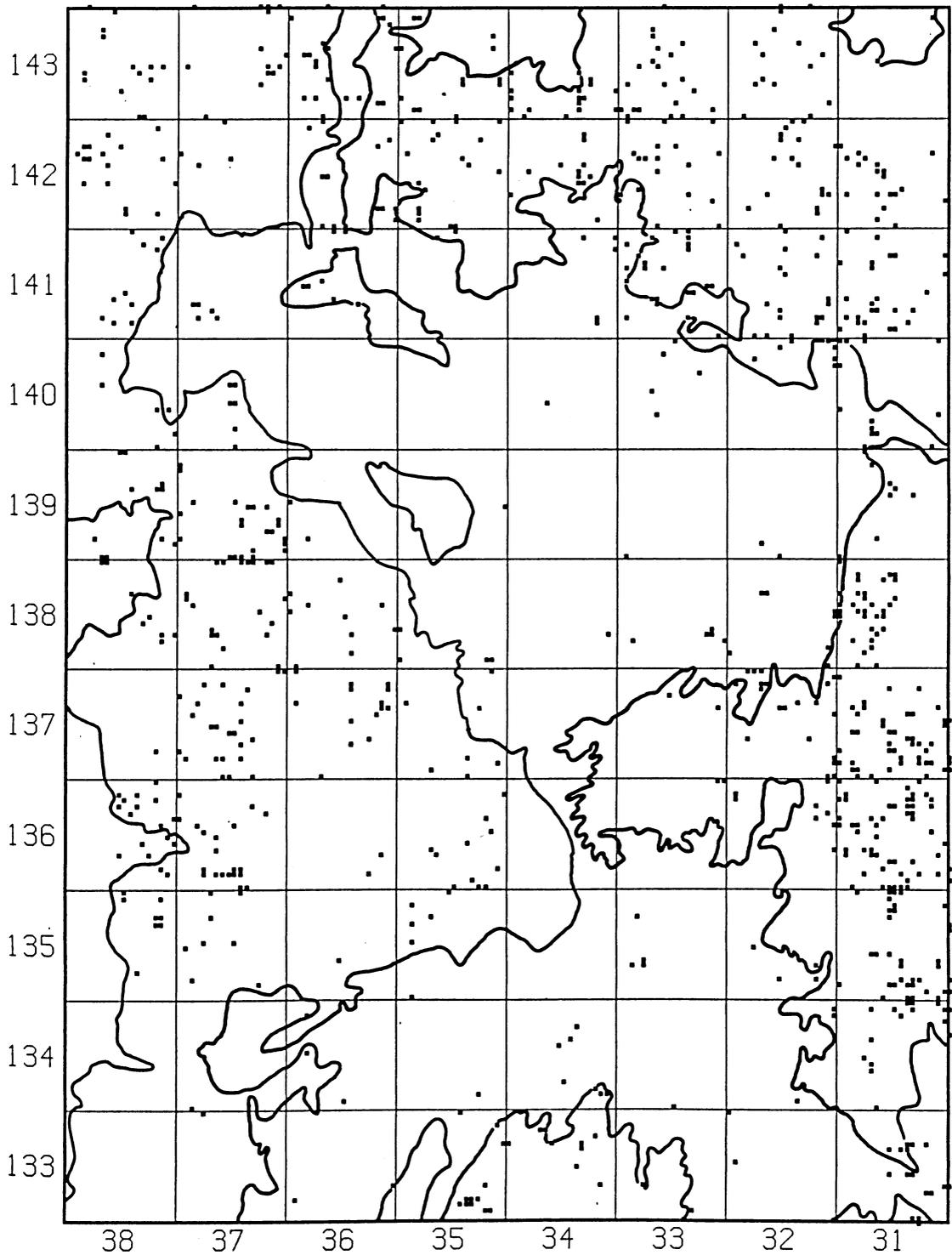


Fig. 1.10. The distribution of paper birch bearing trees, concentrated on areas of till (see Fig. 1.4).

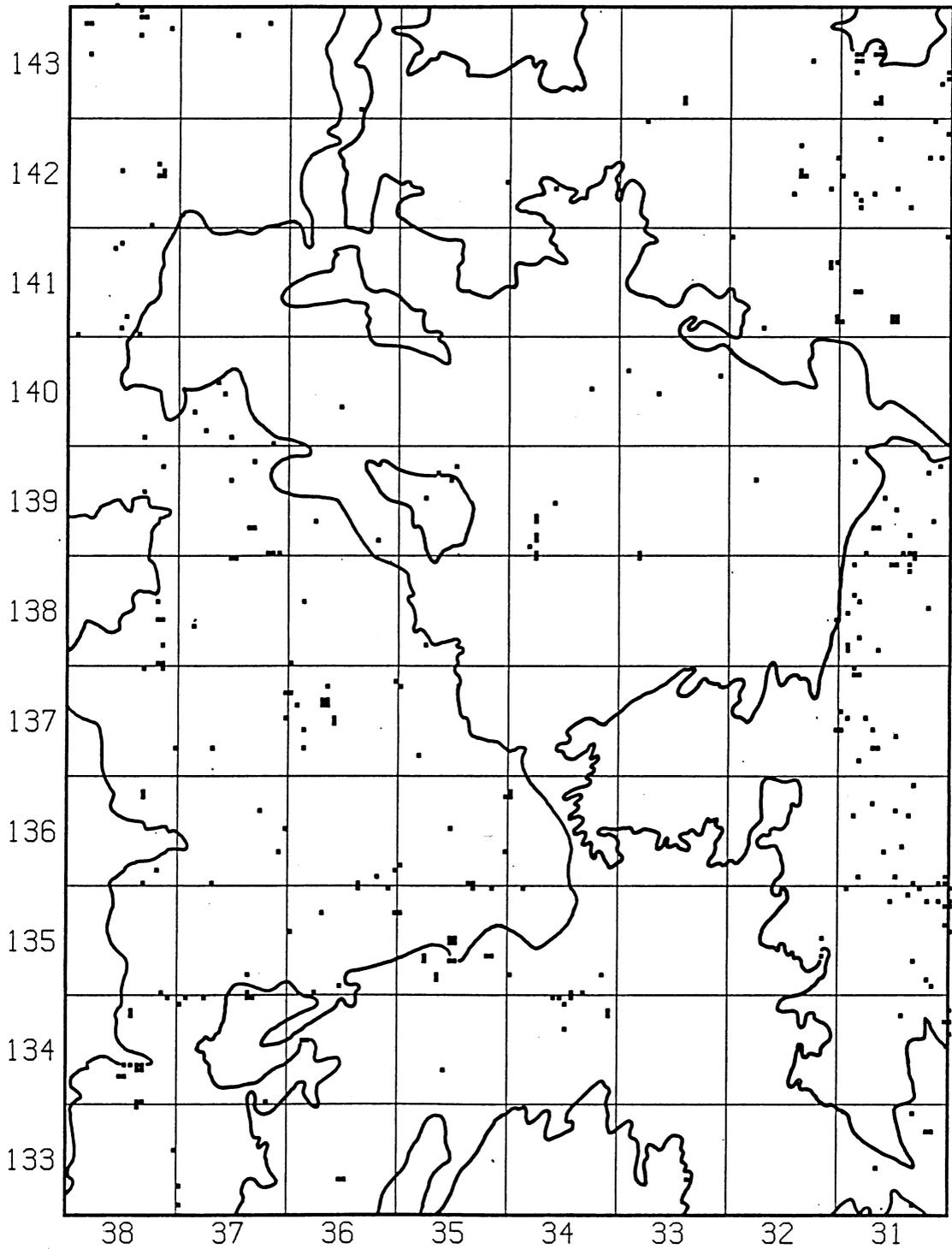


Fig. 1.11. The distribution of red oak bearing trees, occurring mostly on areas of till (see Fig. 1.4).

oak and paper birch are differentially distributed on the two moraines. They account for substantially higher proportions of the bearing trees on the St. Croix moraine (birch 14.6%, red oak 7.1%) than on the Itasca moraine (birch 7.2%, red oak 1.9%).

The restriction of white pine to loamy till-derived soils is peculiar to the western edge of its range. Only rarely does white pine occur on outwash plains in the study area or on sandy soils elsewhere in the state (Jacobson 1979). There are only two patches of white pine growing on outwash in the study area, and they are clearly associated with poorly drained soils (Figs. 1.4.B and 1.9; townships 138-32, 134-33, and 133-33). The probable explanation for the restriction of white pine to finer-textured soils is that the mean annual precipitation in Minnesota is low (50-80 cm., Baker and Kuehnast 1978) as compared to other areas within the range of white pine. In areas of increased precipitation farther east, white pine typically grows on well drained, sandy soils, where it is more successful in competing with hardwoods (Fowells 1965). Curtis (1959) has implied that the occurrence of white pine on poorly drained soils and shallow peat may also be more prevalent in Wisconsin (or Minnesota) than it is eastward.

The association of white pine with red pine (Fig. 1.3) is yet another situation more common at the western edge of their ranges (Heinselman 1981, Curtis 1959). East of Wisconsin, white pine is more typically associated with fire-sensitive hardwoods or conifers

such as hemlock, white spruce, and balsam fir (Fowells 1965). In the study area the denser patches of white pine bearing trees (Fig. 1.9; townships 143-38, 143-37, 142-35, 141-32, 141-31, 139-37, 139-31, 137-31, and 135-31) are mixed with red pine, forming the groves of pine that were the backbone of the early logging industry in Minnesota (ca. AD 1870-1930). Such stands were dependent upon frequent low-intensity fires to provide mineral seedbeds and reduce the height and volume of underbrush that might carry fire to their crowns (Heinselman 1981). From fire scars and stand-origin maps, Frissell (1973) determined the average return interval of fire to be 22 years in the big-pine groves of Itasca State Park (township 143-36 of the study area). Apparently the rugged, well-drained moraines were most conducive to that type of fire regime. The density of white pine and red pine bearing trees is greatest where the Itasca and St. Croix moraines are rugged and dotted with numerous small lakes (Fig 1.4.A). These small lakes are effective firebreaks only at a local scale, because they lack the length and interconnections of waterlogged drumlin-swales and channels on flatter units of till.

The patch of white pine bearing trees in the Henning till plain (Fig. 1.9; townships 137-37, 136-38, 136-37, and 135-37) is the only region where white pine is mixed with hardwoods alone. This patch is wholly outside the range of red pine. The southwestern extension of white pine beyond that of red pine can be observed throughout Minnesota. Not only is this the present case, but white pine has

always occurred west and south of red pine as these taxa migrated westward across the the state in the late Holocene (Jacobson 1979).

Aspen.- Aspen is the second-most abundant bearing-tree taxon in the study area. It is believed to comprise both Populus tremuloides and P. grandidentata, with the former being more abundant. When all corners (upland, lowland, and wetland) are summarized, aspen accounts for 18.2% of the bearing trees (Table 1.1). Although aspen is a common upland tree (Table 1.2), its overall abundance and highest concentrations are the result of its ability also to dominate regions of poorly drained soils (Figs. 1.4.A and 1.12; townships 138-37, 138-36, 137-37, 137-36, 134-31, and 133-31). On poorly drained soils and alluvium derived from till, aspen accounts for 27% of the bearing trees in comparison to 13% of the bearing trees at upland corners. Aspen bearing trees did occur on outwash plains, but they were mostly restricted to outwash in the southwestern corner of the study area, where relict-prairie soils occur (Fig. 1.2). There aspen occurred mostly as brush along with oak brush and scattered oak timber (see above). The only place where aspen did not commonly grow was on outwash plains within the range of jack pine. South of township tier 141, the distributions of aspen (Fig. 1.12) and jack pine (Fig. 1.5) are clearly inversely related. North of township tier 141, the distributions of aspen and jack pine overlap, but they do not occur in the same township-sized areas. The scattered occurrence of aspen and oak on outwash within the range of jack pine is on relict prairie

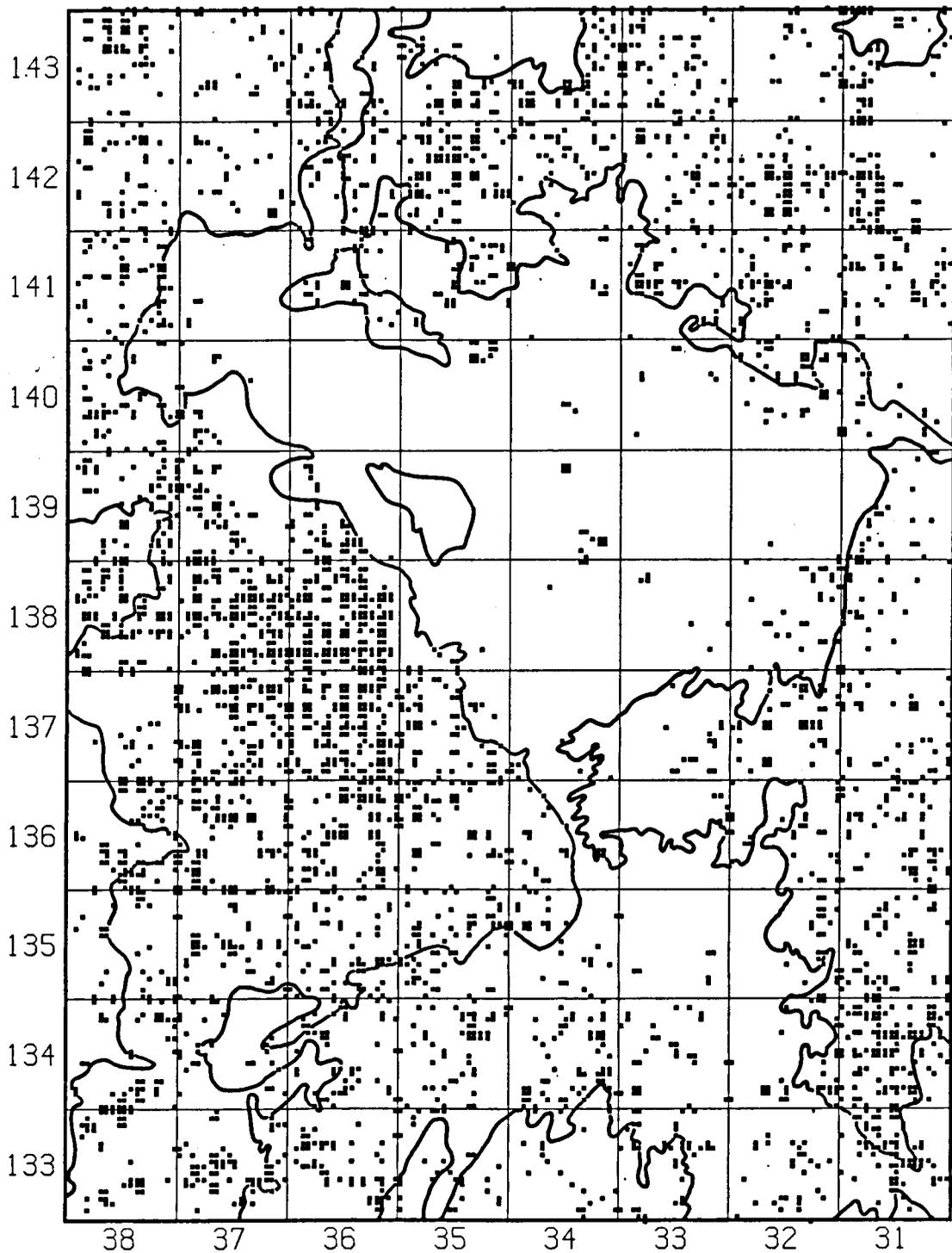


Fig. 1.12. The distribution of aspen bearing trees, concentrated on areas of till and on outwash with relict-prairie soils (see Figs. 1.2 and 1.4).

soils recently invaded by jack pine (Figs. 1.2, 1.8, 1.12; townships 141-37, 140-35, and 139-34).

Sugar maple, basswood, and elm.- Sugar maple, basswood, and elm are rare in the study area. Together they constitute just 5.0% of the bearing trees (Table 1.1). Although these taxa are rare, their bearing trees are distributed in sufficiently dense patches to show some pattern (Figs. 1.13 - 1.15). These patches occur in two types of fire-protected areas. First, these taxa occur on well-drained areas of till that are surrounded by aspen-dominated lowlands (Figs. 1.4.A, 1.12, 1.13, 1.14, and 1.15; townships 138-38, 137-38, and 135-37). Second, the fire-sensitive taxa occurred on drumlin crests where the adjacent swales are filled with peat (Fig. 1.4.A, townships 136-35, 136-34, 135-36, and 135-31) or where swales have poorly drained soils (Fig. 1.4.A, townships 133-35, 136-34, 135-36, and 135-31). To demonstrate the latter situation, the fire-sensitive taxa occurring on the northern tip of the Todd drumlin field are plotted at a larger scale, along with a physiographic map of the same area, in Fig. 1.16. George B. Wright, the surveyor of township 133-34, described the area as follows:

"This Tp. (133-34) is mostly hard timbers 1st to 2nd rate Clayey Soil. The surface, Generally undulating sufficient to give good drainage to the land but nowhere rising to any considerable Height - The Eastern part is very marshy and swampy and all through The Township there are long narrow marshes and meadows bearing N&S which furnish good grass and serve to drain the timbered ridges intervening"

The occurrence of mesic deciduous taxa on fluted topography,

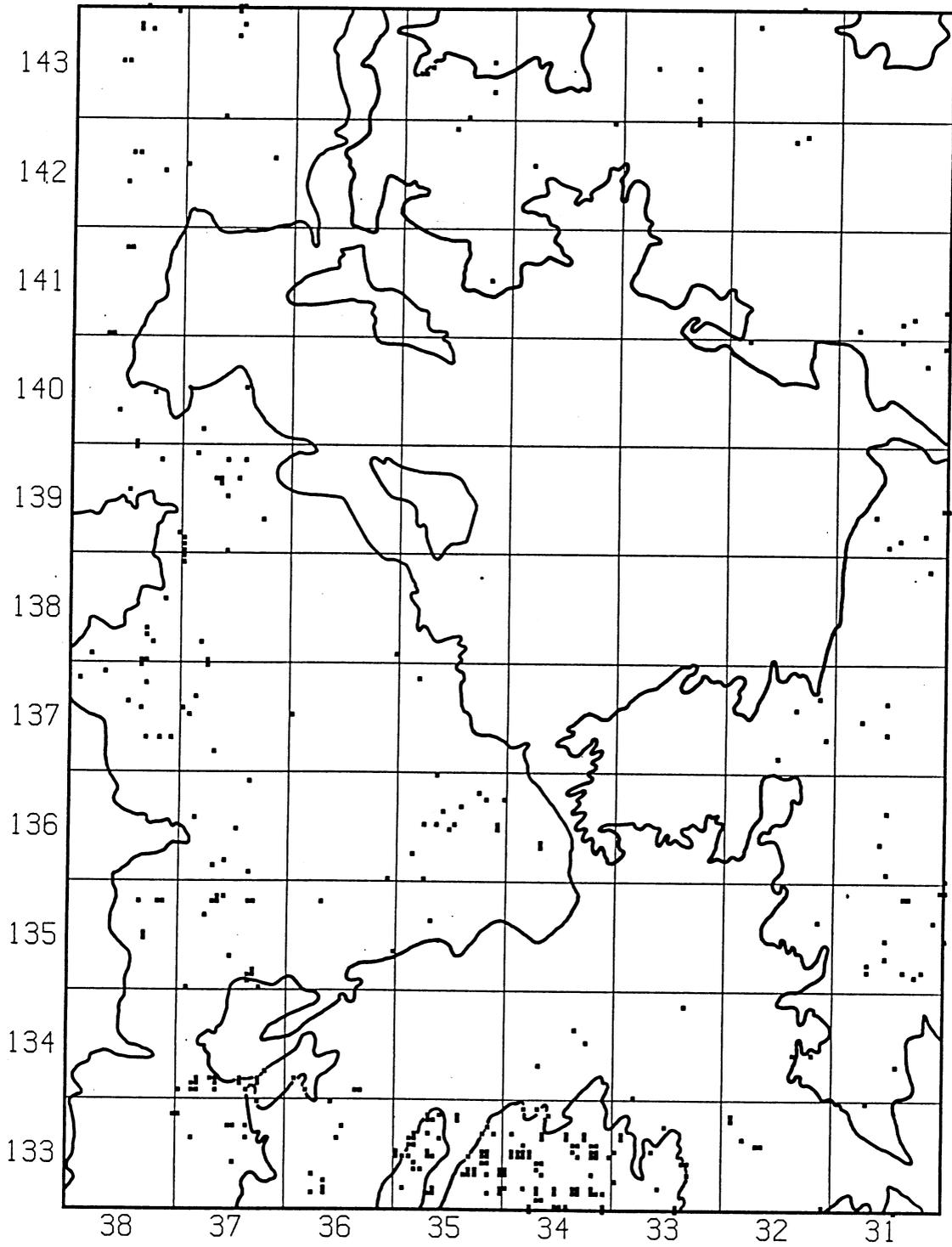


Fig. 1.13. The distribution of sugar maple bearing trees, concentrated on areas of till (see Fig. 1.4).

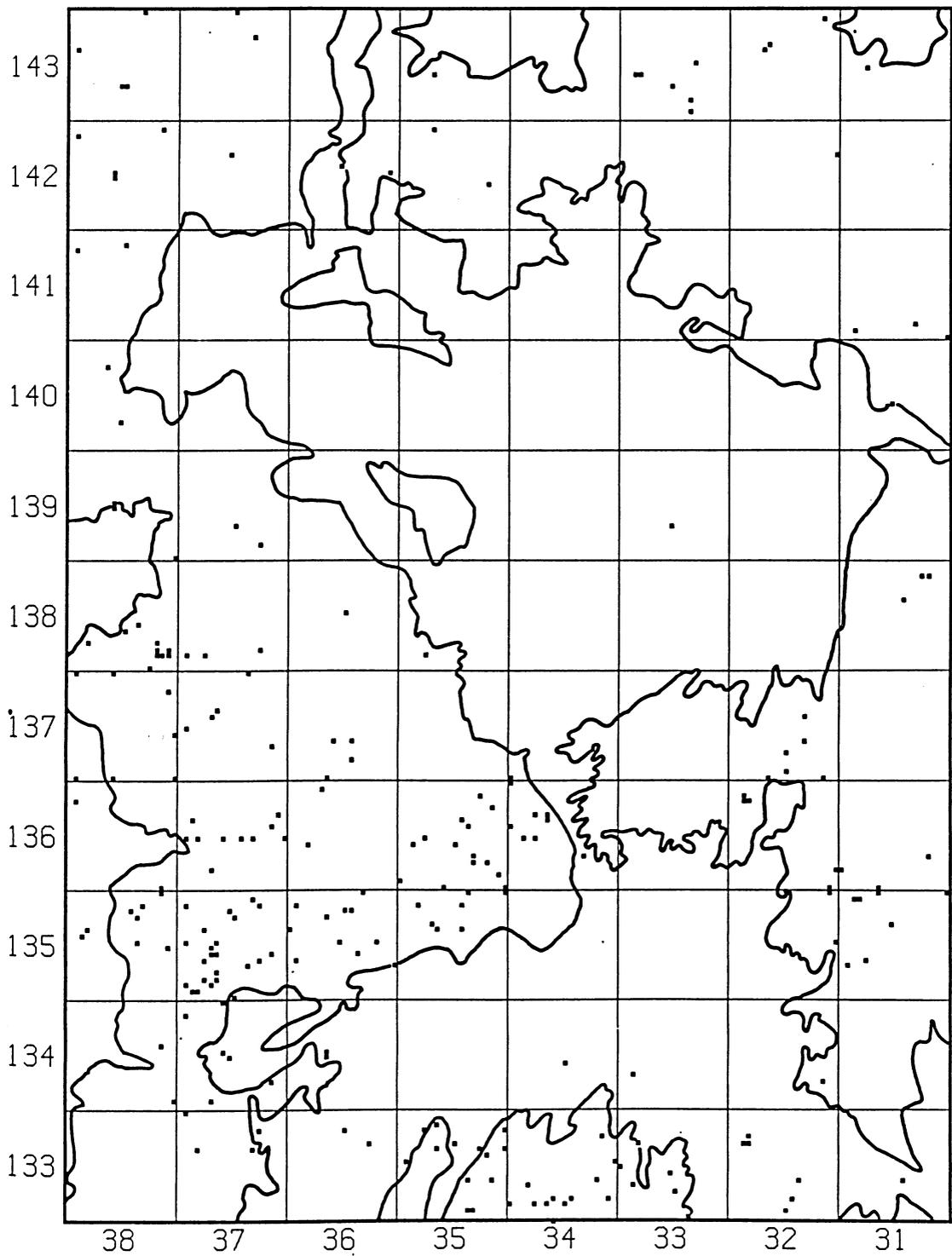


Fig. 1.14. The distribution of basswood bearing trees, concentrated on areas of till (see Fig. 1.4)

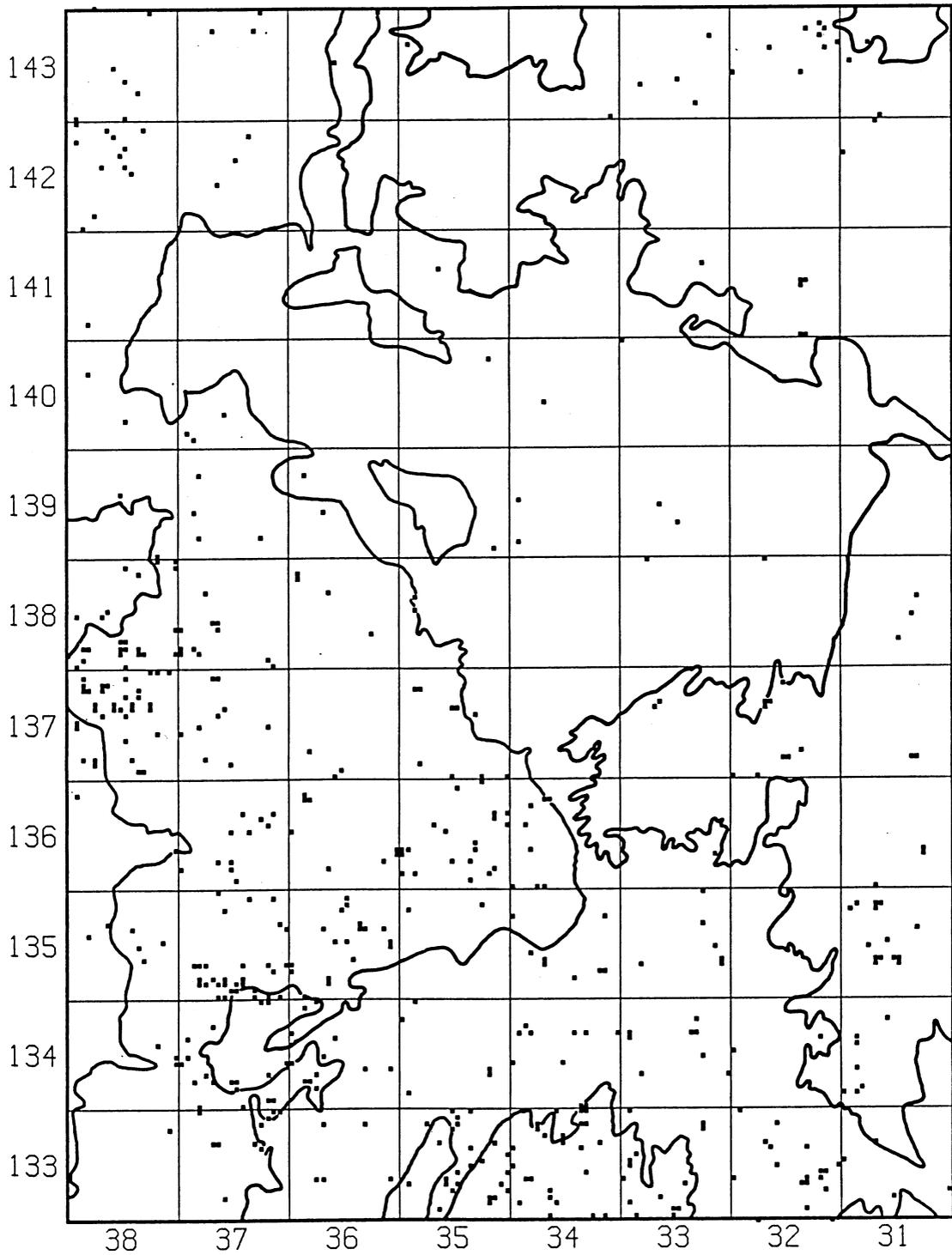


Fig. 1.15. The distribution of elm bearing trees, concentrated on areas of till (see Fig. 1.4).

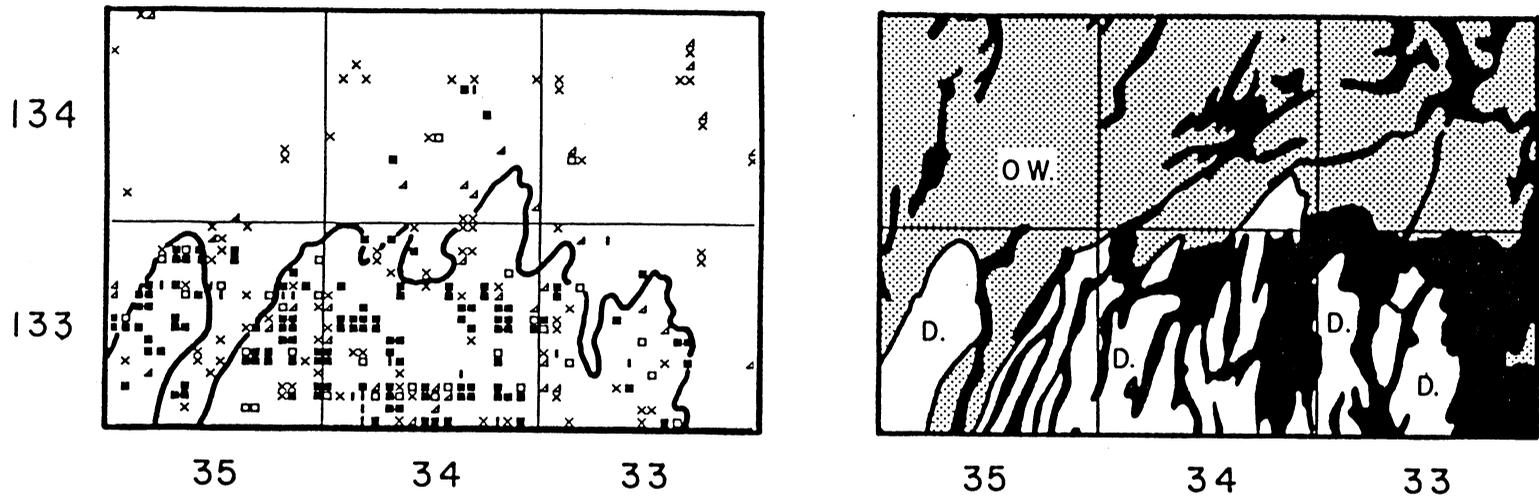


Fig. 1.16. The distribution of sugar maple (solid squares), basswood (open squares), elm (x), ash (triangles), and ironwood (bars) bearing trees along a contact of an outwash plain (OW) and till with drumlins (D). The black areas are areas of poorly drained soils and peat (Redrawn from the Minnesota Soil Atlas 1969).

drumlin fields and the ground moraine at their terminus, is of considerable historical interest because the poorly drained soils and peat deposits in the swales probably have recently developed and were most likely prerequisite for the establishment of the fire-sensitive taxa. If the paludification of the swales is coincident with the paludification of the Glacial Lake Agassiz lowlands to the north (Glaser et al. 1981) and the lake-level rises on the adjacent sand plains (see Chapter 2), it probably began about 2,000-3,000 yr B.P. and has continued until the present. The depth of the swale peat is highly variable locally, ranging from 0.5 to 4.0 m, with a mean of 1.5 m (Elwell 1926). This indicates that it took some time for the peat to rise above substrate irregularities and form the long continuous peatlands so apparent in the firebreak maps (Fig. 1.4). Precisely when swales became sufficiently wet and interconnected to isolate crests from frequent fire is unknown. If the rise in the water table on the drumlin fields was similar to the rise on outwash plains, it was probably highly variable and dependent upon local hydrologic conditions. The occurrence of sugar maple and associated taxa on drumlin fields is not unique to the study area. The entire Wadena drumlin field as it extends south of the study area is occupied by sugar maple forest, as is much of the Pierz drumlin field (Minnesota Soil Atlas 1969, 1980) in central Minnesota, where white pine is an associate (Marschner 1974). In any event, the manner in which peat-filled channels as firebreaks influenced the distribution of sugar

maple, basswood, and elm is probably a recent phenomenon.

CONCLUSIONS

In north-central Minnesota, the distributions of bearing-tree taxa across the prairie/deciduous-forest/conifer-forest ecotone are related to physiography. The strongest distributional pattern of bearing trees is correlated with the distribution of outwash plains or physiographic units composed of till. Jack pine, red pine, aspen, and oak represent 90% of the bearing trees occurring on outwash. It is not that these early successional taxa are restricted to outwash, but rather the other taxa in the study area do not commonly occur on outwash. In fact, these species account for 44% of the bearing trees occurring on till, which indicates the importance of fire and other disturbance factors in maintaining the early successional nature of the ecotone on both outwash and till.

Late-successional taxa are not abundant in the study area, and they often occur in habitats generally considered atypical for most of their range in eastern North America. White pine is nearly restricted to loamy soils and rugged terrain in the study area, where it is often associated with red pine. To the east, where precipitation is higher and fires less frequent, white pine often grows in association with hardwoods on sandy soils. Also to the east, mesic hardwoods such as sugar maple, basswood, and ironwood generally occur on well drained soils. The abundance of these taxa on poorly drained soils and

alluvium in the study area might also be interpreted as a response to lower precipitation and frequent fires, which characterize the ecotone at the western margin of their ranges.

The analysis of association resulted in an abundance of positive associations among the deciduous taxa. The interpretation is that across the ecotone, deciduous trees may occur in almost any combination, regardless of their presumed successional status or ranking along an inferred environmental gradient. Four factors contributed to this result. First, because only four individuals were sampled at a survey corner, joint absences were higher than they would be for sample units containing more individuals (eg. plots). High joint absence values cause high values of Cole's Coefficient. Second, by including regions of nearly pure pine stands, joint absence values among the deciduous taxa were higher than they would be for a study area covering areas of deciduous forest only. Third, the sampling was systematic and included sample points falling along vegetational boundaries and in areas disturbed by fire, windthrow, or disease. Such areas are often excluded from vegetational studies reporting fewer positive associations. The survey records, however, indicate that disturbed areas were characteristic of the ecotone. It is possible that repeated disturbance helped to maintain a variety of successional stages and to promote compositionally diverse deciduous forests. Fourth, the study area includes a wide variety of equally-represented habitats ranging from flat outwash to rugged moraine.

This, in conjunction with the complexity of the local climate, may have created a set of extremely heterogeneous habitats which were occupied by equally heterogeneous deciduous forests.

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CHAPTER 2: THE LATE-HOLOCENE HISTORY OF PRAIRIE, BRUSH-PRAIRIE, AND
JACK PINE FOREST ON OUTWASH PLAINS, NORTH-CENTRAL MINNESOTA.

INTRODUCTION

Isopoll maps prepared by Webb et al. (1983) summarize the Holocene shifts in the distribution of pollen taxa characteristic of prairie, deciduous forest, and conifer forest in northern Minnesota. These maps indicate that during the mid-Holocene, the prairie expanded eastward into regions of northern Minnesota that are now forested. The mid-Holocene displacement of the 20% isopoll for prairie herbs, which roughly indicates the position of the prairie/forest border, was about 90 - 160 km east of the position of the prairie/forest border at the time of agricultural settlement, ca. 100 yr B.P. (Fig. 2.1). Unlike conditions during settlement, when prairie occurred only on the flat terrain of western Minnesota, the mid-Holocene prairies developed in a region of central Minnesota where four different ice lobes had deposited a complex mosaic of rugged moraine, drumlin fields, till plains, and outwash plains (Hobbs and Goebel 1982, Wright 1972). In this region the mid-Holocene isopoll maps of Webb et al. (1983) are based entirely upon sites located on till, where the often rugged terrain was presumably not favorable for the establishment and persistence of prairie (Grimm 1983). In contrast, prairie should have been favored over forest on the large outwash plains (Fig. 2.1), because their flat topography and droughty soils encourage frequent fires. With the exception of an undated pollen diagram from Stevens Pond (Janssen 1967) and Jacobson's (1979) late-Holocene pollen diagram from Ondris Pond (Fig 2.2), no pollen records have been available to

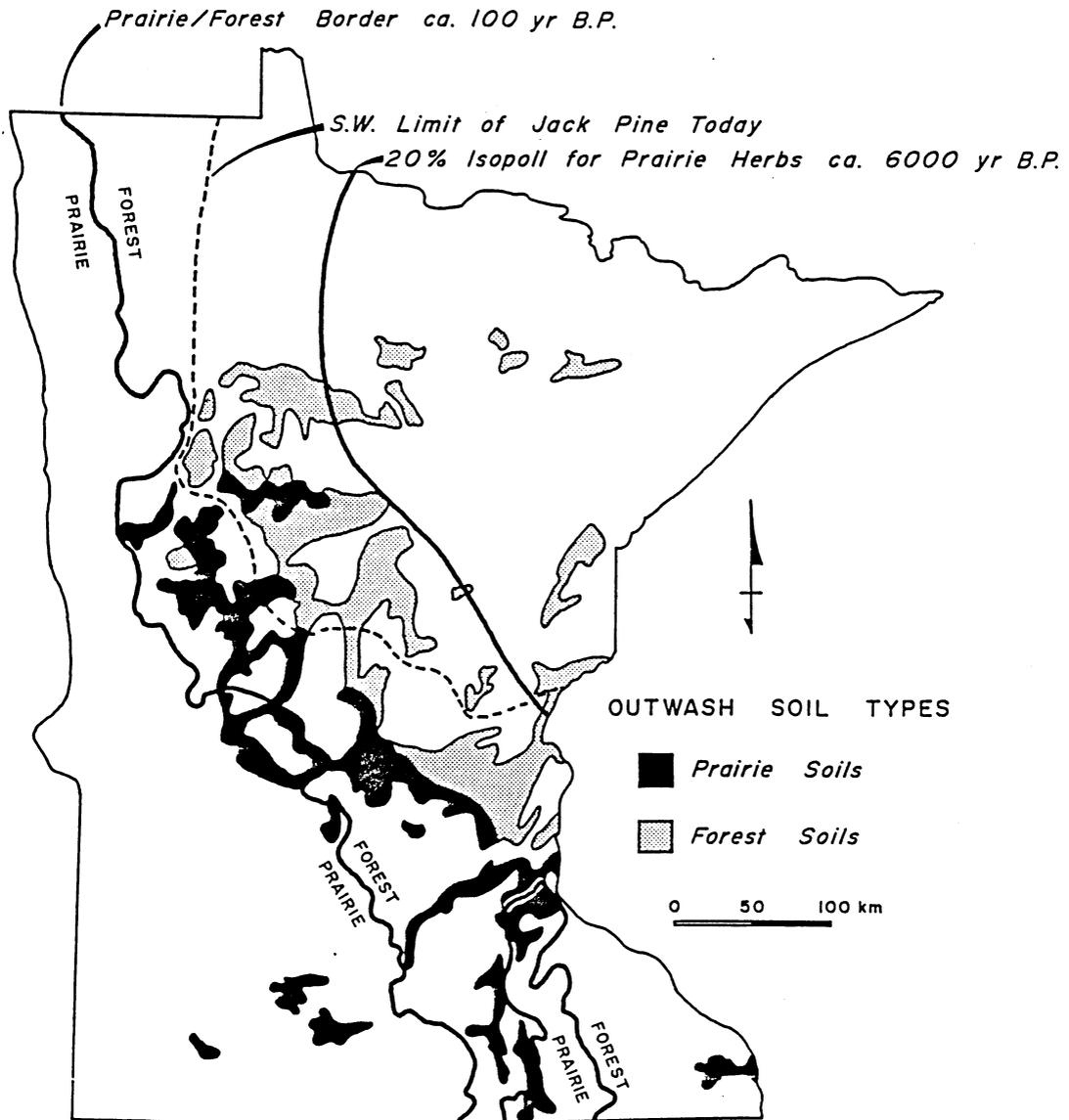


Figure 2.1. The distribution of Minnesota's sandy soils and outwash with respect to the prairie/forest border at 100 yr B.P. The 20% isopoll for prairie herbs (Webb et al. 1983) represents a reasonable estimate of the position of the prairie/forest border at 6,000 B.P. Where prairie soils occur northeast of the prairie/forest border, forest replaced prairie more recently than on the forest soils. The outwash between the range limit of jack pine and the isopoll line is almost entirely occupied by jack pine and serves as the study area. (Soil distributions redrawn from Arneman, 1963).

document the occurrence, persistence, and the mid-Holocene spread of prairie on a favorable habitat like the northern Minnesota outwash plains.

The former presence of prairie on the outwash plains of northern Minnesota had long been inferred from the vegetation and soils. In fact, historical descriptions of presettlement forests on outwash often refer to occasional prairie openings within the forest matrix (public land survey records, ca. AD 1850-1880; see Chapter 1). Where presettlement stands of oak (predominantly Quercus macrocarpa) or aspen (Populus tremuloides) occurred, the soils are characteristically dark-colored and clearly of prairie origin (McMiller 1930, Elwell 1926). Mixed stands of jack pine (Pinus banksiana) and oak, described physiognomically as "barrens" by the early surveyors, also occurred on relict prairie soils. By the time of settlement, however, large areas of outwash were occupied by jack pine forest growing on highly leached forest soils. The only indication that these jack pine forests had developed on outwash formerly occupied by prairie is that the groundlayer of these stands includes several grasses and herbs that characteristically occur in tallgrass prairie (see Chapter 3). That the soil biosequence is out of phase with the existing vegetation (Fig. 2.1) strongly suggests that the west-to-east spatial sequence across the ecotone (prairie, to oak-aspen brush or woodland, to jack pine) has occurred in time as well.

The purpose of this study was to determine if prairie occurred on

all outwash plains in northern Minnesota during the mid-Holocene and also to determine the nature and chronology of the afforestation at sites where jack pine eventually replaced prairie. The pollen stratigraphy of six study sites (Fig 2.2) was investigated and correlated by radiocarbon dating. The fossil pollen spectra were ordinated together with presettlement samples (ca. 100 yr B.P.) that might serve as analogues.

SITE DESCRIPTIONS

Peterson Slough

Peterson Slough (long. $95^{\circ} 19' W$, lat. $46^{\circ} 58' N$) is in the SW 1/4 of section 2, T.140 N, R.37 W, Becker County, Minnesota, 4.8 km west and 5.0 km north of the town of Osage. The slough is presently an elongate Typha marsh (800 x 250 m, 14 ha) with about one hectare of open water in its eastern end where the core was taken. The slough occupies a steep-walled E-W trending channel that is 4-6 m lower than the surrounding level outwash. A small east-flowing stream enters the slough at its western end, and the present water-level (elev. 460 m, max. depth 3.9 m) is controlled by a concrete dam (ca. 1 m high) at the east end of the slough. Past water-level was probably a meter lower, but the possibility that it was controlled by beaver dams is suggested by wood chips in the 12 m core.

The portion of the Park Rapids outwash plain (Fig. 2.2) that

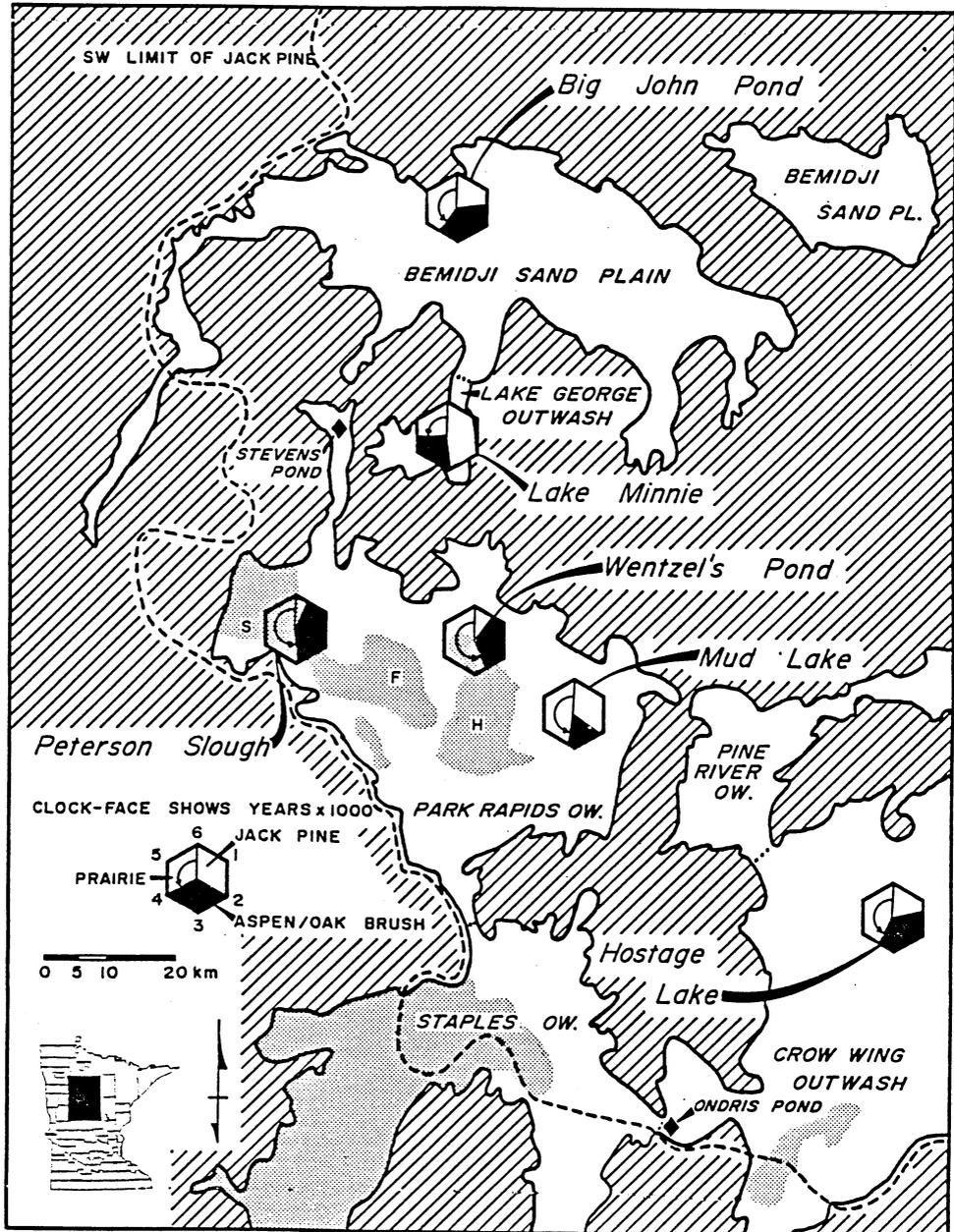


Figure 2.2. The location of the paleoecological study sites on outwash plains in north-central Minnesota. Each study site is located at the center of a hexagonal clock-face that runs counterclockwise from 6,000 yr B.P. to the present. The durations of prairie occupation, reforestation by aspen and oak, and jack pine occupation are indicated on the clock-faces. The shaded (stippled) regions of outwash are areas where prairie soils occur, and the approximate locations of the Shell (S), Fishhook (F), and Hubbard (H) prairie openings on the Park Rapids outwash plain are indicated. The black diamonds show the location of the study sites of Janssen 1967 (Stevens Pond) and Jacobson 1979 (Ondris Pond). (Redrawn from the Minnesota Soil Atlas 1969, 1980).

surrounds Peterson Slough is exceptionally flat (local relief, < 2 m) and slopes gradually (3 m/km) to the southeast. The soils are dark-colored relict-prairie soils (Udic Haploborolls) and have a loamy epipedon (Minnesota Soil Atlas, 1969). The most striking feature of the outwash is the lack of permanent lakes, Peterson Slough being the only known exception. Several depressions shown as marshes on topographic maps (U. S. Geological Survey, 1:24,000) and apparent on air photos (1976) were cored and found to contain no sediments (Appendix 2.A, Table 2.A.1).

The present upland vegetation consists mostly of isolated woodlots of jack pine and oak among fields. Most of these woodlots are characterized by a sparse canopy of jack pine, a continuous subcanopy of Quercus macrocarpa, Q. borealis, and Corylus americana, and a sparse groundcover. The channel in which Peterson Slough lies is occupied by several taxa that do not occur outside of the catchment, such as Picea glauca, Larix laricina, Abies balsamea, and Betula papyrifera. Surveyors described the presettlement vegetation as jack pine barrens with openings of brush prairie (Quercus macrocarpa and Populus tremuloides thickets) and small patches of grassland (the Shell and Fishhook prairies, Fig. 2.2).

Wentzel's Pond

Wentzel's Pond (long. 94° 57' W, lat. 46° 57' N) is in the NE 1/4 of the SW 1/4 of section 11, T.140 N, R.34 W, Hubbard County,

Minnesota, 0.5 km east of the town of Dorset. The oval pond (270 x 130 m) lies in a steep-sided ravine at an elevation of 435 m, 10-20 m lower than the surrounding outwash. Several of these ravines lie end-to-end, forming a discontinuous channel and a chain of small, closed-depression ponds crossing sections 11, 12, and 15. Wentzel's Pond is the largest (2 ha) and deepest (1.6 m) of the ponds in section 11 and the only site having sediments that show no signs of recent drying and humification.

The portion of the Park Rapids outwash plain (Fig. 2.2) that surrounds Wentzel's Pond is strongly rolling (local relief 5-10 m), and several of the hills are composed of gravel rather than sand. The soils are dark-colored relict-prairie soils (Boralfic Udic Argiborolls, Minnesota Soil Atlas 1969), and their textures range from sandy loams to coarse sands with gravel (McMiller et al. 1930). The ponds described above are the only lakes occurring on the dark-soil region around Wentzel's Pond (ca. 25 km²).

The present upland vegetation consists of scattered woodlots that are similar to those described for Peterson Slough. Unlike Peterson Slough, the vegetation of the catchment is composed of taxa that occur on the uplands. Patches of jack pine, Populus tremuloides, and Quercus macrocarpa cover the catchment slopes to the lake margin. The understory is a dense thicket of Quercus macrocarpa grubs, Corylus americana, Prunus virginiana, P. pensylvanica, and Amelanchier humilis-complex. As inferred from surveyor's notes, the presettlement

vegetation consisted of scattered patches of jack pine, thickets of Quercus macrocarpa and Populus tremuloides, scattered individuals of Pinus resinosa, and some grassland (the Hubbard prairie, Fig 2.2).

Hostage Lake

Hostage Lake (long. 94° 8' W, lat. 46° 33' N) is in the SW 1/4 of the NW 1/4 of section 31, T.136 N, R.27 W, Crow Wing County, Minnesota, 11 km N and 3 km E of the town of Merrifield. The teardrop-shaped lake (380 x 190 m) lies in a district of numerous lakes in closed ice-block depressions, which are highly variable in size and depth. Hostage Lake is one of the smaller (4.6 ha) and shallower (max. depth 1.5 m) lakes in the district, and it lies just 1 km southeast of one of the district's larger lakes, Pelican Lake (3,340 ha). Within a 10 km radius of Hostage Lake, the ratio of land area to lake area is approximately one.

The portion of the Crow Wing outwash plain that surrounds Hostage Lake is level (local relief 2-5 m) and generally less than 5 m higher than the lakes (most lake elevations ca. 368 m). The outwash is composed of well-sorted sands, and the soils are light-colored forest soils (Typic Udipsamments, Minnesota Soil Atlas, 1969).

The present vegetation is largely jack pine forest with a discontinuous subcanopy of Quercus borealis, Q. macrocarpa, Corylus cornuta, C. americana, Prunus virginiana, P. pensylvanica, and Amelanchier intermedia-complex. Where there are gaps in the

subcanopy, the ground is carpeted with Pleurozium schreberii, Vaccinium angustifolium, broadleaf evergreens, herbs, and grasses. Stands of Populus tremuloides are common around lake margins and where jack pine has been logged. Stands of Quercus borealis and Betula papyrifera are common on small outcrops of till, which are scattered across the outwash plain (Arneman et al. 1965).

Big John Pond

Big John Pond (long. 94° 58' W, lat. 47° 33' 30" N) is in the SE 1/4 of the SE 1/4 of section 10, T.147 N, R.34 W, Beltrami County, Minnesota, approximately 10 km west and 8 km north of Bemidji. The small (1.8 ha), oval lake (240 x 110 m) lies in a closed depression. With an elevation of 421 m, it is 2-5 m lower than the surrounding level outwash. The pond is flat-bottomed, and it has a maximum depth of 0.6 m.

The portion of the Bemidji sand plain (Fig. 2.2) surrounding Big John Pond is characterized by patches of flat well-sorted outwash with few lakes, alternating with patches of gently rolling, moderately sorted outwash with several shallow lakes or peatlands. The size of these patches ranges from about 25-100 km². Big John Pond is one of the few lakes on the flatter outwash. The soils are sandy light-colored forest soils (Psammentic Eutroboralfs, Minnesota Soil Atlas 1980).

Jack pine occurs in nearly pure stands on the level outwash

around big John Pond. The understory is similar in both composition and structure to that described for Hostage Lake.

Mud Lake

Mud Lake (long. 94° 45' W, lat. 46° 52' N) is in the NE 1/4 of section 17, T.139 N, R.32 W, Hubbard County, Minnesota, 2.4 km west of the Badoura State Nursery. The lake consists of two basins partially separated by a point on the northwest side of the lake. The southwest basin is shallow (< 2 m), whereas the northeast basin, where the core was taken, has a maximum depth of 11 m. Mud Lake lies in a NE-SW trending channel as a middle member of a four-lake chain (between Tripp and Mow lakes). It has an area of 20.5 ha, and with an elevation of 424 m it is 3-10 m lower than the surface of the surrounding, undulating outwash.

The outwash around Mud Lake is mapped as a part of the Park Rapids outwash plain (Fig. 2.2), but the outwash is a relatively thin veneer of well-sorted sand that blankets a former drumlin field (Wright 1962). The underlying drumlins create the local undulating topography, with NE-SW trending crests and swales. Most swales are filled with peat (McMiller et al. 1930) or chains of lakes like the Mud Lake chain.

The sand-capped drumlins are presently occupied by jack pine forest, with a sparse understory of Corylus cornuta, C. americana, Salix humilis, Viburnum rafinesquianum, and lesser amounts of Quercus

macrocarpa, Q. borealis, and Populus tremuloides. Near the margins of the peat-filled swales the subcanopy coverage is greater and the canopy of jack pine is often mixed with Populus tremuloides and some Betula papyrifera. Typically, Pleurozium schreberi provides a continuous moss carpet that is interrupted by clones of Vaccinium angustifolium, Arctostaphylos uva-ursi, and Ceanothus ovatus.

Lake Minnie

Lake Minnie (long. 95° 00' 30" W, lat. 47° 14' 40" N) is in the SE 1/4 of section 32, T.144 N, R.34 W, Hubbard County, Minnesota, 1.5 km west, and 5.3 km north of Lake George. The oval lake (900 x 410 m) has an area of 28.5 ha and a maximum depth of 8.5 m at the point where the core was taken by J. H. McAndrews. The lake elevation is 429 m.

Moraine occupies the northwest quadrant of a circle of 6 km radius with Lake Minnie at its center. The remaining quadrants are outwash (Lake George outwash plain, Fig. 2.2) that is interrupted by several peat-filled channels and steep-sided, widely spaced, elongate hills that are 25-40 m higher than the intervening flat outwash. Both the peat-filled channels and the elongate hills trend N-S and are probably fluvial features. The sandy soils of the flat outwash are light-colored forest soils (Typic Udipsamments, Minnesota Soil Atlas 1980).

Jack pine, common on the moraine northwest of Lake Minnie, forms nearly pure stands on the outwash. On the well-drained portions of

the outwash plain, Pinus resinosa is the only other taxon to commonly share the canopy with jack pine. Populus tremuloides, Betula papyrifera, Quercus macrocarpa, and Q. borealis occur as seedlings, but they rarely reach a height of 2 m. The shrub layer is essentially absent, consisting of a few scattered individuals of Corylus cornuta, Prunus virginiana, P. pensylvanica, P. pumila, and Amelanchier intermedia-complex. The ground is carpeted with a continuous mat of Pleurozium schreberi and other mosses, except for small patches of Cladonia rangiferina and C. alpestris on drier spots. Large clones of Vaccinium angustifolium are common, as are several broadleaf evergreens, including Arctostaphylos uva-ursi, Pyrola secunda, P. rotundifolia, Epigaea repens, and Chimaphila umbellata.

METHODS

Coring Methods

For all but Lake Minnie, the sediment cores were collected in late February and March (1980-1981) from the ice surface. An electronic depth-finder was used to locate the deepest part of the lake basin, where the cores were taken. The cores were collected with two types of piston samplers. First, the soft surface-sediments were collected with a clear plastic tube, 5 cm in diameter, fitted with a piston (Wright 1980). The tubes were sealed and transported in an upright position to the laboratory, where they were extruded

vertically in alternating 1 cm and 4 cm segments for storage in glass vials and plastic bags respectively. Second, beginning at the end of the surface sample drive and in the same hole, a modified Livingstone sampler (5 cm diameter and 1 m length, Wright 1967) was used to collect the deeper, firmer sediments. These core segments were extruded in the field and then wrapped in plastic and aluminum foil. The coring logs, which record drive depths, recovery, assigned stratigraphic position of the core segments, coring dates, and water depths, are given in Appendix 2.A.

Sediment Description

The sediment lithology was described (Table 2.1) in the Troels-Smith (1955) system. The percentage loss-on-ignition was determined from subsamples of 1 cm³ for firm sediments and 0.86 cm³ for softer, often flocculent sediments (see below). The samples were (1) placed in dried, pre-weighed crucibles, (2) dried overnight at 110° C, (3) cooled 30 minutes in a desiccator under vacuum, (4) reweighed, (5) ignited at 500° C for one hour, (6) cooled as above, (7) reweighed, (8) ignited at 900° for one hour, (9) cooled overnight, and (10) reweighed. Calcium carbonate controls were also ignited at 500° and 900° C to check for CaCO₃ decomposition.

Table 2.1. Sediment lithology according to the Troels-Smith system (1955).

Depth (cm)	Sediment type	Color	Turfa	Detritus	Limus	Argilla	Grana
Peterson Slough							
0-45	calcareous gyttja	5Y 3/2		Dh+	Ld ⁰ ₃ , Lc1		
45-87	gyttja	10YR 3/2		Dh+	Ld ⁰ ₄		
87-91	calcareous gyttja	2.5Y 4/2		Dh+	Ld ⁰ ₃ , Lc1		
91-140	gyttja	2.5Y 3/2		Dh+	Ld ⁰ ₄ , Lc+		
140-262	gyttja	5Y 2.5/2		Dh+	Ld ⁰ ₄		
262-432	banded gyttja, bands (1-5 cm)	5Y 3/2		Dh+	Ld ⁰ ₄ , Lc+		
		5y 4/3		Dh+	Ld ⁰ ₃ , Lc1		
		5Y 4/2		Dh+	Ld ⁰ ₂ , Lc2		
432-450	gyttja	5Y 2.5/2		Dh+, D1+	Ld ⁰ ₄ , Lc+	Ag+	
Wentzel's Pond							
0-50	slightly humified detrital gyttja	5Y 2.5/2		Dh1	Ld ¹ ₃		
50-102	detrital gyttja	5Y 2.5/2		Dh1	Ld ⁰ ₃ , Lc+		
102-135	calcareous detrital gyttja	5Y 3/2		Dh1	Ld ⁰ ₂ , Lc1		

[continued on next page]

[Table 2.1. continued]

135-156	humified detrital gyttja	2.5Y 2.5/0		Dh1	Ld ¹ ₃ , Lc+		Gs+
156-195	humified detrital gyttja	2.5Y 2.5/0		Dh1	Ld ¹ ₃		Gs+, Gg+
195-215	humified detrital gyttja	2.5Y 2.5/0		Dh1	Ld ² ₃		Gs+, Gg+
215-225	organic sands						Gg4
225-234	humified detrital gyttja	5Y 2.5/1		Dh1	Ld ³ ₃		Ga+
234-235	sand						Gs4
235-242	humified detrital gyttja	5Y 2.5/1		Dh1	Ld ³ ₃		Ga+
242-243	sand						Gs4
243-280	humified silty gyttja	5Y 2.5/1	Th+		Ld ³ ₃	Ag1	Ga+
280-282	sand						Ga2, Gs2
282-291	slightly humified silty gyttja	10YR 2.5/1		Dh+	Ld ¹ ₃	Ag1	Ga+, Gs+
291-293	sand						Ga2, Gs2
293-338	slightly humified silty gyttja	10YR 2.5/1			Ld ¹ ₃	Ag1	Ga+, Gs+
338-405	banded organic silt	2.5Y 2.5/0	Tl+		Ld ¹ ₂	Ag1, As1	
		10YR 2.5/1		Dh+	Ld ⁰ ₃	As1, Ag+	
		5Y 3/2		Dh1	Ld ¹ ₁	As2, Ag+	

[continued on next page]

[Table 2.1. continued]

Hostage Lake

0-25	gyttja	5Y 3/2		Dh+	Ld ⁰ ₄	
25-40	aquatic mosses	5Y 3/2	Tb ⁰ ₃		Ld ⁰ ₄	
40-61	gyttja with moss fragments	5Y 3/2	Tb+	Dh+	Ld ⁰ ₄	
61-91	gyttja	5Y 3/2		Dh+	Ld ⁰ ₄	
91-100	gyttja with moss fragments	5Y 3/2	Tb+	Dh+	Ld ⁰ ₄	
100-280	gyttja	5Y 3/2		Dh+	Ld ⁰ ₄	
280-443	gyttja	5Y 2.5/2		Dg+	Ld ⁰ ₄	Ag+
443-475	calcareous detrital gyttja	5Y 4/2		Dh1	Ld ⁰ ₂ , Lc1	Ag+
475-483	marly detrital gyttja	5Y 4/2		Dh1	Ld ⁰ ₁ , Lc2	Ag+

Big John Pond

0-66	detrital gyttja	10YR 2.5/1	Tl+	Dh1	Ld ⁰ ₃	
66-120	humified detrital gyttja	10YR 3/2		Dh1	Ld ¹ ₂ , Lc1	
120-158	humified silty gyttja	10YR 2.5/1		Dh+	Ld ¹ ₃	Ag1

[continued on next page]

[Table 2.1. continued]

158-162	humified organics and sand	10YR 2.5/1	Dh+	Ld ¹ 2	Ag1	Gs1
162-218	humified silty gyttja	7.5YR 2.5/0	Dh+	Ld ² 3	Ag1	

Mud Lake

0-384	gyttja	5Y 2.5/0	Dh+	Ld ⁰ 4		
384-427	calcareous gyttja	5Y 3/2	Dh+	Ld ⁰ 3, Lc1		
427-437	gyttja	5Y 2.5/1	Dh+	Ld ⁰ 4		
437-467	calcareous gyttja	5Y 2.5/2	Dh+	Ld ⁰ 3, Lc1		
467-550	gyttja	5Y 2.5/1	Dh+	Ld ⁰ 4, Lc+		
550-561	calcareous gyttja	5Y 3/1	Dh+	Ld ⁰ 3, Lc1		
561-573	detrital gyttja	5Y 2.5/1	Dh1	Ld ⁰ 3		
573-578	marly gyttja	5Y 3/2	Dh+	Ld ⁰ 2, Lc2		

Pollen-analytical Methods

Quantitative subsamples of sediment were taken for pollen analysis and loss-on-ignition (see above). For firm sediments, 1.0 and 0.5 cm³ subsamples were taken with a volumetric brass sampler (Birks 1976). For softer or flocculent sediments, a ceramic spoon was used to take 0.86 cm³ subsamples.

Samples were prepared for pollen analysis (Faegri and Iversen 1975) as follows: (1) addition of 0.5 cm³ of a suspension of polystyrene microspheres ($116.5 \pm 5.58 \times 10^3$ microspheres/cm³), (2) dispersion in hot 10% KOH, (3) 3-10 water washes to remove colloidal particles, (4) hot 10% HCl to remove carbonates, (5) 2 hot water washes, (6) treatment with hot 48% HF to remove silicates, (7) glacial acetic acid wash, (8) acetolysis solution for 1 minute, (9) glacial acetic acid wash, (10) 2 water washes, (11) safranin stain, (12) dehydration in tertiary butyl alcohol, (13) suspension in silicone oil (2000 centistokes) as a mounting medium (Andersen 1960).

Routine counting was done on a Leitz Dialux microscope at 400x magnification with a 40x apochromatic objective (n.a. = 0.95). More critical examinations were made with a 100x oil-immersion objective (n.a. = 1.30). Whole or half-slides were counted with equally spaced traverses to avoid errors associated with the nonrandom distribution of pollen on slides (Brookes and Thomas 1967). The number of pollen grains and spores (excluding aquatic and wetland taxa) counted per sample was 210-556, with a mean of 328. Fossil pollen and spores were

identified by comparison with a collection of modern pollen and spores at the Limnological Research Center, University of Minnesota. Pollen-type definitions follow Cushing (1963), McAndrews et al. (1973), Faegri and Iversen (1975), and Grimm (1981). Pollen-preservation classes follow Cushing (1967). The relative proportions of undifferentiated pine grains assigned to the subgenus Haploxylon (Pinus strobus) or Diploxylon (Pinus banksiana/resinosa) were based upon a minimum of 30 differentiated grains per sample. Additional, low-sum (50-100 grains) counts from unprepared sediments were made to locate the cultural horizon more precisely by differentiating only pine, Ambrosia, and cultivars from other pollen grains. Pollen counts are given in Appendix 2.B.

Pollen Diagrams

Several pollen sums were used in preparing the pollen diagrams (Plates 1-6, in back pocket). The basic sum, *P, includes all upland taxa; the sum *Q includes all obligate aquatic and obligate wetland taxa; and the sum *L includes all upland taxa that typically grow on outwash plains. Cyperaceae (Y) and indeterminable (X) grains are excluded from the above sums. Cyperaceae was excluded because it occurs in high percentages at Wentzel's Pond and Big John Pond that are almost certainly derived from local populations of sedges (see Lichti-Federovitch and Ritchie 1965). The percentages of upland taxa are based on the sum *P and plotted on Plates 1-6 as silhouettes, with

or without a 10x exaggeration (stippled curves). The percentages of aquatic and wetland taxa are based on $*P + *Q$ and plotted as thick bars with a thin-line 10x exaggeration. The percentage of Cyperaceae pollen is based on $*P + Y$ and plotted as a curve filled with a pattern of small squares. The percentage of indeterminable pollen is based on $*P + *Q + Y + X = \text{total grains encountered}$, and it is plotted as a curve filled with diagonal lines. Four taxa, Pinus banksiana/resinosa, Quercus, Artemisia, and Poaceae, have their percentages plotted as double curves as suggested by Wright and Patten (1963). The black portion of their curves is based upon the sum $*P$. The portion of their curves filled with horizontal lines indicates the percentage increase when the more restricted (smaller) sum $*L$ is used. The sum $*L$ excludes several taxa that do not commonly occur on outwash (e.g. Pinus strobus, Betula, Ostrya, and Ulmus).

The zonation of the diagrams is based entirely upon the behavior of the curves for Pinus banksiana/resinosa, culturally influenced taxa, and the sum of prairie taxa. These restrictive zoning criteria were used to provide, for all six study sites, matching zones that are consistent with the inferred history of prairie and jack pine, which is the focus of the paper. The zone boundary based upon the culturally influenced taxa (Zone 1/Zone 2 boundary) was determined so that a radiocarbon date could be obtained for a core segment of known age (ca. AD 1880).

The taxa were placed in local, extralocal, and regional

categories, which differ slightly from the definitions proposed by Janssen (1966). Local taxa are defined as representing those plants growing in the lake (Aquatic) or in the lake-margin wetland (Wetland). Extralocal taxa refer to types that grow on the surrounding outwash plains. Extralocal taxa may be either upland types or types that characteristically grow in peatlands, which are common on outwash plains in north-central Minnesota (see Chapter 1). Regional taxa are those that are generally restricted to moraines within the study area or do not occur within the study area.

Numerical Methods

To compare visually the prairie-to-jack pine transitions among the six study sites and to compare the fossil pollen spectra with presettlement pollen spectra (ca. 100 yr B.P.), 109 fossil spectra were ordinated with 105 presettlement samples (unpublished data made available by E. J. Cushing). Detrended Correspondence Analysis (Hill 1979) was used to ordinate the samples. The sample scores were based upon the relative proportions of 21 taxa (Fig. 2.3) that are important in distinguishing pollen-assemblage zones in Minnesota.

RADIOCARBON DATES

Three radiocarbon dates were obtained for each study site except Lake Minnie (Table 2.2). Lake sediments provided the organic material for dating in all cases. The dates as reported by the radiocarbon

Table 2.2. Radiocarbon dates.

Sample depth (cm)	Sediment type (abbreviations follow Troels-Smith, 1955)	Laboratory reference number	Reported date in radiocarbon years B.P.	Date corrected for ^{14}C deficiency
Peterson Slough				
21-30	Calcareous gyttja Ld ⁰ ₃ Lc1 Dh+	WIS-1606	510 ₋ 70	uncorrected
40-50	Calcareous gyttja Ld ⁰ ₃ Lc1 Dh+	WIS-1316	840 ₋ 80	112
390-400	Gyttja Ld ⁰ ₄ Dh+	WIS-1660	3740 ₋ 80	3012
Wentzel's Pond				
46-55	Detrital gyttja Ld ¹ ₃ Dh1 Lc+	WIS-1605	590 ₋ 70	154
70-80	Detrital gyttja Ld ⁺ ₃ Dh1 Lc+	WIS-1303	800 ₋ 80	364
180-190	Detrital gyttja Ld ¹ ₃ Dh1 Gs+ Gg+	WIS-1654	2860 ₋ 80	2424
Hostage Lake				
16-35	Detrital gyttja Ld ⁰ ₃ Dh1 Tb ⁰ ₊	WIS-1661	240 ₋ 70	uncorrected
215-225	Gyttja Ld ⁰ ₄ Dh+	WIS-1314	1870 ₋ 80	1596
380-390	Gyttja Ld ⁰ ₄ Dh+ Ag+	WIS-1655	3760 ₋ 80	3486

[Continued on next page]

[Table 2.2. continued]

Big John Pond

16-20	Detrital gyttja Ld ³ Dh1 Tb+	WIS-1659	450 ₈₀	256
60-65	Detrital gyttja Ld ³ Dh1 Tb+	WIS-1315	1700 ₈₀	1506
125-135	Silty gyttja Ld ¹ ₃ Ag1 Dh+	WIS-1658	3690 ₈₀	3496

Mud Lake

37-50	Gyttja Ld ⁰ ₄ Dh+	WIS-1656	900 ₇₀	92
330-340	Gyttja Ld ⁰ ₄ Dh+	WIS-1305	3060 ₈₀	2252
440-450	Calcareous gyttja Ld ⁰ ₃ Lc1 Dh+	WIS-1657	3680 ₈₀	2872

laboratory were calculated with 5,568 years as the half-life of ^{14}C . The standard deviations reported were calculated from counting statistics of background, sample, and standard counts and indicate the precision of the radiocarbon measurements only, not the accuracy of the date.

The accuracy of the dates is affected by past fluctuations in atmospheric ^{14}C and by the natural contamination of sediments with ancient carbon. The corrections for fluctuations of atmospheric ^{14}C are small over the last 4,000 years (Damon et al. 1974) and were not applied. The most serious problem affecting the accuracy and hence the comparability of the dates among study sites is the incorporation of ancient carbon in the sediments, causing a deficiency of ^{14}C . The radiocarbon dates were adjusted to account for this bias. The Zone 1/Zone 2 boundary (Plates 1-6, in back pocket), which is the cultural horizon, was identified and assigned the date of 70 yr B.P. (AD 1880), which is the time of increased logging and agriculture in the study area (see Results and Discussion). The corrections were then obtained as the difference between 70 yr B.P. and the date of the cultural horizon as estimated graphically by plotting the radiocarbon dates against depth. The corrections used are as follows: -808 years for Mud Lake, -728 years for Peterson Slough, -436 years for Wentzel's Pond, -274 years for Hostage Lake, and -194 years for Big John Pond. The date from Lake Minnie was not adjusted.

Application of the above corrections to radiocarbon dates down-

core assumes that the incorporation of ancient carbon is constant with depth and equal to the presettlement estimate. This is a poor assumption for the study sites; however, applying the corrections probably does increase the comparability of the study-site chronologies. The most probable sources of ancient carbon are the lignin or other carbon in Paleozoic rocks or Cretaceous shales in the outwash (Hobbs and Goebel 1982), redeposited lake sediment, and organics leached from the mid-Holocene prairie soils under a canopy of jack pine. Both the influx and the relative contribution of these sources to the lake sediments has certainly varied in time. The radiocarbon samples near the decline in prairie herbs (Plates 1-6, in back pocket) were probably most influenced by sediment redeposition or focusing (Davis 1968, 1973) because of lower water levels at that time. The inorganic sediment fraction, possibly including Cretaceous shale, is also higher for these samples, as shown by the loss-on-ignition curves (Plates 1-6) and recorded in the sediment lithologies (Table 2.2). The radiocarbon dates near the point of pine establishment were possibly contaminated with leached soil organics, but the fate of soil organic matter following the degradation of prairie soils is unknown. The ranking of the study sites by the magnitude of their corrections is not consistent with any patterns of physiographic or limnological features that might influence the influx of ancient carbon.

RESULTS AND DISCUSSION

Zone 4, Prairie Occupation

Zone description.- This zone is characterized by high percentages of prairie herbs that, when summed, have maxima between 47% at Peterson Slough to nearly 70% at Wentzel's Pond (Plates 1-6, in back pocket). The taxa contributing most to the higher percentages of summed prairie types are Ambrosia 2-10%, Artemisia 6-28%, Chenopodium-type 1-3%, Poaceae 12-45%, and undifferentiated Tubuliflorae 1-12%. The upper boundary of the zone is placed between sample levels where the sum of prairie herbs begins a continued decline to values generally less than 20%. Indeterminable pollen grains can be common in this zone (2-12%), and they consist mostly of crumpled grains or grain fragments that are apparently inaperturate (probably Cyperaceae, Populus, or broken Poaceae).

Presettlement analogues.- In the ordination (Figs. 2.3 - 2.6) the high percentages of prairie herbs cause the fossil-pollen samples in Zone 4 to have high first-axis scores and low second-axis scores. These samples generally fall close to, but not within, the cluster of presettlement samples that constitute the Poaceae-Artemisia assemblage (Fig. 2.3). Moderate percentages of pine (8-18%) in the Zone 4 samples of Wentzel's Pond, Big John Pond, Mud Lake, and Lake Minnie cause these sites to be ordinated outside the Poaceae-Artemisia assemblage and to differ from Hostage Lake and Peterson Slough, which

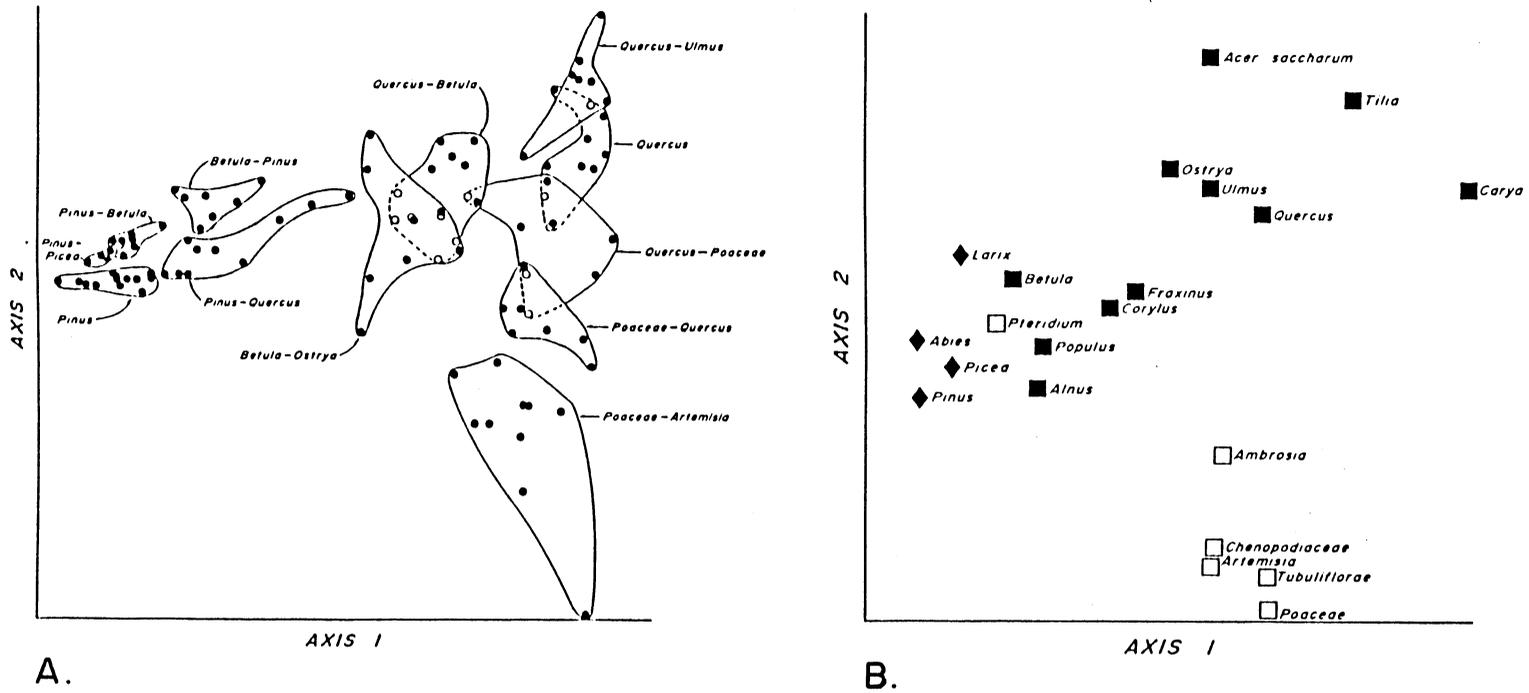


Figure 2.3. Detrended correspondence analysis ordination (Hill, 1979) of 105 presettlement samples, **A**, and 21 pollen taxa, **B**. The pollen assemblages are outlined and labeled in **A**. Where assemblages overlap, the border of the assemblage with generally lower third-axis scores is broken and its sites are indicated by open circles. Not shown in **A** are the positions of 109 fossil samples that were included in the ordination (Figs. 2.4 - 2.6). In **B** conifers, deciduous trees, and herbs are represented by solid diamonds, solid squares, and open squares respectively.

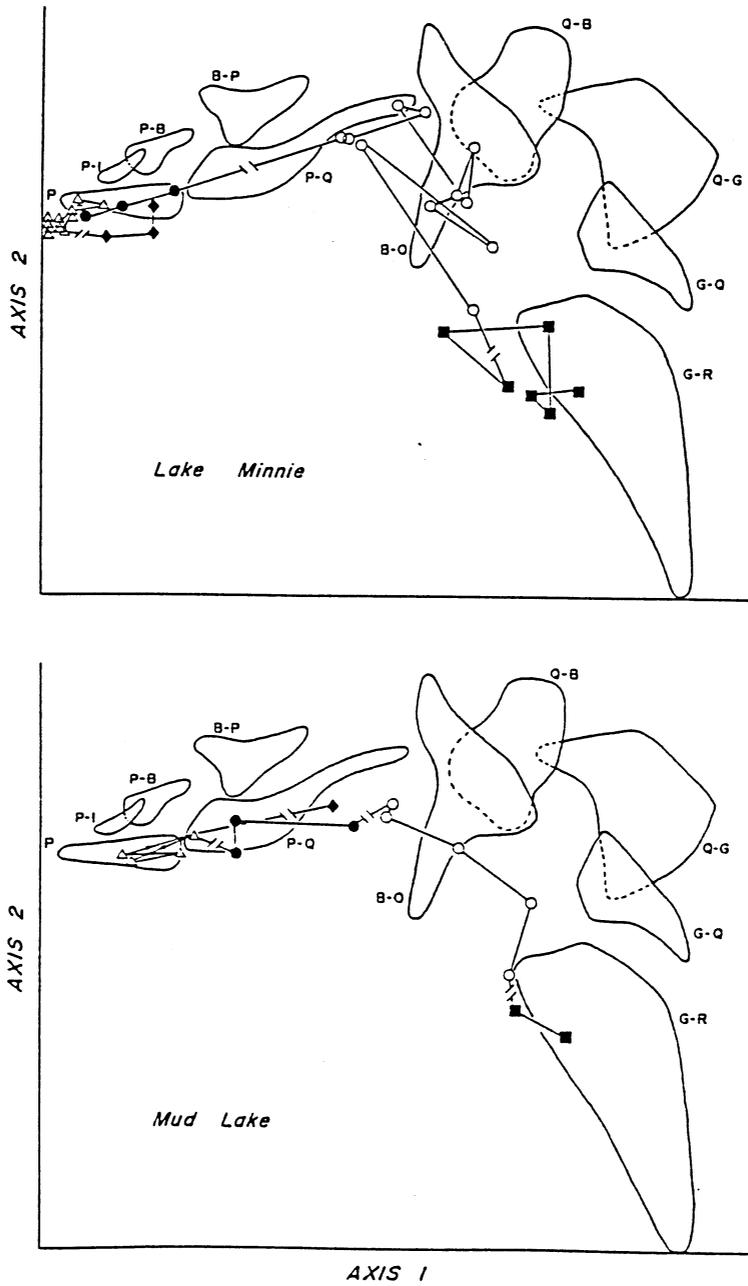


Figure 2.4. Detrended correspondence analysis ordination (Hill 1979) of fossil samples from Lake Minnie (McAndrews, unpublished data) and Mud Lake. Figure 2.3.A serves as the key to the pollen-assemblage abbreviations. Stratigraphically adjacent samples are connected. The symbols and line-breaks separate samples belonging to different pollen zones (Plates 1 and 2) as follows: solid squares, Zone-4; open circles, Subzone 3-B; solid circles, Subzone 3-A; open triangles, Zone-2; and solid diamonds, Zone-1.

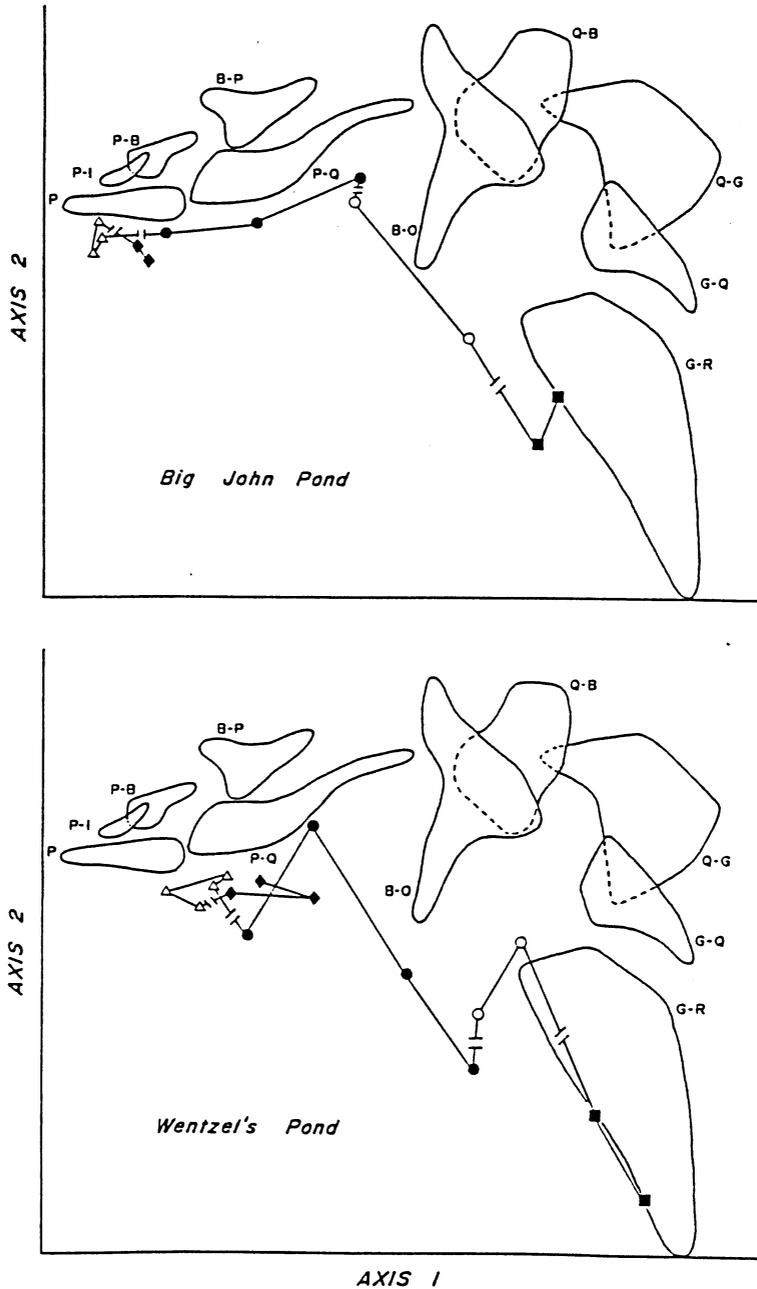


Figure 2.5. Detrended correspondence analysis ordination (Hill, 1979) of fossil samples from Big John Pond and Wentzel's Pond (Plates 3 and 5). Abbreviations and symbols are as in Fig. 2.4.

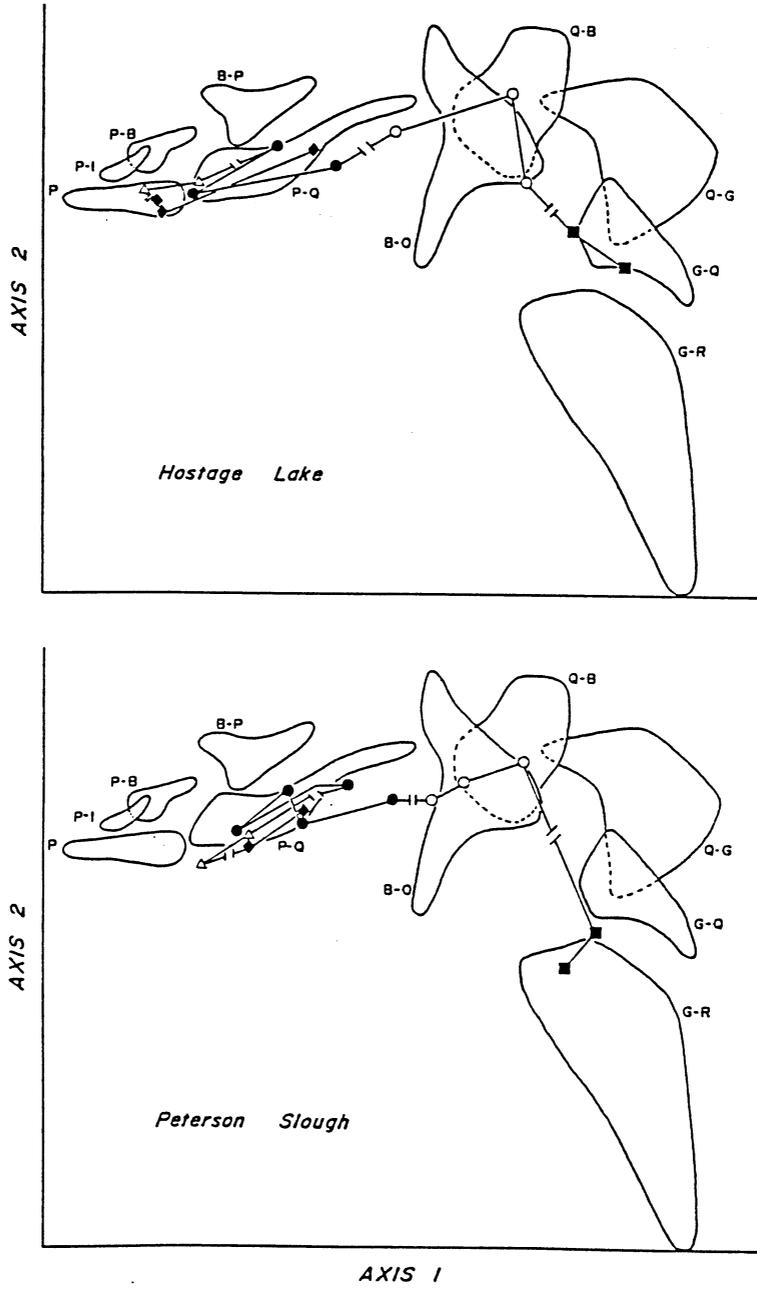


Figure 2.6. Detrended correspondence analysis ordination (Hill 1979) of fossil samples from Hostage Lake and Peterson Slough (Plates 4 and 6). Abbreviations and symbols are as in Fig. 2.4.

have slightly lower percentages of pine (6-12%). Also, Hostage Lake and Peterson Slough have much higher percentages of Quercus (16-27%) than the other sites (5-17%), which cause the Zone 4 samples from these sites to fall within the Poaceae-Quercus assemblage and the upper part of the Poaceae-Artemisia assemblage, respectively.

With the exception of Hostage Lake, the fossil samples are most analagous to presettlement samples of the Poaceae-Artemisia assemblage, which comprises sites in the tallgrass-prairie regions of western Minnesota and eastern South Dakota. The prairie surrounding the presettlement sites was essentially continuous, interrupted only by gallery forests along rivers and by brush that rimmed prairie sloughs. Most of the presettlement sites were more than 40 km west of the nearest woodlands, thus the source of arboreal pollen is presumed to have been distant.

The Zone 4 samples for Hostage Lake are ordinated within the Poaceae-Quercus assemblage, which comprises sites along the prairie/forest border in southern Minnesota. Most of these presettlement sites occurred in prairie, but close to patches of bur oak, Quercus macrocarpa. These oak-dominated patches have been variously described as savanna, openings, and scrub (Daubenmire 1936, McAndrews 1968, Grimm 1983), indicating the stature and density of oaks as they mix with prairie. Apparently the oaks can flower under all of the physiognomic circumstances above (Grimm, 1983) and deliver moderate amounts of oak pollen to sites in nearby prairie.

Interpretation.- Zone 4 represents a period during which prairie occupied the outwash surrounding all six study sites. Unlike their closest presettlement analogues, the study sites probably were occupied by relatively small prairies (10-100 km²) limited to the surrounding outwash. The moraine that encompasses the outwash plains has been forested since about 4,000 yr B.P. (McAndrews 1966, 1969; Jacobson 1979) and has served as a nearby source of arboreal pollen during the period represented by Zone 4. The moderate percentages of total pine and oak, which cause some of the Zone 4 samples to be ordinated outside the presettlement assemblages (Figs. 2.4 - 2.6) may be attributed to oak and white pine growing on the adjacent moraines.

High percentages of locally derived Poaceae (27-45%) and undifferentiated Tubuliflorae (4-12%) in the Zone 4 samples at Wentzel's Pond and Big John Pond cause their exceptionally low second-axis scores (Fig. 2.5). Similarly high percentages of Poaceae pollen have been interpreted as the presence of wild rice, Zizania aquatica, at sites within the study area (McAndrews 1969), but this is probably not the case for these two sites. Apparently both of these sites were sedge meadows at the time (Zone 4), as indicated by exceptionally high percentages of Cyperaceae pollen (43-47%, outside the sum). Humified siltier sediments with sand lenses occurring at and below the lowermost samples prepared for pollen analysis characterize the Zone 4 sediments of these sites (Plates 3 and 5, Table 2.2). These sedimentological features indicate periodic drying. The sand could

have been wind-deposited, as Holocene dunes do occur on these outwash plains (Norton 1982), but the large sand lens at Wentzel's Pond (215-225 cm, Table 2.1) appears to be a mud-crack filling, as it is wedge-shaped in vertical section. Thus it is unlikely that these sites were sufficiently wet to support wild rice. Local populations of Calamagrostis, Glyceria, and other wetland grasses which are present at these sites today may have caused the high percentages of Poaceae. The high percentages of undifferentiated Tubuliflorae (some of which is Bidens-type) is consistent with the interpretation that these sites were wet swales and not wild rice beds. Because of its high percentages in Zone 4 at these two sites, Cyperaceae was removed from pollen sums for all study sites and was not included in the ordination (Figs. 2.3 - 2.6).

Chronology.-- The duration of prairie occupation at the study sites is undocumented except at Lake Minnie, which has a full Holocene pollen diagram (McAndrews, unpublished data). This diagram shows that prairie replaced a Diploxylon pine woodland at about 8,140 yr B.P. (WAT-1032). Thus prairie occupied the outwash plains at Lake Minnie for roughly 3,600 radiocarbon years. Because prairie persisted longer at the other study sites than at Lake Minnie, it is likely that prairie was established sooner at those sites in the early Holocene. If this is true, then 3,600 radiocarbon years is a minimal estimate of the duration of prairie occupation at the other study sites.

It is clear from historical records (public land survey-records

ca. AD 1850-1880, Upham 1888, Todd 1899, West 1907, Watrin 1930) that some patches of outwash were so prone to repeated fire (or were otherwise so suited to the persistence of prairie) that they remained prairie until settlement. This includes the Hubbard, Fishhook, and Shell prairies of the Park Rapids outwash plain (Fig. 2.2) that occurred well within the conifer/hardwood forests, some 40-80 km east of the prairie/forest border. These prairies persisted in spite of the fact that the nearby pollen sites, Peterson Slough and Wentzel's Pond, indicate that afforestation began prior to 2,000 yr B.P. (see below). Thus prairie has probably occupied some small patches of outwash within regions of Minnesota that are mostly forested since about 8,000 yr B.P. -- leaving little evidence of their existence in the pollen record. If Peterson Slough and Wentzel's Pond may serve as models for all of the study sites, then small patches of prairie persisted for more than 2,500 radiocarbon years following the initial decline in prairie herbs (Subzone 3-B/Zone 4 boundary, Plates 1-6).

Zone 3, Afforestation of the Outwash-Plain Prairies

Description of Subzone 3-B. - This subzone represents a transitional period in which the percentages of prairie herbs decline to levels 20% lower than in Zone 4 (Plates 1-6). The Quercus curves show slight to moderate peaks, which are better-defined when the extralocal pollen sum is used. Pinus strobus, Betula, and Ostrya percentages increase and contribute most to the consistent 10-20%

increases in the sum of tree and shrub types that are restricted to moraine (regional taxa). This is in contrast to the slight changes in the sum of tree and shrub taxa that can grow on outwash. The upper boundary of the subzone is placed between sample levels where the Pinus banksiana/resinosa curves begin a consistent rise to percentages exceeding 30%. With the exception of Hostage Lake, the percentages of indeterminable pollen decline largely because the percentages of easily crumpled types (Poaceae and Cyperaceae) also decline. The rise in indeterminable pollen at Hostage Lake is caused by an increase in crumpled and broken pollen grains that are probably Populus. Alternatively, the indeterminable grains at Hostage Lake could be Cyperaceae grains that resemble Populus when they are corroded as well as crumpled.

Presettlement analogues, Subzone 3-B.- In the ordination, the Subzone 3-B samples have the most between-site variability (Figs. 2.4 - 2.6). Peterson Slough and Hostage Lake are the only sites having fossil samples that clearly track through the presettlement assemblages. The Subzone 3-B samples from these sites have ordination scores similar to the presettlement samples that constitute the Quercus-Betula assemblage because they have percentages of Quercus that range from 7 to 30% and because their Betula curves rise prior to increases in Pinus strobus. Low percentages of Quercus (< 12%) and roughly coincident rises in Betula and Pinus strobus cause the samples from Wentzel's Pond, Big John Pond, and Mud Lake to have lower second-

axis scores than the samples constituting the Quercus-Betula assemblage. The ordination scores for the numerous Lake Minnie samples span the range of variability exhibited by all of the other study-site samples in Subzone 3-b.

An analogue-based interpretation of Subzone 3-B suggests that Hostage Lake and Peterson Slough have presettlement analogues in the Quercus-Betula assemblage. The Quercus-Betula assemblage is found at presettlement sites that generally occur in regions mapped as oak-dominated brushland by Marschner (1974). The closest presettlement analogues for the Subzone 3-B samples of the other sites are three presettlement sites that have the lowest second-axis scores of the Betula-Ostrya assemblage. These sites (Cora Lake, Cushing unpublished data; Horse and Faith Ponds, McAndrews 1966) occurred in prairie with oak nearby (< 5 km), and birch in the region. Thus, by analogy, it appears that prairie occurred in the immediate vicinity of Wentzel's Pond, Big John Pond, Mud Lake, and Lake Minnie; and the differences among their Subzone 3-B samples result possibly from different distances to the nearest oak-dominated community.

Interpretation of Subzone 3-B.- Horse Pond and Faith Pond (McAndrews 1966) are not only the closest presettlement analogues to many of the Subzone 3-B samples, but they also occur close to the study area in a region where woody species were actively invading prairie prior to widespread agriculture. Fortunately, these two sites fall within the study area where Ewing (1924) described in detail the

vegetation, succession, and mechanics of the afforestation process. Ewing's observations may provide the best interpretation of Subzone 3-B because they are consistent with sedimentological features and fluctuations of minor taxa that have little or no influence on the ordination scores, and therefore on the interpretation by analogy.

Ewing (1924) observed that the initial invaders of northern Minnesota prairies are willows (Salix interior and S. discolor) and aspen (Populus tremuloides). These taxa are established first along the margins of sloughs or in swales that are wet at least in the spring. The presence of waterlogged soils is critical for the establishment of these taxa for three apparent reasons. First, the woody seedlings are poor competitors for water with an established prairie sod. This is particularly important in prairie regions, where precipitation is seasonal and variable from year-to-year (Transeau 1935). Sloughs and wet swales may provide a more constant and abundant supply of water for tree and shrub seedlings. Second, the sloughs and wet soils may serve as firebreaks and protect woody seedlings from the nearly annual prairie fires (Grimm 1981, 1983). Once willow and aspen seedlings have been spared for several years, Ewing (1924) suggests that their rootstocks are sufficiently developed to produce vigorous post-fire sprouts, even if they burn nearly every fall. Third, prairie sloughs typically draw down in the early summer, leaving exposed mud flats where spring-fruiting taxa like willow and aspen can seed in on mineral soil.

An unfortunate but characteristic property of pollen diagrams from sites where aspen and associated shrubs are actively invading prairie is the lack of positive evidence for tree and shrub establishment. Many of the invading shrubs, such as Salix, Symphoricarpos, Rhus, and Amorpha, are predominantly insect-pollinated and thus poorly represented in the pollen record. Aspen pollen is produced in abundance, but it is poorly preserved in some lake sediments (Lichti-Federovitch and Ritchie 1965, 1968; Janssen 1966). Also, aspen may not flower at all if the sprouts are burned at intervals of less than 10 years (Grimm 1983). Ewing's observations suggest that it is unlikely that the aspen brush-prairie region just west of the study area escaped fire for periods greater than 10 years. Under these circumstances clones of aspen and its associated entomophilous shrubs would create palynological "blind spots" (Davis 1963) in the study-site landscape. This could cause a decrease in the influx of extralocal pollen (prairie types) and a corresponding percentage increase in regional types (sum of regional tree and shrub taxa). This is observed at all of the study sites, along with some direct evidence of tree and shrub establishment. At Peterson Slough, big John Pond, Mud Lake, and Lake Minnie, the percentages of Populus in Subzone 3-B samples range from 1 to 4% and are higher than the percentages in Zone 4. These percentages are slightly higher than those recorded at sites in Manitoba's aspen parkland, where aspen is actively invading prairie (Lichti-Federovitch and Ritchie 1965, 1968).

The percentages of Salix are highest in Subzone 3-B at Lake Minnie, Mud Lake, and Big John Pond, but the percentages are low (< 5%) and the curves appear to be variable. As described by Ewing (1924), the initial stage of Salix domination is short-lived, and any peaks of Salix pollen could be missed by the wide sampling intervals used in this study.

On flat terrain such as outwash plains, aspen can rapidly invade grassland by suckering (Bird 1961, Buell and Buell 1959, Buell and Facey 1960, Grimm 1983). On more rolling terrain, where aspen roots can't reach the water table, the advance of aspen onto the prairie is slower, and the margins of the expanding clones are often invaded by Corylus americana. For all of the study sites, the percentages of Corylus are higher in Subzone 3-B than in Zone 4. Ewing (1924) observed that Corylus reduced the number of aspen sprouts (by shading), and Quercus macrocarpa, Prunus virginiana, and Prunus serotina became established. Because the seeds of these species are not wind-dispersed, Ewing concluded that their establishment was in part due to chance and the proximity to a seed source. Thus the proximity of a study site to moraine (where oak was established) and the ruggedness of the local topography may have determined the degree to which oak became established relative to aspen in the extralocal vegetation around that site. This could explain the high percentages of oak at Lake Minnie, which lies adjacent to moraine. Hostage Lake and Peterson Slough also have high percentages of oak, and they lie

close to areas of rolling ice-contact moraine that presently support oak-dominated forests.

In summary, Subzone 3-B is interpreted as representing a period during which an aspen-dominated brush prairie as described by Ewing (1924) became established around the margins of the study sites. It is probable that aspen brush also became established around other sloughs and wet swales on the surrounding outwash, while the drier portions of the outwash remained prairie. Differences among ordination scores of the Subzone 3-B samples caused by the decline in prairie taxa, and the apparent increase in taxa restricted to moraine, are attributed to aspen replacing prairie which resulted in a relative increase in the proportion of regional versus extralocal pollen. Increases in taxa associated with aspen brush (Salix, Corylus, and perhaps Quercus) and sedimentological evidence of rising water tables during deposition of Subzone 3-B (see Hypotheses below) are consistent with Ewing's observations concerning the afforestation of prairie just west of the study area.

Description of Subzone 3-A.- This subzone is characterized by percentage increases in Pinus banksiana/resinosa from less than 10% to values between 30% and 60%. The upper boundary is placed where the percentages of Pinus banksiana/resinosa cease to increase and begin to fluctuate about a mean upcore (Zone 2). The rise in Pinus banksiana/resinosa is accompanied by falling percentages of Quercus (< 15% at the top of the subzone) and the continued decline of prairie

herb percentages. The sum of regional tree and shrub pollen is essentially constant or rises slightly from Subzone 3-B levels. The percentages of Pinus strobus and Betula tend to be inversely correlated in Subzone 3-A, while Ostrya generally declines. At Peterson Slough, Wentzel's Pond, Big John Pond, and Lake Minnie, the percentages of Picea increase in this zone. At Big John Pond, and to some extent at Lake Minnie, the Picea rise is accompanied by increases in the pollen of other lowland conifers such as Larix, Abies, and Thuja-type.

Presettlement analogues, Subzone 3-A.- Higher percentages of total pine cause the first-axis scores of the Subzone 3-A samples to be much lower than for the Subzone 3-B samples. At the base of Subzone 3-A, Pinus strobus is the major contributor to total pine, whereas at the top of the zone Pinus banksiana/resinosa is the predominant taxon (Plates 1-6). The samples for Lake Minnie have much higher percentages of pine than the other study sites and span a narrow range of first-axis scores within the Pinus assemblage. Samples from the other sites span a broader range of first-axis scores that are higher than those of the Lake Minnie samples and comparable to those of the Pinus-Quercus and the Pinus-Betula assemblages. In two dimensions, the samples from Peterson Slough, Hostage Lake, and Mud Lake fall within the Pinus-Quercus assemblage, but these fossil samples and the presettlement samples that constitute the Pinus-Betula assemblage have considerably higher third-axis scores than does the

Pinus-Quercus assemblage. Thus when three ordination axes are considered the Subzone 3-A samples do not fall within any presettlement assemblage and are equally close to the Pinus-Quercus and the Pinus-Betula assemblages. Higher third-axis scores are caused by higher percentages of lowland conifers such as Picea, Abies, and Larix. Conifer swamps are presently a common feature of the outwash plains and for that reason were included as extralocal taxa. There are no presettlement analogues because of the odd combination of prairie, Quercus, Pinus banksiana/resinosa, and lowland conifer pollen types.

Interpretation of Subzone 3-A.- This subzone represents a period during which jack pine invaded the extralocal vegetation. A straightforward interpretation of the Pinus banksiana/resinosa curves (Plates 1-6) would indicate that jack pine populations had expanded to some limit. If that limit were set by intraspecific competition, then jack pine had formed a closed-canopy forest. At Peterson Slough and Wentzel's Pond, where jack pine became established recently (300-500 radiocarbon years ago), historical descriptions of the vegetation indicate that by the close of Subzone 3-A the coverage of jack pine was sparse and not a closed canopy forest. An analysis of surveyor bearing-trees (see Chapter 1) indicates that jack pine bearing trees occurred at roughly 70% of the survey corners on the outwash surrounding Peterson Slough and Wentzel's Pond, with the remaining corners falling in regions of aspen-oak scrub or open grassland.

Where jack pine occurred, the average distance from the survey corner to a jack pine bearing tree was 35 m, indicating that the trees were scattered. Thus the rise of Pinus banksiana/resinosa percentages to near peak values in Subzone 3-A indicates the development of jack pine barrens or woodland rather than a closed-canopy forest.

The surveyors of the region around Peterson Slough and Wentzel's Pond described the understory of jack pine stands as tall, dense, and composed of oak, aspen, hazel, and willow (Salix humilis ?). Thus the described physiognomy and composition for the jack pine understory is essentially identical to the oak-aspen scrub described by the surveyors (ca. AD 1880) and Ewing (1924). From this it appears that the jack pine around Peterson Slough and Wentzel's Pond invaded patches of oak-aspen scrub rather than open grassland. No historical evidence was found to indicate that jack pine directly invaded prairie. Jack pine stands containing prairie grasses and forbs have an open understory and occur on forest soils where jack pine has been established for more than 1200 radiocarbon years (see below, and Chapter 3). Because the so-called "prairie" plants do not occur in recently established (< ca. 500 B.P.) stands of jack pine on prairie soils (see Chapter 3), these plants are not indicators of former prairie occupation (i.e. relicts) nor do they indicate the direct invasion of prairie by jack pine. Rather, they are simply heliophytes that can apparently grow equally well in prairie and in jack pine stands with an open understory.

The rises in Picea in Subzone 3-A are interpreted as the establishment of extralocal populations of white spruce (Picea glauca) near Peterson Slough, Wentzel's Pond, Big John Pond, and Lake Minnie (Plates 1,3,5, and 6). White spruce presently occurs along the margins of the shallow peatlands that are common on the outwash plains. These peatlands (Badoura and Rifle peats, Elwell et al. 1926) are characteristically open sedge-fens where the peat is deep (> ca. 1.5 m) and forested with Larix laricina where the peat is shallower. Abies balsamea, Thuja occidentalis, and rare individuals of Picea mariana also occur along the peatland margins. Big John Pond and Lake Minnie are the only sites that show rises of lowland conifers other than spruce in Subzone 3-A (Plates 1 and 3). Wood fragments and stumps occur in the upper horizons of the Rifle peats (Elwell et al. 1926). It is possible that the former tree cover of these relatively deep peats was black spruce (Picea mariana) and that the spruce pollen preserved in the Subzone 3-A sediments is a mixture of both white and black spruce pollen. No attempt was made to distinguish white and black spruce pollen grains.

Chronology, Zone 3.- The decline of prairie and the establishment of aspen-dominated brush was asynchronous among the study sites (Fig. 2.7). The dates for this event (Subzone 3-B/Zone 4 boundary, Plates 1-6) are 4,525 yr B.P. at Lake Minnie (uncorrected date), 3,638 yr B.P. at Hostage Lake, 3,255 yr B.P. at Mud Lake, 2,903 yr B.P. at Peterson Slough, and 2,611 yr B.P. at Wentzel's Pond. In view of the

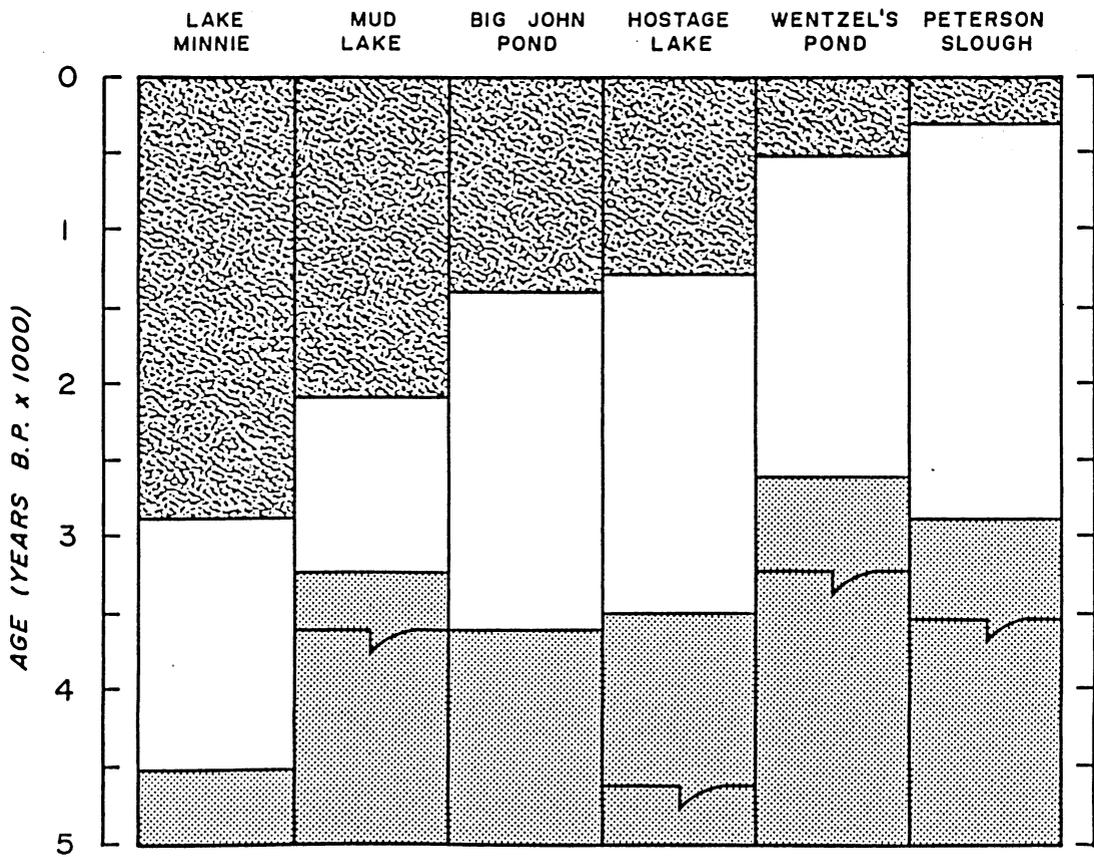


Figure 2.7. The chronology of inferred vegetation at the six study sites. The shaded portions of the bars younger than 3,000 yr B.P. represent a jack pine community. The white bar segments represent the period of reforestation by aspen and oak. The stippled bar segments older than 3,000 yr B.P. represent prairie. The notched lines indicate the age of the lowest pollen samples.

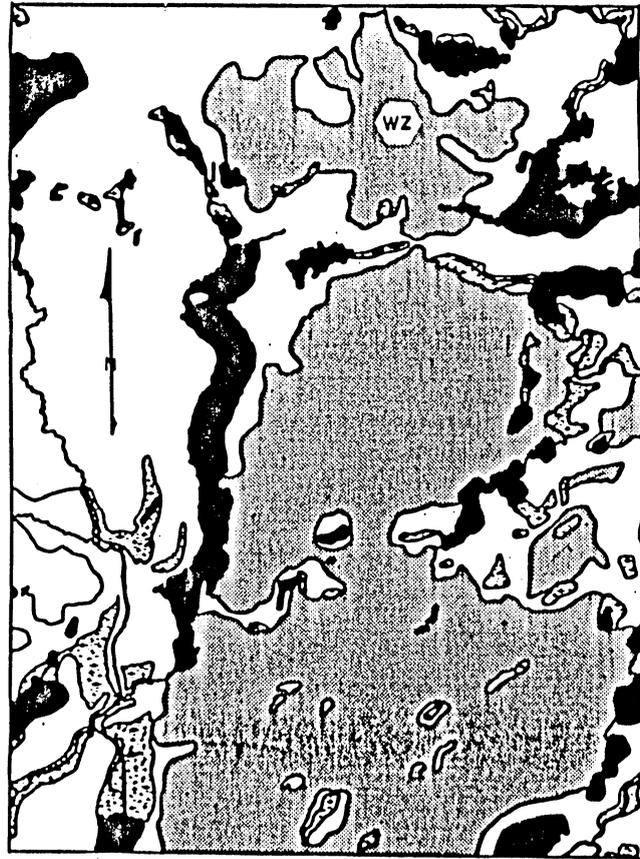
magnitude and variability of the corrections applied to the radiocarbon dates (ca. 200-800 years), it is probable that the oldest and youngest dates are significantly different. However, no date appears to be significantly different from the next older or next younger date. If one assumes that the dates are accurate, the establishment of woody plants on the outwash plains was a continuous process and the result of increasingly moister and perhaps cooler climatic conditions between about 4,500 and 2,500 yr B.P. (Webb and Bryson, 1972). The lack of a clear relation between geography and chronology (Fig. 2.2) suggests that the timing differences among the study sites are caused by local factors rather than spatial variance of climate.

Little emphasis is placed on the relative duration of the Zone 3 subzones. The reason for this is that the initial rises in Pinus banksiana/resinosa, which determine the position of the boundary between the subzones, could be the result of several different vegetational situations. These situations could range from the establishment of a few jack pines within the lake catchment to the establishment of large stands of jack and red pine on distant moraines.

Unlike the subzones, the interpretation of Zone 3 as a whole is consistent among the study sites. The zone begins with the establishment of woody species on the outwash plains and culminates with the establishment of jack pine woodlands or barrens -- i.e. the

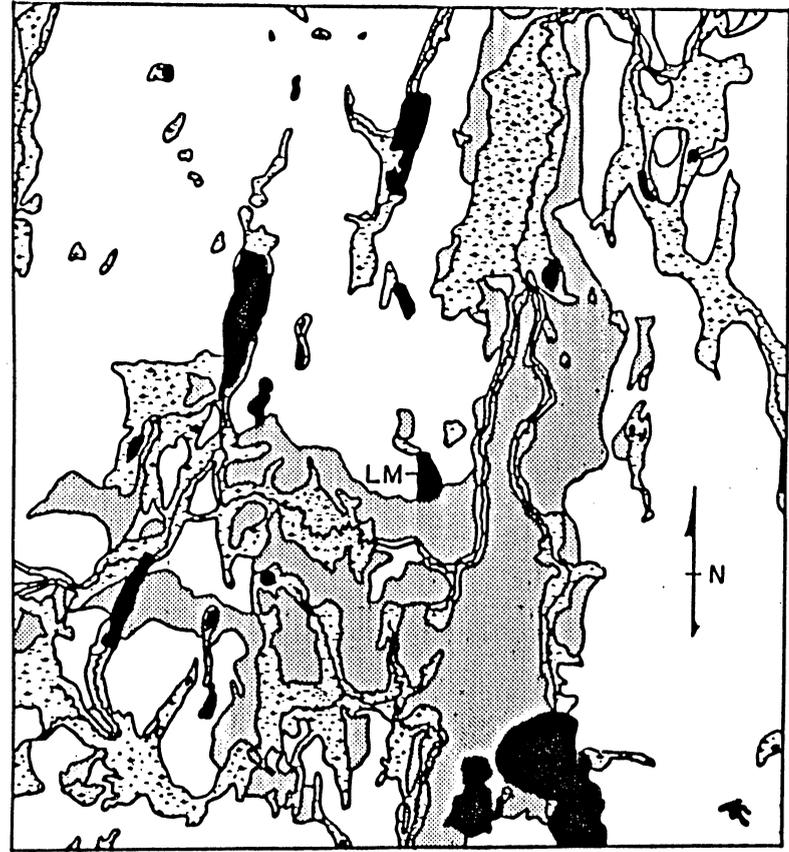
zone represents the period of afforestation. For four of the study sites, the duration of afforestation is similar and recorded as 2,580 years at Peterson Slough, 2,233 years at Big John Pond, 2,175 years at Hostage Lake, and 2,060 years at Wentzel's Pond (Fig. 2.7). In contrast, the duration of Zone 3 was just 1620 years at Lake Minnie and 1,136 years at Mud Lake. It is probably significant that afforestation was most rapid at these two sites where jack pine was first established. The dates for an established jack pine community (Zone 2/Zone 3 boundary) at Lake Minnie and Mud Lake are 2,545 yr B.P. and 2,119 yr B.P. respectively. The corresponding dates for sites with a longer period of afforestation are 1,405 yr B.P. at Big John Pond, 1,334 yr B.P. at Hostage Lake, 551 yr B.P. at Wentzel's Pond, and 323 yr B.P. at Peterson Slough.

Both the rate of afforestation and the timing are correlated with topographic differences among the study sites. Afforestation was completed first (> 2,000 yr B.P.) and most rapidly (< 1,700 years) at Lake Minnie and Mud Lake. Both of these sites occur on the Menahga soil series (McMiller et al. 1930), which is characteristically associated with peat-filled channels. These channels are sinuous and interconnected and break the outwash plain surface into small isolated patches of upland (Fig. 2.8). Where jack pine has been established since 1,200-1,400 yr B.P., the outwash plain surface is pitted, with lakes (Hostage Lake area) or peat (Big John Pond area) occurring in the depressions. Where jack pine was most recently established (300-



A.

0 5 10 km



B.

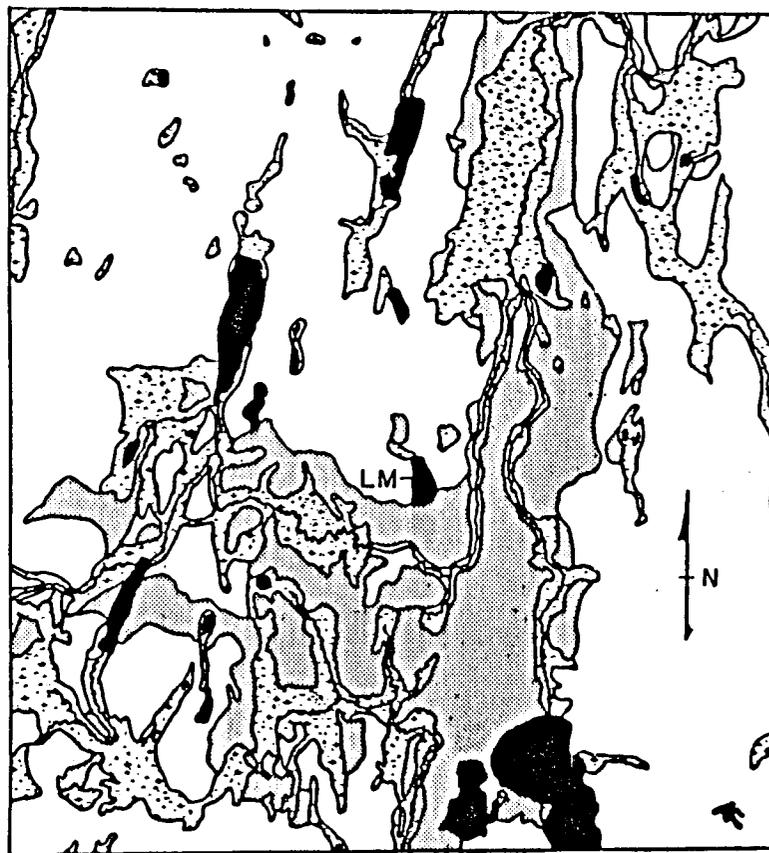
0 5 10 km

Figure 2.8. Maps of the Dorset soil series (a prairie soil) around Wentzel's Pond (A) and the Menahga soil series (a forest soil) around Lake Minnie (B). Note the lack of lakes and peatlands on the Dorset series versus the abundance of peat-filled channels associated with the Menahga soil series. (Redrawn from McMiller et al. 1930).



A.

0 5 10 km



B.

0 5 10 km

Figure 2.8. Maps of the Dorset soil series (a prairie soil) around Wentzel's Pond (A) and the Menahga soil series (a forest soil) around Lake Minnie (B). Note the lack of lakes and peatlands on the Dorset series versus the abundance of peat-filled channels associated with the Menahga soil series. (Redrawn from McMiller et al. 1930).

500 yr B.P.), the outwash plains have few permanently wet depressions (Fig. 2.8).

Hypotheses for the afforestation of outwash-plain prairies.- The asynchronicity (Fig. 2.7) of similar vegetation changes among closely-spaced study sites indicates that locally varying factors largely determined the timing and rate of vegetation change. For example, regionally varying factors like climate can't explain why brush invaded the outwash surrounding Lake Minnie at 4,500 yr B.P. but, just 25 km to the south brush invaded the outwash at Wentzel's Pond nearly 2,000 years later, at 2,600 yr B.P. Climate can't explain why the rate of afforestation is so highly variable among sites occurring on the same outwash plain (Park Rapids, Fig. 2.2), requiring just 1,100 years at Mud Lake, 2,100 years at Wentzel's Pond, and 2,600 years at Peterson Slough. That outwash plains were afforested throughout the late Holocene does indicate that the increasingly moist and cool climate (Webb and Bryson, 1972) was probably the ultimate cause of afforestation; local conditions, however, determined the climatic threshold required to initiate afforestation on each plain (see Grimm 1983). Thus any proposed hypothesis concerning afforestation must be (1) partially influenced by climate, (2) variable at a local scale, and (3) consistent with the ecology and observed succession of species along the prairie/forest border in northern Minnesota, the spatial analogue.

According to Ewing (1924), the presence of permanently or

seasonally wet swales was required for brush to invade established prairie in northwestern Minnesota. Thus the establishment and persistence of brush in Subzone 3-B and the eventual development of jack pine forest in Zone 2 may have been the result of the formation of sloughs and wet swales in depressions that were dry during Zone 4 time. In this study, the patches of outwash that were never afforested (Hubbard, Fishhook, and Shell prairies) are characterized by shallow sloughs that contain no sediment (see site descriptions for Peterson Slough and Wentzel's Pond and Appendix 2.A, Table 2.A.1). The lack of sediment in these depressions indicates that they have been recently flooded. In contrast, the patches of outwash with uplands that are now occupied by jack pine forest generally have 10 to 50% of their surface occupied by lakes with sediments or shallow peatlands.

One hypothesis is that sloughs and wet swales formed during Subzone 3-B time as a result of a rising water table. This hypothesis is particularly attractive because differences in local hydrology among the study sites could account for the filling of sloughs and thus the establishment of brush at various times throughout the late-Holocene -- i.e. the asynchronicity of the Subzone 3-B/Zone 4 boundaries (Fig. 2.7).

The development of the Glacial Lake Agassiz peatlands just north of the study area (Glaser et al. 1981) was almost certainly the result of a regional water-table rise, and it occurred over the same period (4,000-2,000 yr B.P.) during which brush invaded the outwash-

plain prairies. The best evidence for the occurrence and variable timing of water-table rises on a more local scale comes from small ponds that were dry while prairie surrounded the site and have coincident records of increasing lake depth (based on sedimentology) and increasing percentages of tree and shrub taxa. Wentzel's Pond, Big John Pond, and Stevens Pond (Janssen 1967) are three such sites. At Wentzel's Pond the transition from compact, highly humified sediments with sand lenses to looser, slightly humified sediments with no sand lenses is exactly coincident with the decline of prairie taxa at 2,600 yr B.P. (Plate 5, Table 2.1). At Big John Pond the transition from silty, slightly humified sediments with sand lenses to marly sediments occurs within Subzone 3-B, slightly after the decline in prairie taxa at about 3,400 yr B.P. (Plate 3, Table 2.2). At Stevens Pond (Fig. 2.2), a small peat-filled depression on outwash, Janssen (1967, p. 150) describes a transition from "completely decomposed black amorphous peat" to well-preserved woody peat that is exactly coincident with the decline in prairie taxa. Although the Stevens Pond core is undated, a comparison of the Betula, Pinus strobus, and Ostrya curves with those of the dated record at nearby bog D (McAndrews 1966) indicates that conditions favorable for peat preservation, probably a water-table rise, prevailed at Stevens Pond at about 4,000 yr B.P. Thus the shallower (< ca. 1.5 m) study sites like Wentzel's Pond, Big John Pond, and Stevens Pond contain a record of increasing water depth that is coincident with asynchronous

declines of prairie pollen taxa and corresponding rises in tree and shrub pollen (see also Appendix 2.A, Table 2.A.1 for other truncated records). Cores taken in water depths greater than about 1.5 m contain no record of lake levels low enough to expose their sediments. Therefore it appears that on outwash plains the depression of mid-Holocene lake levels below present levels generally did not exceed 1.5 m plus the thickness of sediment accumulated in the late Holocene.

A second hypothesis is that increased precipitation as snow could account for the establishment of brush in depressions above the water table. Depressions may trap enough snow that it persists throughout much of the spring fire season, thereby protecting woody seedlings from spring fire. Freeze and thaw cycles of snow and ice in the depressions promotes spring flooding and cryoturbation that could cause the breakup of upland prairie sod and favor the establishment of wetland graminoids and woody plants such as Salix and Populus. Increased precipitation as snow was probably not an important mechanism for the outwash plains first invaded by brush (4,500-3,500 yr B.P.) because it seems that the depressions were already filled with peat (Lake Minnie, Mud Lake, and Big John Pond) or with water (in the lake district around Hostage Lake). This mechanism may have been important at Peterson Slough and Wentzel's Pond, where most of the depressions are well above the water table or have just recently been flooded. This mechanism poorly explains the asynchronicity of brush invasion among the study sites because it would have been a regional

climatic event that should have been recorded synchronously at the study sites. All of the outwash plains have depressions deep enough to trap snow, but not all depressions are deep enough to reach the water table, which is why the water-table hypothesis is favored.

The inundation of depressions either seasonally or permanently may explain the establishment and persistence of aspen-dominated brush, but it does not explain the eventual spread of aspen onto the uplands. It also does not explain the spread of taxa like oak and jack pine, which require fire return-intervals greater than their minimum age of seed production, about 30 and 10 years respectively (Fowells 1965), in order to spread by sexual means. The most likely explanation is that the clones of aspen themselves, because they are less flammable than prairie, provided the firebreaks that allowed some upland patches of outwash to escape fire for several years (Grimm 1981, 1983). Therefore the abundance of brush-filled depressions and the degree to which they are interconnected may have determined how well they could insulate a particular patch of outwash from prairie fires -- and thus determine the probability that woody species could invade that patch. This would explain why afforestation was most rapid (see above) at sites where depressions occur as channels (1,100-1,700 years) versus sites where depressions are scattered or rare (2,000-2,600 years, Fig. 2.8).

Zone 2, Jack Pine Occupation

Zone description.- This zone is characterized by the highest percentages of Pinus banksiana/resinosa (30-60 %) and the lowest percentages of Quercus (2-15 %). The percentages of Pinus strobus, Betula, and Ostrya generally decline throughout the zone (Plates 1-6). The summed percentages of regional trees and shrubs are 5-20 % lower than in Zone 3. The lowest percentages of prairie taxa are recorded in this zone, from about 10% at most sites to 15-20 % at Peterson Slough and Wentzel's Pond. The upper boundary of Zone 2 is placed between sample levels where total pine percentages decline and Ambrosia percentages increase as a result of logging and land clearance.

Presettlement analogues.- In the ordination (Figs. 2.4 - 2.6), the Zone 2 samples for Peterson Slough, Wentzel's Pond, Hostage Lake, and Mud Lake are ordinated near the contact between the Pinus assemblage and the Pinus-Quercus assemblage. The samples for Lake Minnie and Big John Pond have lower first-axis scores than the above sites and are ordinated near the Pinus assemblage. The differences in first-axis scores among the Zone 2 samples is the result of different percentages of total pine that range from 30 to 35% at Peterson Slough to nearly 60% at Lake Minnie. The Lake Minnie samples with near-zero first-axis scores have the highest percentages of total pine recorded in Minnesota sediments. With the exception of a single sample for Peterson Slough, the second-axis scores vary little among the sites,

and these differences cannot be attributed to a particular taxon. The study sites themselves constitute the bulk of presettlement samples from outwash plains dominated by jack pine and therefore serve as their own analogues.

Interpretation.- The vegetation represented by the Zone 2 samples is presumed to be analogous to the presettlement vegetation around the study sites as described by the early land surveyors. All of the study sites are in regions mapped as jack pine barrens and openings by Marschner (1974). A detailed examination of land-surveyor records reveals two distinctive types of jack pine communities on outwash plains in the study area (see Chapter 1). Outwash plains with light-colored forest soils were occupied by an essentially continuous forest of jack pine that was not extensively mixed with deciduous trees. Outwash plains with dark-colored relict-prairie soils were occupied by jack pine barrens, described by the surveyors as a mosaic of jack pine, oak and aspen thickets, and some open grassland. Hostage Lake, Big John Pond, Mud Lake, and Lake Minnie occur in the regions of jack pine forest, whereas Peterson Slough and Wentzel's Pond occur in regions of presettlement jack pine barrens. The only palynological distinction between sites occurring in jack pine barrens versus jack pine forest are slightly higher first-axis scores (Figs. 2.4 - 2.6) and somewhat higher percentages of prairie types (Plates 1-6) for the barrens sites. Apparently, the overwhelming abundance of pine pollen in these samples influences the percentages of minor taxa and

ordination scores in such a way that it is difficult to differentiate palynologically the pine-dominated communities that have considerable compositional and physiognomic differences.

Chronology.- because all of the study sites are now occupied by jack pine, the dates of establishment are equivalent to the duration of occupation. They are recorded as follows: 2,545 years at Lake Minnie, 2,119 years at Mud Lake, 1,405 years at Big John Pond, 1,334 years at Hostage Lake, 551 years at Wentzel's Pond, and 323 years at Peterson Slough (Fig. 2.7). These periods of jack pine occupation represent the historical factor most correlated with the present vegetation and levels of soil organic matter (SOM). A detailed examination of the present vegetation and SOM levels indicates that SOM declines from ca. 4% to less than 2% during the first 1,000 years of jack pine occupation (see Chapter 3). The most striking vegetational change that accompanies falling percentages of SOM is a decrease in both the height and cover of deciduous trees and shrubs growing as associates of jack pine. On sandy soils with little silt and clay, SOM is probably the most important soil component governing cation-exchange capacity and soil-moisture retention (Brady, 1974). Thus this is a clear case of a shift from the deciduous habit on sandy soils with ca. 4% SOM to the evergreen habit (conifers, broadleaf evergreens, and mosses), because sandy soils with less than 2% SOM are impoverished in both nutrients and water. Because the percent SOM is correlated with the duration of jack pine occupation (Zone 2/Zone 3

boundary) rather than the time since the establishment of deciduous taxa (Zone 3/Zone 4 boundary), it is probable that the establishment of jack pine and its associated litter and microflora caused the decline of SOM, and the gradual loss of deciduous elements probably resulted from this process.

Postsettlement, Zone 1

Zone description and interpretation.- This zone is characterized by rising percentages of Ambrosia, declining percentages of total pine, and the occurrence of introduced or agricultural pollen types. The agricultural and introduced pollen types recorded are cf. Avena, undifferentiated Cerealia, Zea mays, Medicago sativa, Melilotus-type, Trifolium repens-type, and Salsola kali. Ambrosia percentages are typically 5% higher than those in Zone 2. The peak values of Ambrosia are between 5 and 10 %, which is low in comparison to Ambrosia percentages recorded from sites in agricultural regions of southern Minnesota. The declines in pine pollen range between 10 and 30 % and result from logging. The fluctuations of culturally influenced taxa are accompanied by percentage rises in Quercus and Populus at all sites and percentage rises in Betula at Lake Minnie, Hostage Lake, and Mud Lake. These increases are interpreted as the expansion of these taxa into regions logged for pine. The Zone 1 percentages of Chenopodium-type are 1-4% higher than those recorded in Zone 2 and are probably the result of timber harvest or land clearance for farming.

The increased percentages of Quercus, Populus, Betula, Ambrosia, and Chenopodium-type cause the Zone 1 samples to have higher first-axis scores than Zone 2 samples in the ordination (Figs. 2.4 - 2.6).

Settlement by Europeans.- The accounts of Alvin Wilcox, the surveyor of several townships in the western portion of the study area, indicate that settlement was sparse in the early 1870's, and many townships had no settlers (West 1907). Agriculture at this time consisted largely of sustenance farming and providing for livestock. Some of the first cash-crop farms in the study area were established on the dark-soil outwash in Wadena and Hubbard counties. In Hubbard county, these initial farms were established in 1879 on the Hubbard and Fishhook prairies, which are within 10 km of Wentzel's Pond and Peterson Slough respectively. By 1890 Hubbard County had 194 farms and 17,000 acres (6,682 ha) under cultivation (McMiller et al. 1930). Most of the acreage was in wheat (Triticum) and oats (Avena). The early agricultural practices in small-grain farming produced ideal conditions for the spread and flowering of Ambrosia (Grimm 1981). Farmers were most likely attracted to these dark-soil outwash plains. initially because of their scattered timber, their well-established wagon trails for grain transport, and their rich, stoneless prairie soils.

By 1880, local sawmills were established along rivers and streams that were sufficiently deep to float timber. The large sawmills, such as the one at Akeley, established in 1891, followed the spread of

railways in the study area. These railways were largely completed between 1880 and 1895 (Bourgeois 1974). Much of the initial cutting was on the moraines, where Pinus strobus and Pinus resinosa groves occurred. It is unlikely that the initial decline in total pine pollen (Plates 1-6) is the result of jack pine logging on outwash.

SUMMARY

Pollen diagrams from six study sites on outwash plains of north-central Minnesota are interpreted as records of similar extralocal vegetation changes since ca. 5,000 yr B.P. All of the study sites have undergone a shift from prairie to an aspen-oak community, followed by the jack pine-dominated vegetation that now occupies the sites.

It is probable that all of the species capable of directly invading prairie (aspen, bur oak, willow, and some entomophilous shrubs) were established on the surrounding moraines prior to their invasion of the adjacent prairie-occupied outwash plains. Thus the movement of these taxa onto the outwash plains probably involved only short distances (< 20 km) and the chronology of their establishment does not indicate a regional westward migration of these taxa in the late Holocene.

Because climate varies little over the short distances separating the study sites, the asynchronicity of the dates for the establishment of aspen brush (Zone 3/Zone 4 boundary) and the following

establishment of jack pine (Zone 2/Zone 3 boundary) indicates that locally varying conditions determined where and when these vegetational shifts occurred. Sloughs and wet swales are apparently prerequisite for aspen to invade prairie, and they probably appeared on the outwash plains at different times because locally varying hydrologic conditions determined the absolute increase in precipitation required for the water table to rise and flood depressions. The rate at which afforestation proceeded, culminating with the establishment of jack pine, appears to be related to local variability in the distribution of wet depressions as they serve as firebreaks. Where peat-filled channels and chains of lakes occur, afforestation occurred first and was relatively rapid. Where lakes and peatlands are scattered, afforestation occurred later and required more time. Where wet depressions are rare, some patches of prairie remained open.

The biosequence of prairie soils to forest soils on outwash may also be viewed as a chronosequence. The most obvious characteristic of prairie soils, the percent soil organic matter, is correlated with the period of jack pine occupation and not with the date of initial invasion by woody plants. Where jack pine has been established for less than ca. 500 years, soil organic matter levels range between 3% and 4% (see Chapter 3). Where jack pine has been established for more than 1,200 years, the soils have less than 2% soil organic matter.

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CHAPTER 3: VEGETATION PATTERNS IN JACK PINE FORESTS ON OUTWASH,
NORTH-CENTRAL MINNESOTA

INTRODUCTION

Jack pine (Pinus banksiana Lamb.) occupied sandy outwash plains in north-central Minnesota at the time of European settlement, about AD 1860 (Marschner, 1974). These stands form the southwestern range limit of jack pine (Fig. 3.1). Early surveyors and settlers of the region recognized that some areas of jack pine probably had replaced prairies recently. Surveyor line descriptions often noted prairie openings in these jack pine woodlands, and early settlers cleared large areas of jack pine and oak scrub in order to cultivate the dark-colored relict-prairie soils (McMiller et al. 1930, Todd 1899, Upham 1899). Other areas, characterized by light-colored soils, were more densely forested with jack pine and some red pine (Pinus resinosa Ait.). Although the soils of these areas do not indicate former occupation by prairie, the presence of typical prairie plants in the understories of these stands suggest that hypothesis. These observations indicate that jack pine has recently extended its range southwestward in north-central Minnesota.

Pollen diagrams from these areas (Jacobson 1979, see Chapter 2), confirm the recent establishment of jack pine. These diagrams indicate that all outwash plains dominated by jack pine in north-central Minnesota were prairie during the mid-Holocene. Apparently jack pine did not invade these prairies directly, but rather it succeeded a Populus-Quercus brush stage that is poorly represented in the pollen record (see Chapter 2). The diagrams also show that the prairie-to-

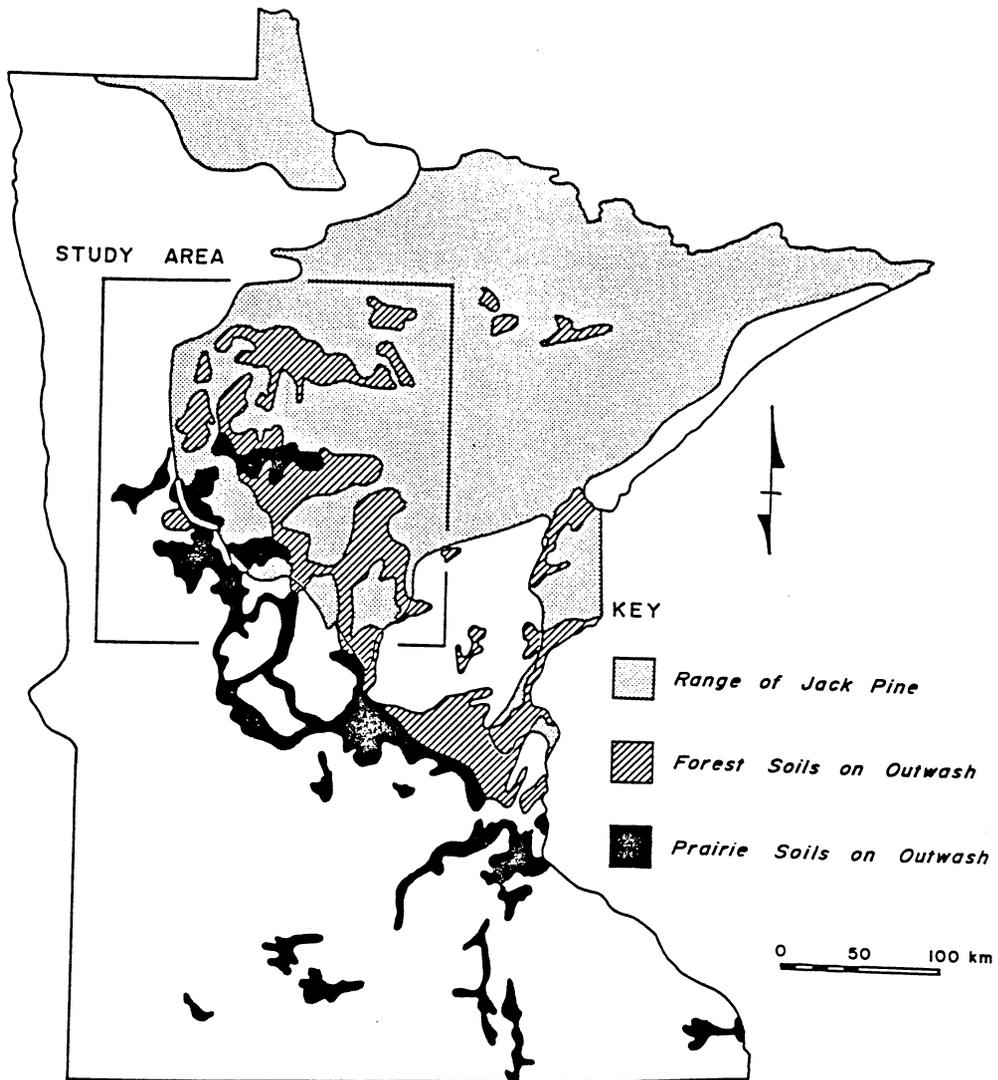


Figure 3.1. The distribution of outwash in Minnesota, showing forest soils (hatched areas) or prairie soils (black areas). Nearly all of the outwash within the study area, including the regions of prairie soils, is now forested. Jack pine dominates the outwash-plain vegetation within its range. (Outwash redrawn from Arneman, 1963; range of jack pine redrawn from Schoenike, 1961).

jack pine transition was similar at different study sites, required 1,000-2,600 years for completion, and was sporadic -- with some areas of jack pine forest being established as early as 2,500 radiocarbon years B.P. and other areas as recently as 300 radiocarbon years B.P. Soils occupied by jack pine for less than 1,000 years have more organic matter and higher nutrient content than soils occupied by jack pine for longer periods (Minnesota Soil Atlas 1969, 1971, 1977, 1980). Thus the levels of soil organic matter in these soils is believed to indicate a soil chronosequence initiated by the development of jack pine forest on prairie soils that developed during the mid-Holocene.

The purposes of this study are (1) to describe the structure and species composition of jack pine forests occurring on either forest or relict-prairie soils (hereafter termed light and dark soils respectively) and (2) to relate these results to the period of jack pine occupation, the levels of soil organic matter, and the previous vegetation as inferred from pollen diagrams. To this end, the relationship of soil properties to the vegetation was determined by comparing ordination scores and classification groupings of vegetation samples with soils maps and actual measurements of soil organic matter. The behavior of individual species is illustrated in phytosociological tables showing species abundances relative to four soil-based units that are interpreted as a soil chronosequence. Paleoecological information is used to estimate the length of time required for the amount of soil organic matter characteristic of sand

prairies (about 5%, Brady 1974) to be reduced to levels more typical of jack pine forest soils (about 1.5%). Additionally, patterns of species occurrence along the soil chronosequence are used to infer the degree to which species commonly found in prairies and deciduous woodlands have persisted in these jack pine forests.

METHODS

Sample Location and Criteria

Sample stands of jack pine forest were chosen systematically with regard to geography and soil types. Geographically separate areas supporting jack pine forest at the time of European settlement were identified from Marschner's vegetation map (1974). The dominant Soil Landscape Unit (SLU) of each of these areas was determined from the Minnesota Soil Atlas (1969, 1971, 1977, 1980). For this study, SLU's are particularly useful because (1) light (forest) and dark (relict-prairie) soils are primary classes, (2) gross textural differences in the rooting zone (top 76 cm of the soil profile) are identified, and (3) the scale (1:250,000) is sufficiently coarse to match vegetation patterns on Marschner's map (1:500,000).

For each area of jack pine, I attempted to locate a sample stand in each of the common SLU's in that area. I used aerial photographs to locate existing stands of jack pine for sample plots, choosing the largest, most continuous stands. The criteria for accepting a targeted

stand were: (1) at least 80% of the canopy coverage was jack pine, (2) the stand covered a minimum of 2 ha (3) the dominant trees were older than 40 years, and (4) there were no obvious signs of grazing. Rejecting stands because of logging proved to be unrealistic. Most of these stands have been logged and it is difficult to distinguish consistently between stands of fire origin or logging origin on the basis of age structure.

Vegetation Sampling

Relevés (Mueller-Dombois and Ellenberg 1974) were made in 59 sample plots (Fig. 3.2, in back pocket). Thirty of these relevés are distributed evenly over the range of jack pine in north-central Minnesota. The remaining 29 relevés are concentrated within about 3 km of six paleoecological study sites. Five relevés accompany each paleoecological study site, except at Peterson's Slough, where only four stands met the above criteria. Exact relevé locations are given in Appendix 3.A.

Each relevé was made in a 20 x 20 m quadrat located in a representative spot in the stand. Stand edges were avoided. Physiognomy was determined by recording visual estimates of height (6 classes) and coverage (7 classes) of plants in 6 life-form categories according to Kùchler's (1967) system. The life-forms recorded in this study are: (1) needleleaf evergreen, (2) broadleaf evergreen, (3) broadleaf deciduous (woody), (4) graminoid, (5) forb, and (6) lichen-moss. The height strata, recorded either singly or as groups of

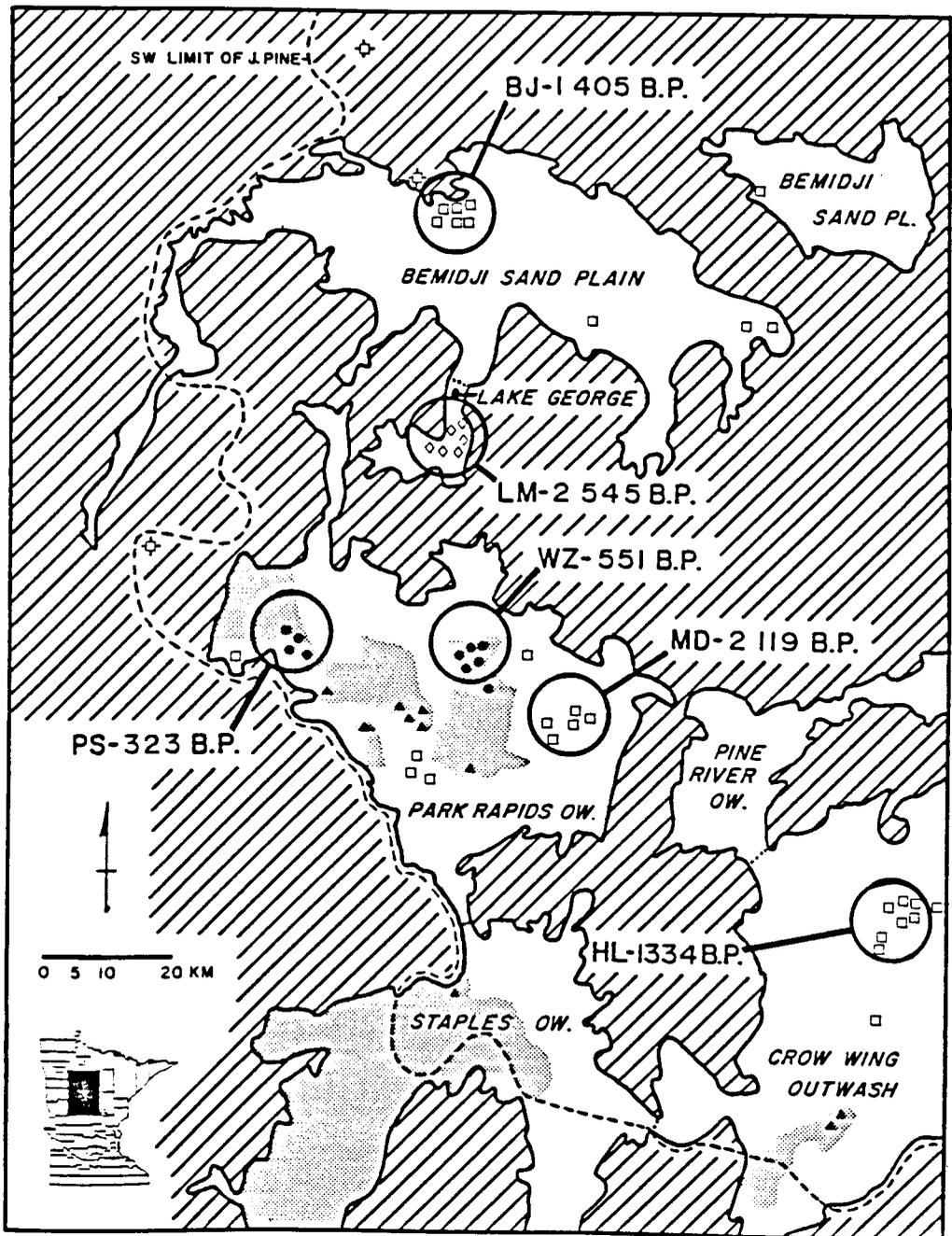


Figure 3.2. The location of paleoecological study sites, relevés, and major outwash plains of north-central Minnesota. The large circles show the location of the study sites, and the abbreviations are as follows: BJ, Big John Pond; LM, Lake Minnie; PS, Peterson Slough; WZ, Wentzel's Pond; MD, Mud Lake; and HL, Hostage Lake. After each site abbreviation is the date of jack pine forest establishment there (see Chapter 2). The small symbols show relevé locations as they occur on forest soils (open symbols) and relict-prairie soils (solid symbols and shaded areas). The symbol shapes correspond to Figures 3.3 and 3.5.

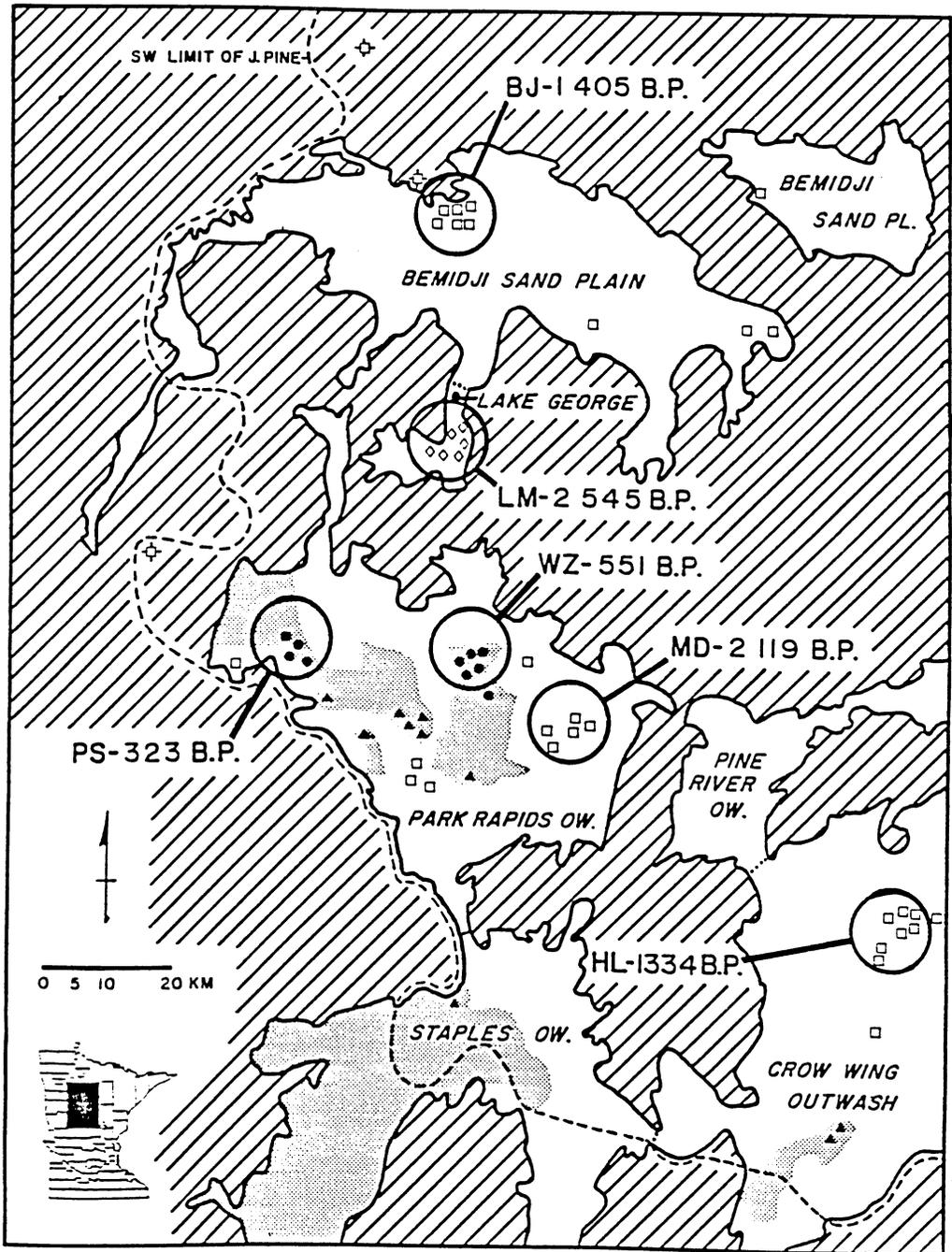


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contiguous strata, are: 1 = <0.1 m, 2 = 0.1-0.5 m, 3 = 0.5-2.0 m, 4 = 2-5 m, 5 = 5-10 m, 6 = 10-20 m. Within each life-form stratum, the coverage of each vascular species was estimated visually using the 7 standard Braun-Blanquet cover-abundance classes (Mueller-Dombois and Ellenberg 1974). The coverages of the common moss species were recorded as well.

Vascular species identification and nomenclature follow Fernald (1950) with the following exceptions: Quercus (Gleason and Cronquist 1963), Aster (Rosendahl and Cronquist 1949), Solidago (Rosendahl and Cronquist 1945), Viola (Russell 1957-1958), Gramineae (Allison 1959). Bryophyte nomenclature follows Ireland et al. (1980).

Codes for reliability of identification, indicating certainty at the family to variety levels, were assigned to the taxa recorded in each releve'. Only plants identified with equal certainty were used as a single entity in the numerical analyses. Groups of species that were indistinguishable for any reason (juveniles, fruits or flowers lacking, etc.) are indicated in Tables 3.2 and 3.B.1 (in back pocket). Whenever possible, a difficult specimen was identified by direct comparison with herbarium material and left as a voucher specimen (Appendix 3.B) in the University of Minnesota herbarium (152 species, 387 specimens).

Relevés were taken over a period of four years (1979-1982) in the late summer (July-September).

Soil Analysis

In each of the 29 releve' plots located near pollen sites (Fig. 3.2), soil samples were collected and analyzed to define the range of percent soil organic matter. Ten samples of the upper 18 cm of mineral soil (epipedon depth, Soil Survey Staff 1975) were taken with a soil probe 2 cm in diameter along a line at 10-m intervals. These soil samples were combined, homogenized, and then sieved (3-mm openings) to remove all but the finest rootlets. The weight loss of samples burned at 500° C was used to estimate the soil organic matter as percent dry weight. For these sandy soils, weight loss due to the decomposition of hydrated clays (see Black et al. 1965) is assumed to be negligible. Three replicates for each of the 29 samples were averaged; the coefficients of variation ranged from 0.26 to 4.91.

Numerical Analyses

Indirect-gradient analyses (Gauch 1982) were performed to examine the vegetational differences among the relevés. The relevés were classified floristically by two-way indicator-species analysis (TWINSPAN, Hill 1979a; Hill et al. 1975). The relevés were ordinated floristically by detrended correspondence analysis (DECORANA, Hill 1979b) and ordinated physiognomically by polar ordination (ORDIFLEX, Gauch 1977, Bray and Curtis 1957). Ordination scores and classification groupings were compared with releve' groups based upon their respective soil-mapping units. The patterns of soil-mapping

units along ordination axes and in classification groupings were then used to infer soil differences that may account for much of the vegetational variation among jack pine stands.

RESULTS AND DISCUSSION

Ordination and Classification

Floristic pattern.- Both the classification and the ordination indicate that jack pine stands growing on dark relict-prairie soils differ floristically from those growing on light forest soils (Fig. 3.3). Only five exceptions (3 light, 2 dark) prevent complete segregation of relevés into light-soil and dark-soil groups in the classification's first division. The same pattern appears in the ordination as well, with the dark-soil group of relevés having higher scores on the first axis. Further separation along the first axis of the ordination, as well as at division level 2 of the classification, is apparently related to soil texture in the rooting zone. For the dark-soil group, relevés where the rooting zone is loamy are separated from those having a sandy rooting zone. Nearly all of the relevés in the light-soil group are from the same soil-mapping unit, making further distinction by soil-mapping unit impossible. Within the light-soil group, relevés from stands in the Lake George area (Fig. 3.2) form a cohesive group at division level 3 of the classification and have the lowest first-axis scores in the ordination. Field

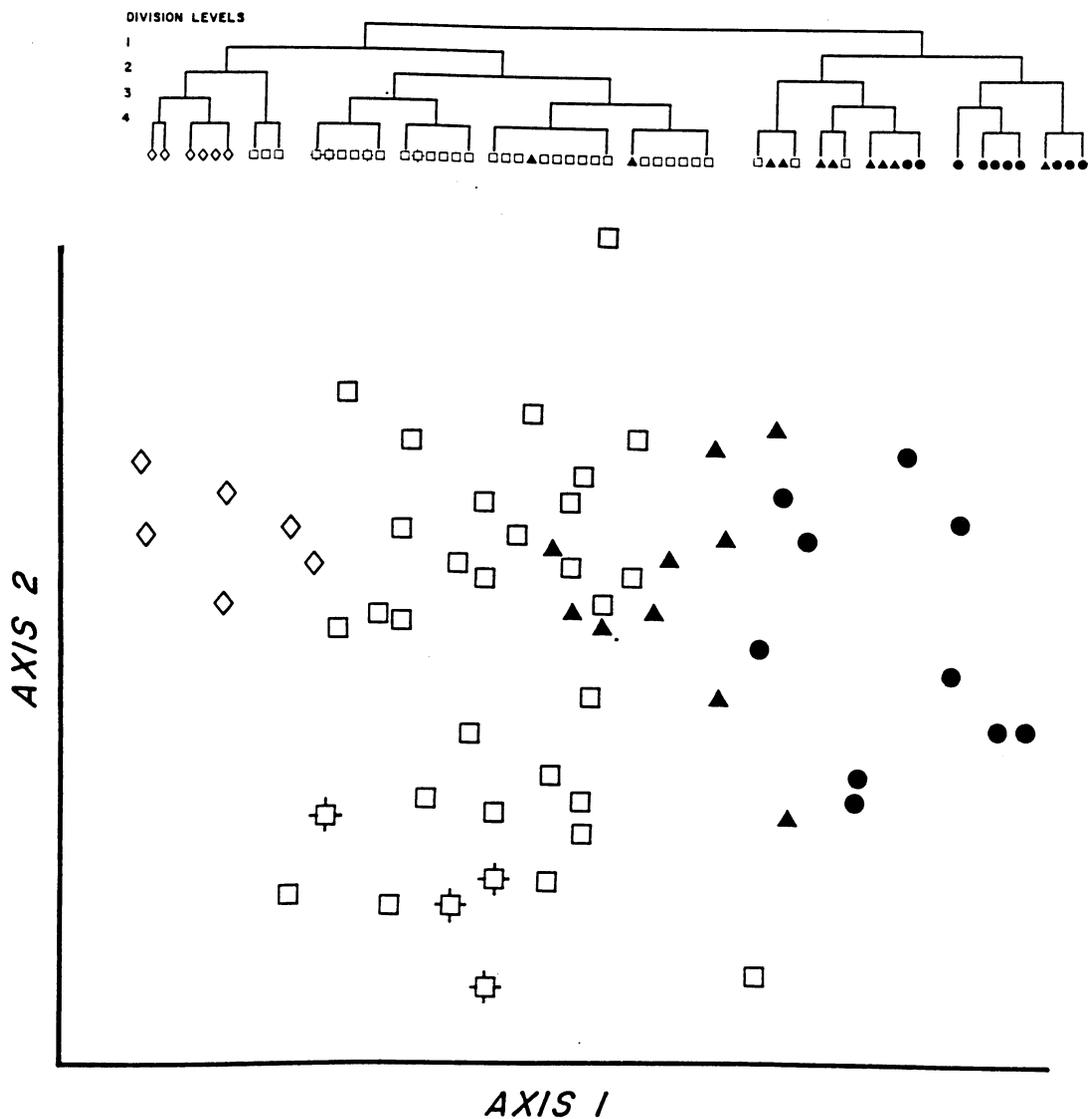


Figure 3.3. A two-way indicator-species analysis classification (above) and a detrended correspondence analysis ordination of 59 relevés from jack pine forests in north-central Minnesota. Open symbols represent relevés on light-colored forest soils as follows: diamonds, sandy outwash soils at Lake George; squares, sandy outwash soils not at Lake George; and crossed squares, loamy soils on till. Solid symbols represent relevés on dark-colored relict-prairie soils as follows: triangles, sandy outwash soils; circles, loamy outwash soils.

descriptions of the soils in each relevé plot suggest that the sands at Lake George are generally better-sorted and contain less silt and clay than the parent material of the other light-soil relevés. Thus the relevés at Lake George are distinct from the other members of the light-soil group, which are highly variable with respect to the parent-material sorting, topography, and soil-unit area. The second axis of the ordination results from this variability, as it separates mainly members of the light-soil group not at Lake George. Light-soil relevés with the lowest second-axis scores generally occur on ice-contact moraine or on smaller patches of outwash isolated by moraine, lakes, or peatlands.

The pattern of soil-mapping units in Figure 3.3 indicates that the numerical techniques effectively separate jack pine stands on light soils from those on dark soils. The principal difference between the light-soil and dark-soil mapping units is the amount of soil organic matter. In general, dark soils have more than 3% organic matter and light soils have less. To understand better the influence of soil organic matter on the understory composition and the rate at which it decreases under jack pine, I determined the percent of soil organic matter in the upper 18 cm of the soils for 29 relevés, that are evenly distributed around the six sites having fossil-pollen records (Table 3.1), and I plotted those percents against relevé ordination scores (Fig. 3.4). The amount of organic matter in dark-soil samples is more variable (2.0 - 4.5%) than that of light-soil

Table 3.1. The relationship among soil color, soil texture, soil-based units (see text), date of jack pine forest establishment (radiocarbon years B.P.), and percent soil organic matter near each pollen site. Also given are the probable soil series in the immediate vicinity of the pollen sites and the series' taxonomic placement. All radiocarbon dates are corrected for ^{14}C deficiency ("carbonate error," see Chapter 2) except for Lake Minnie (McAndrews, unpublished data).

COLOR	TEXTURE	SOIL-BASED UNIT	POLLEN SITE	DATE B.P.	ORGANIC MATTER	ASSOCIATED SOIL SERIES	TAXONOMIC PLACEMENT
light	sandy	Lake George	Lake Minnie	2545	1.48%	Menahga	Typic Udipsamment
light	sandy	other light	Mud Lake	2119	1.62%	Menahga	Typic Udipsamment
light	sandy	other light	Big John Pond	1405	1.77%	Marquette	Psammentic Eutroboralf
light	sandy	other light	Hostage Lake	1334	1.51%	Menahga	Typic Udipsamment
dark	sandy	sandy dark	none	----	-----	Hubbard	Udic Haploboroll
dark	loamy	loamy dark	Wentzel's Pond	551	2.71%	Dorset	Boralfic Udic Argiboroll
dark	loamy	loamy dark	Peterson Slough	323	4.10%	Arvilla or Verndale	Udic Haploboroll Udic Argiboralf

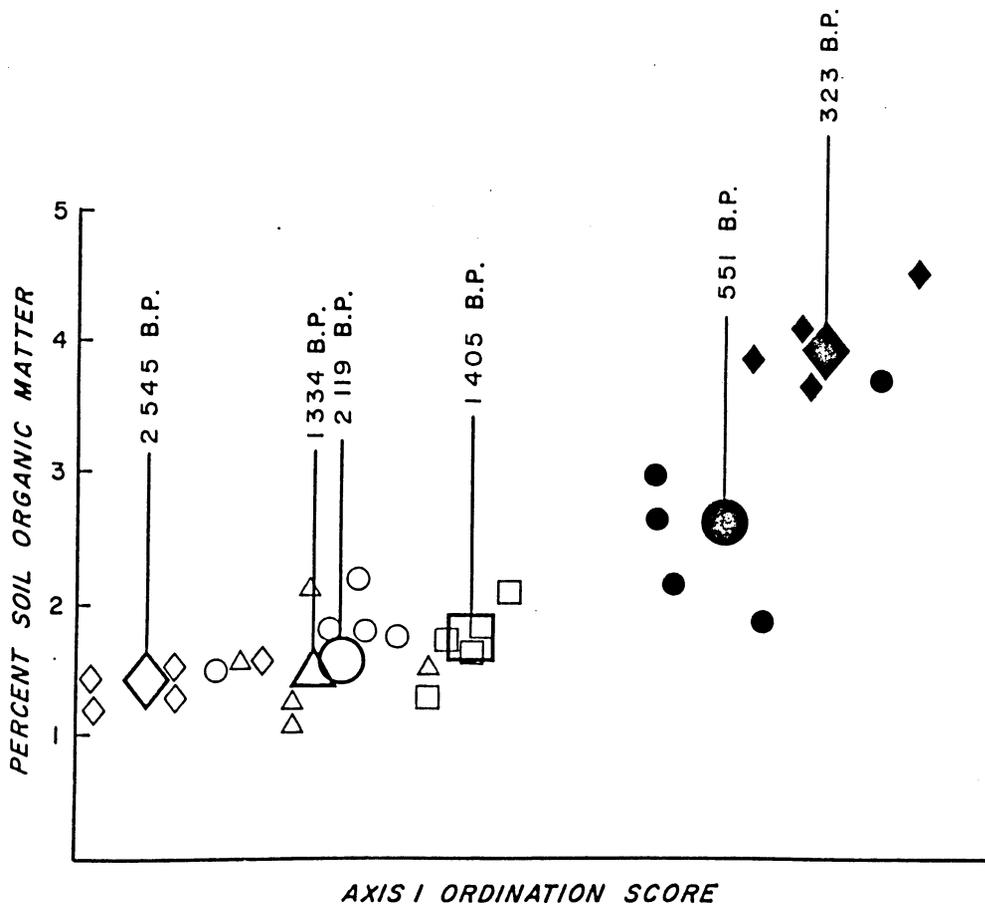


Figure 3.4. A scatter plot of percent soil organic matter and first-axis ordination scores (detrended correspondence analysis) for 29 relevés that occur in the immediate vicinity of six paleoecological study sites. Study site symbols are as follows: open diamonds, Lake Minnie; open triangles, Hostage Lake; open circles, Mud Lake; open squares, Big John Pond; solid circles, Wentzel's Pond; and solid diamonds, Peterson Slough. The corresponding large symbols are the centroids of the smaller ones, and the date of jack pine forest establishment is indicated above each centroid.

samples (1.2 - 2.2%). On sandy soils, organic matter declines from about 5% a few hundred years after jack pine invasion to about 2% after 1,000 years of jack pine occupation.

Physiognomic pattern.- For the polar ordination, relevés 52 and 58 were chosen as the first axis endpoints, because they were the most physiognomically distinct of the widely separated relevés in the floristic analysis. The separation of relevés by soil unit in this analysis (Fig. 3.5) is less clear than in the floristically-based ordination. Nevertheless, the separation of light-soil and dark-soil groups is apparent. Stands in the Lake George region again form a tight group, but the boundaries between the other soil-mapping units are more diffuse than in the floristic analysis. The relative influence of the ten physiognomic/life-form groups on the ordination can be inferred from Table 3.3 as the relevés are ranked by their first-axis ordination scores.

Inferred soil gradient.- The above analyses suggest that differences among jack pine forests are correlated with slight differences in soil organic matter (range, 1.0 - 4.5%) and that the greatest loss of organic matter occurs 500 -1000 years after the establishment of jack pine forest. Soil organic matter directly affects a number of soil properties that govern nutrient, water, and gas availability to plants, including cation-exchange capacity, moisture-retaining capacity, bulk density, and structure (Brady 1974). Soil organic matter is correlated with soil nitrogen, and in the

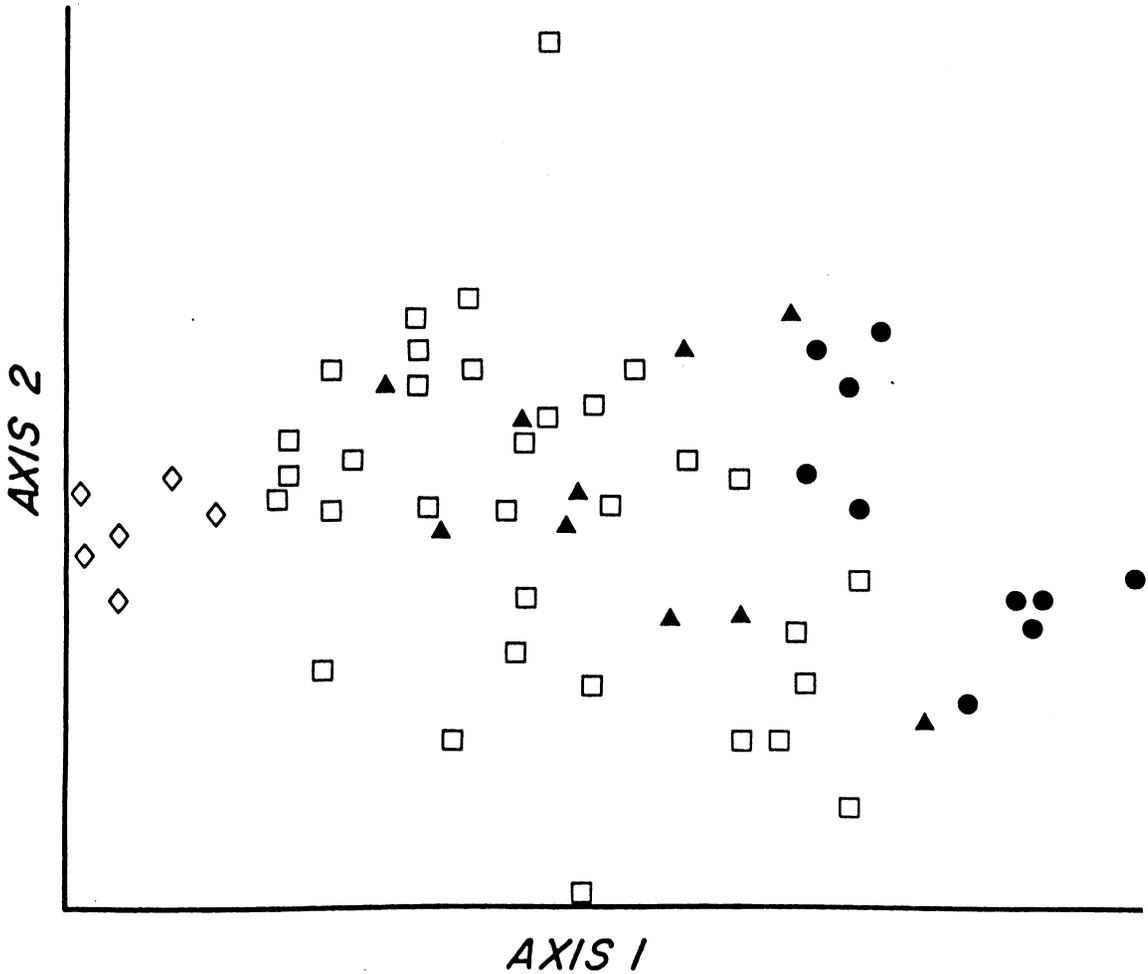


Figure 3.5. A polar ordination of 59 relevés from jack pine forests in north-central Minnesota. The ordination was based upon scores in ten physiognomic/life form classes. The symbols correspond with those of the floristically based ordination and classification (Fig. 3.3).

presence of divalent cations it can form organomineral complexes that serve to stabilize the small amounts of silt and clay in the upper horizons of sandy soils (Jenny 1980). Because soil organic matter affects so many soil properties and because it is correlated with the period of jack pine occupation (Fig. 3.4, Table 3.1), a gradient in soil organic matter must be considered environmentally complex and the correlated vegetation subject to historical complications that accompany long-term understory succession in jack pine forests. Soil organic matter may be particularly important in sandy soils with little silt and clay, inasmuch as organic matter influences soil properties much as does the fine-grained inorganic fraction.

Vegetation Patterns in Four Soil-based Units

Ranking the four soil-based units.- The ranking of the four soil-based units in Tables 3.2, 3.3, and 3.4 (Tables 3.2 and 3.4 in back pocket) represents a chronosequence of soil development as inferred from soil series descriptions for Hubbard and Wadena counties (McMiller et al. 1930, Elwell et al. 1926), from pollen diagrams for sites within the soil-based units (see Chapter 2), and from levels of soil organic matter (Table 3.1). Relevés on light forest soils were assigned to one of two soil-based units: (1) those on the well-sorted level outwash north of Lake George (Fig. 3.2), and (2) those on generally coarser and topographically rougher outwash. Relevés on dark relict-prairie soils were likewise assigned to one of two additional

soil-based units: (3) those with sandy rooting zones and (4) those with loamy rooting zones. Paleoeological study sites occur in three of the four soil-based units. Sites on light soils have been occupied by jack pine forests for more than 1,300 years, and sites on dark soils have supported stands of jack pine for less than 600 years (Table 3.1).

Stands at Lake George occur in the region with the longest record of jack pine forest occupation and with the lowest levels of soil organic matter; however, the range of soil organic matter levels on light soils is small (0.29%) in comparison to the range in periods of jack pine forest occupation (1,200-2,500 years). Thus the placement of the Lake George relevés at the extreme end of the ranking in Tables 3.2, 3.3, and 3.4 results mostly from the striking vegetational differences between stands at Lake George and stands on other light soils and is not related to major differences in chronology or to levels of soil organic matter.

For dark soils, the distinction between those with sandy rooting zones and those with loamy rooting zones may or may not reflect chronological differences. Although the vegetation of jack pine stands on sandy dark soils is intermediate between those on loamy dark soils and light soils (Figs. 3.3 and 3.5), no satisfactory paleoeological sites are available to establish a relative chronology. Where detailed soil surveys are available (Hubbard county, McMiller et al. 1930; Wadena county, Elwell et al. 1926) many of the sandy, dark soils are

the Nymore series, which is described as intermediate between the Hubbard series (a loamy dark soil) and the Menahga series (a sandy light soil). Also, if the loss of soil organic matter with time involves the destruction of organomineral complexes and consequently the loss of silt and clay-sized particles, these sandy, dark soils may well have been occupied by forest for a longer period of time.

Physiognomy.- Relevés were assigned to their respective soil-based unit, and within that unit they are ranked by their first-axis ordination scores (Fig. 3.5). Classes that show similar cover-abundance trends were placed in one of three physiognomic/life-form groups (Table 3.3, groups A-C). Members of Group A (all evergreen) are more abundant and more frequent on light soils. Conifer seedlings (1-2 m) and saplings (2-10 m) are much more common on light soils, but they do occur on sandy dark soils. Moss and lichen cover ranges from nearly continuous on light soils to less than 50% on dark soils. Broadleaf evergreen species, which typically grow among the mosses, show a similar pattern. Broadleaf deciduous (woody) species (Group B) occur in nearly all jack pine stands, but their coverage and heights are much greater in the dark soil groups. The height and cover of deciduous shrubs is the most striking physiognomic difference among jack pine stands, and they provide the most consistent field estimates of the period of jack pine occupation and soil organic matter. Graminoids have slightly greater coverages on dark soils (Group B), and forbs exhibit no obvious trend (Group C).

Table 3.3. Phytosociological table of relevés from *Pinus banksiana* forests in north-central Minnesota. Relevé order was fixed by (1) assignment to one of four soil-based units (Table 3.1) and by (2) ordination scores from Figure 3.5. Table values are for cover-abundance: 1, cover < 1%; 2, cover 1-5%; 3, cover 5-25%; 4, cover 25-50%; 5, cover 50-75%; 6, cover 75-100%. Physiognomic/life-form classes showing similar presence-abundance patterns were grouped (A-C) to facilitate discussion.

Soil-based unit	-LAKE- GEORGE	-----OTHER----- -----LIGHT SOILS-----										---SANDY--- DARK SOILS	---LOAMY--- DARK SOILS
Relevé number	524353 896072	5 114 54	4 5 33	1324 244 4 3 32 133	70544 30561 79681 189	12231 21121	25425 15455	42117 53265	70703 64812				
GROUP A													
Needleleaf evergreen 1-2 m	222322	22112 22222	21.1. 2.1.1	.211. 1.1.. ...	22.1.1..							
Needleleaf evergreen 2-10 m	222..1	22... .2.1.	2..11 1....	.212. 2..	11..2 .22..	2.1..							
Lichen-Moss	655465	63456 54545	66545 34334	33434 44434 133	33422 221..	34324 .2222							
Broadleaf evergreen	443432	33322 43323	22232 22223	23222 11222 .23	23232 2.11.	23211 1.1..							
GROUP B													
Graminoid	336446	53656 44424	26566 53663	54335 63653 633	65556 65465	66535 66322							
Broadleaf deciduous 1-2 m	444353	33454 44434	44443 63433	53455 55555 565	44543 56544	65645 46666							
Broadleaf deciduous 2-10 m	1...2 22212	33233 22223	23323 32333 244	22223 22334	44545 44566							
Broadleaf deciduous > 10 m1. 2...11 .413. .13.3 ..3	.222. 23212	.32.2 24223							
GROUP C													
Needleleaf evergreen > 10 m	555665	55655 55565	66656 66566	54655 65555 555	65655 55565	55555 44555							
Forbs	324335	46334 43364	43443 33335	33543 34333 333	33343 33342	34443 42533							

Different management practices have probably differentially influenced the physiognomy of jack pine stands on dark and light soils. The dark soils are valuable agriculturally and the jack pine stands are scattered woodlots (most < 50 ha) among fields. Jack pine stands on light soils have been logged to varying degrees but are essentially continuous, often covering many square kilometers. Logging has probably affected the understory composition less than the division of once continuous forest into scattered woodlots. The effect of this subdivision is to reduce fire frequency dramatically and to favor the reproduction of oak (Quercus macrocarpa and Q. borealis) rather than jack pine. Present woodlots have a jagged supercanopy of senescent jack pine with a continuous subcanopy of oak. Many stands have taken on this appearance between the time of aerial photographs in 1969 and my field checks in 1979-1982. Although these senescent stands of jack pine were not sampled, at least some of the extensive development of shrubs and deciduous trees in the sampled stands of jack pine on dark soils (Table 3.3) is probably owing to reduced fire frequency and not to soils exclusively. However, early land surveyors (AD 1855-1880, see Chapter 1) and H.L. Hansen (1946, and Hansen's personal field notes) describe a well-developed shrub layer and a mixed canopy of deciduous trees and jack pine in stands on dark soils, in contrast to more open, monotypic stands of jack pine on light soils. Thus, my relevés are probably representative of presettlement stands on dark soils; however, reduced fire frequency on dark soils

has probably sharpened any natural vegetational differences between stands on dark and light soils.

Associated tree species.- Except for occasional jack pine seedlings, conifers are unimportant in the understory of jack pine stands on dark soils as they occur in < 10% of the relevés. Seedlings and saplings of Pinus resinosa, Abies balsamea, and Picea glauca frequently occur in the understory of jack pine stands on light soils, but only Pinus resinosa commonly shares the canopy (Table 3.4, group A). These occasional Pinus resinosa trees are typically old, having survived selective logging or fires, which initiated the development of the surrounding younger jack pines. Picea glauca and Abies balsamea are common understory components near poorly drained portions of some outwash plains, particularly along the margins of abandoned drainage channels (of glacial origin) that are now filled with peat. Pinus strobus does not usually occur with jack pine on coarse-textured soils (Jacobson, 1979), but it occasionally grows with jack pine on light soils (Table 3.4, group B).

Stands of jack pine on light soils other than those at Lake George often have deciduous taxa in the understory (58% of the relevés). Acer rubrum, Quercus macrocarpa, and Fraxinus pensylvanica occur as seedlings and saplings but rarely share the canopy with jack pine (Table 3.4, group B). Betula papyrifera is the only species that regularly reaches the canopy on light soils, to which it is restricted. betula papyrifera was recorded in only one relevé on dark

soils as 3 seedlings (Table 3.4). During the four field seasons, I saw only two Betula papyrifera trees on undisturbed dark soils, but they do occur on eroded slopes around lakes and in gravel pits located within the dark-soil regions.

In contrast to the absence of deciduous trees on light soils, Quercus borealis, Quercus macrocarpa, and Populus tremuloides frequently occur on dark soils (80% of the relevés in Table 3.4, group C). The simplest explanation for increased canopy mixture on dark soils is that dark soils, by virtue of having higher amounts of soil organic matter (Table 3.1), are richer in nutrients and retain more water than light soils, thereby favoring deciduous trees. An alternative hypothesis is that the Quercus borealis, Q. macrocarpa, and Populus tremuloides on dark soils are relicts of former woodlands that jack pine has recently invaded (see Chapter 2).

Jack pine regeneration.- Nearly all jack pine trees in the study are open-coned (Schoenike et al. 1959, Schoenike 1962), and the stands are typically multi-aged. Seedlings occur in all jack pine stands except on loamy dark soils (Tables 3.2 and 3.4). Jack pine seedlings are common in open areas on dark loamy soils, such as along roadsides and in abandoned fields, suggesting that dense shade from the thick shrub layer (Table 3.3) inhibits seed germination or seedling development on loamy, dark soils.

A hypothesis of allelopathy is an alternative to the shade hypothesis. Water extracts of some species occurring with jack pine

inhibit or enhance seed germination (Brown 1967). Prunus serotina, which occurs in seven of the ten relevés on loamy, dark soils, is a strong inhibitor (Table 3.2, groups F and G). Jack pine seedlings do not occur on loamy, dark soils. Also, jack pine seedlings on light soils or sandy, dark soils are often associated with Oryzopsis pungens (Table 3.2, group D), which Brown found to enhance jack pine seed germination. Other inhibitors however, (Gaultheria procumbens, Prunus pumila, Solidago juncea) do tend to co-occur with jack pine seedlings (Table 3.2).

Shrubs.- Shrub height and coverage gradually change along the soil organic-matter gradient, with stands on loamy dark soils having the tallest and most continuous shrub canopy. This gradual change, which occurs in the broadleaf deciduous physiognomic class (Table 3.3) is largely responsible for the diffuseness of the boundaries of the soil-based units in Figure 3.5. This pattern is complicated because the broadleaf deciduous physiognomic class includes juvenile trees that by themselves show the same pattern (Table 3.4, group C). The height and coverage of both shrubs and juvenile trees are probably influenced by levels of soil organic matter.

Soil organic matter may limit the distribution of some shrub species. The species that are restricted to light soils (Prunus pumila and Ceanothus ovatus) or that are more common on them (Ribes cynosbati, Rubus allegheniensis, and Corylus cornuta) occur in fewer than 25% of the relevés on soils with more than 2% soil organic matter

(Table 3.2). Amorpha canescens, Spiraea alba, Crataegus sp., Symphoricarpos occidentalis, and Viburnum rafinesquianum are absent from Lake George (1.48% soil organic matter) and rarely occur on soils having less than 2% soil organic matter.

The coverages of Vaccinium angustifolium and Corylus americana are influenced by levels of soil organic matter (Table 3.2). Relevés having a continuous cover of Vaccinium angustifolium have less than 1.59% soil organic matter (average 1.38%), whereas relevés with a continuous cover of Corylus americana have more than 2.69% (average 4.42%).

Groundlayer species.- Many groundlayer species are also associated with particular amounts of soil organic matter (Table 3.2). Shading by tall shrubs rather than levels of soil organic matter may be primarily responsible for the correlation between soils and groundlayer species, however. As is true for Pinus banksiana seedlings and Betula papyrifera, some groundlayer species (mostly Compositae and Gramineae) rarely occur on dark soils, except in open disturbed areas. Agrostis scabra, Bromus kalmii, Oryzopsis pungens, Solidago nemoralis, and Pteridium aquilinum are examples of these species. This pattern also applies to some common species that occur in most light-soil relevés and in slightly more than 20% of the dark-soil relevés (and therefore do not appear in Table 3.2). Agropyron trachycaulum, Muhlenbergia glomerata, Aster laevis, Solidago hispida, and Lithospermum canescens are examples of this latter group.

Soil conditions probably control the distribution of species not showing the above pattern. In particular, the broadleaf evergreens are nearly restricted to either light soils (e.g. Epigaea repens, Pyrola virens, Pyrola rotundifolia, Linnaea borealis) or to light soils plus sandy dark soils (e.g. Arctostaphylos uva-ursi, Gaultheria procumbens, Chimaphila umbellata). That broadleaf evergreens and conifer seedlings (other than jack pine) rarely occur on dark soils under any circumstance (shaded or not) suggests that these plants grow or compete better on poorer soils, which is the situation described for evergreens elsewhere (Monk 1966, Small 1973).

Groundlayer species probably limited by light are species that commonly occur in prairies and open woodlands west of the limit of jack pine in north-central Minnesota. Some of these species are Agropyron trachycaulum, Bromus kalmii, Koeleria cristata, Muhlenbergia mexicana, Stipa spartea, Aster azureus, Aster ptarmicoides, Helianthus laetiflorus, Liatris aspera, Liatris ligulistylis, Lilium philadelphicum, Phlox pilosa, Zizia aptera, Monarda fistulosa, Ceanothus ovatus, and Lithospermum canescens. In the absence of paleoecological information, the presence of such prairie plants has been used to infer the former presence of prairie in regions now forested (Transeau 1935). If these species are prairie relicts, they should be more abundant in the most recently established jack pine forests. This is not the case, however. All of the above species occur more frequently in open jack pine forests on light soils (Table

3.2), which were last occupied by prairie about 1,000-2,500 radiocarbon years B.P. These species are rare or absent from jack pine stands on dark soils that were last occupied by prairie less than 1000 radiocarbon years B.P. If a dense shrub canopy similar to that of jack pine stands on dark soils also occurred in the early stages of jack pine forest development throughout north-central Minnesota, the above species would probably not have survived the intermediate shrubby stage to later become abundant in open jack pine stands now growing on light soils. Other heliophytes, such as Amorpha canescens, Veronicastrum virginianum, Polygonum convolvulus, Thalictrum dasycarpum, and Symphoricarpos occidentalis, are more common on dark soils and may be relicts, as was suggested for the co-occurring deciduous trees.

SUMMARY

The distribution and abundance of some species in Minnesota jack pine forests are correlated with soil-mapping units. Ordination and classification produce a ranking and hierarchy of releve' soil-mapping units that represent a gradient of soil organic matter and perhaps texture. Based on vegetation, the three most common soil-mapping units in the study area have the following order: (1) light-colored forest soils with a sandy rooting zone, (2) dark-colored relict-prairie soils with a sandy rooting zone, and (3) dark-colored relict-prairie soils with a loamy rooting zone. The amount of soil organic matter is a

function of the time period of jack pine occupation (Figure 3.4). The loss of soil organic matter is most rapid during the first 500-1,000 years following the establishment of jack pine on prairie.

The present spatial patterns in the vegetation of jack pine forests are possibly homologous to a long-term forest succession. This succession may apply to other areas where conifers have been recently established (or planted) on relatively organic sandy soils.

Prairie and deciduous woodlands occupied the outwash plains prior to the establishment of jack pine. One might assume that species commonly found in prairies or deciduous woodlands should occur more frequently in more recently established jack pine forests. This pattern pertains to only a handful of understory species, however. In fact, prairie plants are more common in jack pine stands that have been established for longer periods of time and have a poorly developed shrub layer. Thus these species are simply heliophytes that can grow equally well in prairies or open jack pine forests.

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APPENDIX 1.A

COLE'S COEFFICIENTS

Table 1.A.1 Table of Cole's coefficients for common bearing-tree taxa.

	Sugar maple	Birch	Ash	Black ash	Ironwood	Aspen	Balsam poplar	Red oak
Birch	-0.025
Ash	+0.103	-0.328
Black ash	-0.121	+0.083	+0.035
Ironwood	+0.371**	-0.022	+0.027	-1.000
Aspen	-0.310*	+0.172**	-0.402	-0.281	-0.255	.	.	.
Balsam pop	-1.000	-0.469	+0.019	+0.038	+0.030	+0.299	.	.
Red oak	+0.109**	+0.176**	-1.000	-1.000	-0.090	+0.065	+0.064	.
Bur oak	+0.037	-0.082	-0.139	+0.149	+0.118	+0.142*	+0.041	+0.060
Basswood	+0.301**	-0.144	+0.220**	+0.124*	+0.149**	-0.388*	-0.049	+0.073*
Elm	+0.107**	-0.168	+0.465**	+0.437**	+0.125	-0.366**	+0.010	+0.017
Balsam fir	-0.241	+0.128	+0.038	-1.000	-1.000	-0.193	+0.012	-1.000
Jack pine	-0.974**	-0.624**	-0.917**	-1.000**	-1.000**	-0.612**	-0.607*	-0.722**
Red pine	-0.851**	-0.296**	-0.880**	-1.000*	-1.000*	-0.512**	-1.000**	-0.553**
White pine	-0.091	+0.052*	-0.325	-0.621	-0.673	-0.086	-0.200	+0.122**
Spruce	+0.004	+0.028	-0.022	+0.100	-1.000	+0.168*	+0.011	-1.000*

[continued on next page]

* P < 0.05, ** P < 0.01

[Table 1.A.1 continued]

	Bur oak	Basswood	Elm	Balsam fir	Jack pine	Red pine	White pine
Birch
Ash
Black ash
Ironwood
Aspen
Balsam pop
Red oak
Bur oak
Basswood	+0.115**
Elm	+0.143**	+0.266**
Balsam fir	-0.374	+0.054	+0.003
Jack pine	-0.681**	-1.000**	-1.000**	-0.819**	.	.	.
Red pine	-0.723**	-1.000**	-0.863**	-0.476	+0.137**	.	.
White pine	-0.309	-0.785*	-0.228	+0.023	-0.656**	+0.197**	.
Spruce	-0.499	+0.011	+0.008	+0.320**	-0.831**	-0.581**	-0.084

* P < 0.05, ** P < 0.01

APPENDIX 2.A

CORING RECORDS

CORE LOGS FOR STUDY SITES

Mud Lake, Hubbard County, Minnesota

Access: Hemerick's resort on east side of lake

Date: 29 March 1980

Water depth: 8.27 m, drives in meters below water surface

DRIVE-DEPTH	RECOVERY	REMARKS
8.00 - 10.30	2.20	Core in plastic tube, stored and extruded vertically
10.30 - 11.30	1.00	Firm, homogeneous gyttja
11.30 - 12.30	1.00	"
12.30 - 13.30	1.00	"
13.30 - 14.30	.99	Firm, mottled (olive and dk. brown) gyttja
14.30 - 15.30	1.00	"
15.30 - 16.30	.99	"
16.30 - 17.30	1.00	" , dark banding at 16.60, 16.75 - 16.85
17.05 - 18.03	.98	25 cm recored, bottom 10 cm silty with trash layer of moss and detritus, out of rods

Big John Pond, Beltrami County, Minnesota

Access: County road at pond

Date: 15 February 1981

Water depth: 0.60 m, drives in meters below water surface

DRIVE-DEPTH	RECOVERY	REMARKS
0.40 - 1.40	.76	Core in plastic tube, stored and extruded vertically
1.40 - 2.40	.96	
2.40 - 3.40	.80	lost portion from bottom
3.40 - 4.13	.56	"
4.13 - 5.03	.76	banding at bottom
5.06 - 5.56	.48	banding and two sand lenses
5.56 - 5.65	.09	sand
5.62 - 6.12	.47	sand, 3 cm recored
5.82 - 6.46	.34	sand, 30 cm recored

Hostage Lake, Crow Wing County, Minnesota

Access: Logging road north from E/W county road south of lake

Date: 7 March 1981

Water depth: 1.51 m, drives in meters below water surface

DRIVE-DEPTH	RECOVERY	REMARKS
1.20 - 2.90	1.44	Core in plastic tube, stored and extruded vertically
2.90 - 4.20	1.27	" , 20 cm hiatus
4.40 - 5.40	1.00	detrital gyttja
5.40 - 6.40	1.00	" , banded below
6.40 - 7.40	1.00	" , banded above
7.40 - 8.40	.94	carbonate band near top, silty towards bottom
8.40 - 9.40	.95	10 cm organic sed, 4 cm trash layer, sand below
9.31 - 10.19	.88	sand, 9 cm recored

Wentzel's Pond, Hubbard County, Minnesota

Access: trail leading north from Wenzel residence south of pond

Date: 30 March 1980

Water depth: 1.57 m, drives in meters below water surface

DRIVE-DEPTH	RECOVERY	REMARKS
1.50 - 3.20	1.66	Core in plastic tube, stored and extruded vertically, core in different hole than Livingstone
1.30 - 2.30	.50	Livingstone core, lost top 20 cm of flocculent sed.
2.30 - 3.30	.96	detrital gyttja, bottom 25 cm dark (humified ?)
3.30 - 4.30	.91	peaty top, black organic silt at bottom sand lenses at 3.25-3.80, 3.94, 4.02
4.30 - 4.68	.29	silty, detrital gytja, sand lenses at 4.40 and 5.52
4.68 - 5.18	.44	pebble at 4.68, 3 cm hiatus below
5.21 - 5.81	.52	sand lens 5.44, 5.54-5.81 inorganic silt

Peterson Slough, Becker County, Minnesota

Access: Peterson residence east of slough

Date: 16 February 1981

Water depth: 3.90 m, drives in meters below water surface

DRIVE-DEPTH	RECOVERY	REMARKS
3.70 - 5.35	1.32	Core in plastic tube, stored and extruded vertically
5.35 - 6.35	.99	gyttja
6.35 - 7.35	.98	"
7.35 - 8.35	1.00	"
8.35 - 9.35	.80	" , two lenses of wood chips (beaver ?)
9.35 - 10.35	.95	"
10.35 - 11.35	1.00	silty gyttja
11.35 - 12.33	.83	" , with fine sand
12.33 - 13.33	.94	" , "
13.33 - 14.22	.81	banded silts
14.24 - 14.98	.67	4 cm recored, carbonate band above, dark organic below
14.98 - 15.42	.33	4 cm recored, organic with silt bands
15.38 - 15.67	.29	4 cm recored
15.67 - 16.00	.26	banded silts to sand and gravel

Table 2.A.1. Coring sites on relict-prairie soils investigated, but not used in the study. The site names indicate ownership except for Shinker Lake, Lake Moran, and unnamed sites.

SITE	LOCATON	WATER DEPTH	SEDIMENT RECOVERED	REMARKS
Sites near Peterson Slough and the Fishhook and Shell prairies				
unnamed	NW of SE of S.22 T.141 N, R.37 W	< 0.5	none	highly organic, cumulic soil
unnamed	SW of NW of SE of S. 22 T.141 N, R.37 W	< 0.5	none	highly organic, cumulic soil
Kastama pond	SW of NE of SE of S. 17 T.141 N, R.37 W	0.9	none	gravel bottom, wet during the 1930' drought
Peterson pond	SE of SW of SE of S. 2 T.140 N, R.37 W	2.4	15 cm calc. gyttja over 2.3 m sedge peat	small dam at east end has raised lake level, basin appears natural
Crandall pond(s)	N of NE of S. 30 T.140 N, R.35 W	< 0.5	----	dry during 1930's drought, not cored
Lake Moran	NW of SE of S. 14 T.139 N, R.35 W	4.7	13.3 m limnic sed.	silty pine zone at base, pollen diagram complete to 6 m, one radiocarbon date

[continued on next page]

[Table 2.A.1 continued]

Sites near Wentzel's Pond and the Hubbard prairie

Gruis pond(s)	NE of SW of SE of S. 11 T.140 N, R.37 W	1.2	1.2 m humified detrital gyttja	sed. over black, organic silt and sand, 3 ponds to NE were dry during the 1930's drought
Hemmenway slough	SW of SW of SE of S. 10 T.139 N, R.34 W	2.1	60 cm detrital gyttja	sed. over black, organic silt and sand
unnamed	SW of NW of SW of S. 34 T.139 N. R.34 W	1.9	none	mat of macrophyte remains on sand bottom
Shinker Lake	NW of NW of S. 31 T.140 N, R.33 W	4.0	7.4 m limnic sed.	sed. over sand and gravel, raw smear counts show lower pine zone

APPENDIX 2.B

POLLEN AND SPORE COUNTS

Peterson Slough, Becker County, Minnesota

COUNTS OF POLLEN AND SPORES

SYM	VARIABLE	DEPTH OF SAMPLE (CM)						
		0	30.	50.	60.	80.	100.	120.
.	MICROSPHERE	229.0	173.0	145.0	141.0	151.0	136.0	173.0
A	ALNUS CF. RUGOSA	5.0	17.0	6.0	5.0	8.0	7.0	8.0
B	BETULA	11.0	45.0	37.0	28.0	34.0	28.0	26.0
C	CORYLUS	0	4.0	3.0	2.0	13.0	1.0	2.0
D	DRYOPTERIS-TYPE	0	0	0	0	0	0	0
E	PINUS BANKSIANA/RESINOSA	21.8	89.0	45.0	56.5	12.0	35.5	29.5
F	FRAXINUS NIGRA-TYPE	0	3.0	2.0	3.0	0	2.0	0
G	POACEAE	3.0	19.0	12.0	12.0	16.0	10.0	16.0
H	PINUS STROBUS	6.7	39.5	20.5	45.5	18.0	68.5	30.5
I	PICEA	8.5	13.0	12.0	8.0	8.5	5.5	7.5
J	THUJA-TYPE	0	11.0	2.0	2.0	2.0	1.0	0
K	CHENOPODIUM-TYPE	4.0	3.0	1.0	4.0	1.0	1.0	2.0
L	LARIX	1.0	3.0	1.5	1.0	3.0	3.0	2.0
M	AMBROSIA	10.0	17.5	11.0	5.0	9.0	1.0	1.0
N	FRAXINUS PENNSYLVANICA-TYPE	1.0	0	1.0	7.0	2.0	2.0	3.0
O	OSTRYA-TYPE	8.0	6.0	9.0	10.0	5.0	10.0	9.0
P	PINUS UNDIFFERENTIATED	63.5	111.0	142.5	109.0	71.0	115.0	77.5
Q	QUERCUS	30.0	45.0	18.0	43.5	54.5	46.0	49.0
R	ARTEMISIA	5.0	17.0	14.0	13.5	7.5	26.0	5.0
S	SALIX	3.0	9.0	3.0	2.5	2.0	0	3.0
T	TILIA	1.0	0	0	1.0	0	1.0	3.0
U	ULMUS	6.0	13.0	5.0	9.0	7.0	9.0	5.0
V	TUBULIFLORAE UNDIFF.	5.0	8.0	10.0	10.0	4.0	4.0	1.0
W	UNKNOWN OR RARE	0	4.0	2.0	1.0	1.0	3.0	1.0
X	INDETERMINABLE POLLEN	17.0	5.0	7.0	5.0	5.0	8.0	5.0
Y	CYPERACEAE	8.5	9.0	7.0	9.5	13.0	9.0	7.0
AB	ABIES	0	1.0	.5	2.5	3.5	0	1.5
AC	ALNUS CF. CRISPA	1.0	1.0	3.0	2.0	1.0	0	1.0
AE	ANEMONE-TYPE	0	0	0	0	0	0	0
AI	ACER SACCHARINUM-TYPE	0	0	0	0	0	0	0
AM	AMORPHA	0	0	0	0	0	0	1.0
AN	ACER NEGUNDO-TYPE	3.0	0	1.0	0	0	0	1.0
AR	ACER RUBRUM	0	0	0	1.0	1.0	0	0
AS	ACER SACCHARUM	0	0	0	0	2.0	0	0
CA	CARYA	0	0	0	0	0	0	0
CZ	CEREALIA CF. AVENA	1.0	2.0	0	0	0	0	0

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[Peterson Slough pollen counts continued]

DZ	ZIGADENUS	0	0	0	0	0	0	0
EQ	EQUISETUM	0	0	0	0	0	3.0	0
GA	GALIUM	0	0	0	0	0	1.0	0
HU	HUMULUS-TYPE	1.0	0	0	0	0	0	0
IC	IVA CILIATA-TYPE	0	1.0	0	0	0	0	0
IX	IVA XANTHIFOLIA-TYPE	0	2.0	1.0	1.0	1.0	2.0	0
JC	JUGLANS CINEREA-TYPE	0	0	0	0	0	0	0
LM	LEMNA	0	0	0	0	0	1.0	0
MO	MORUS	0	0	0	1.0	0	0	0
MR	MYRICA	0	0	0	0	0	0	0
MY	MYRIOPHYLLUM EXALBESCENS-TYPE	0	1.0	0	0	0	0	0
NS	NYSSA	0	0	0	0	0	0	0
NU	NUPHAR	0	0	0	0	1.0	0	0
NY	NYMPHAEA	0	0	0	0	0	0	1.0
OS	OSMUNDA CLAYTONIANA	0	1.0	0	0	0	0	0
PB	POPULUS BALSAMIFERA-TYPE	0	0	0	0	0	1.0	0
PL	PLATANUS	0	0	0	0	1.0	0	0
PS	PETALOSTEMUM CANDIDUM-TYPE	0	0	0	0	0	0	0
PT	POPULUS TREMULOIDES-TYPE	1.0	14.0	2.0	2.0	7.0	0	5.0
QN	XANTHIUM	0	0	0	0	0	0	0
RH	RHUS	0	0	0	0	1.0	0	1.0
RO	ROSACEAE	0	0	0	2.0	0	0	0
SF	SPHAGNUM	0	0	0	0	0	0	0
SL	SALSOLA KALI	0	3.0	0	0	0	0	0
SP	SPARGANIUM-TYPE	0	0	0	0	1.0	0	0
SR	SARCOBATUS	0	0	0	0	0	0	0
TH	THALICTRUM	1.0	1.0	1.0	1.0	0	1.0	0
TR	PTERIDIUM-TYPE	0	2.0	0	1.0	0	1.0	0
TS	TSUGA	0	0	0	0	1.0	0	0
TY	TYPHA LATIFOLIA	0	1.0	0	0	0	0	0
UM	UMBELLIFERAE	0	0	0	0	0	1.0	0
UP	POTAMOGETON (EUPOTAMOGETON)	1.0	0	4.0	1.0	4.0	7.0	1.0
UR	URTICA-TYPE	0	0	0	0	1.0	0	0
VL	VIBURNUM LENTAGO	0	0	0	0	0	0	1.0
VT	VITIS	0	0	0	0	0	0	0
WH	HYPERICUM	0	2.0	0	0	0	0	0

Peterson Slough, Becker County, Minnesota

COUNTS OF POLLEN AND SPORES

SYM	VARIABLE	DEPTH OF SAMPLE (CM)						
		150.	200.	250.	300.	350.	400.	450.
.	MICROSPHERE	93.0	117.0	151.0	131.0	115.0	125.0	69.0
A	ALNUS CF. RUGOSA	11.0	11.0	21.0	16.0	13.0	27.0	16.0
B	BETULA	26.0	41.0	60.0	37.0	65.0	24.0	16.0
C	CORYLUS	6.0	4.0	14.0	5.0	5.0	5.0	1.0
D	DRYOPTERIS-TYPE	1.0	0	0	0	0	0	0
E	PINUS BANKSIANA/RESINOSA	34.0	7.1	5.0	9.5	3.0	.8	1.4
F	FRAXINUS NIGRA-TYPE	5.0	1.0	5.0	1.0	1.0	1.0	2.0
G	POACEAE	20.0	11.0	29.0	25.0	26.0	57.0	33.5
H	PINUS STROBUS	59.5	5.9	30.0	26.5	4.5	3.2	6.1
I	PICEA	10.5	14.0	8.0	4.0	3.5	2.0	1.0
J	THUJA-TYPE	1.0	1.0	3.0	3.0	1.0	3.0	3.0
K	CHENOPODIUM-TYPE	2.0	0	2.0	7.0	4.0	7.5	6.0
L	LARIX	4.5	1.0	2.0	3.0	2.5	0	0
M	AMBROSIA	5.0	21.0	13.0	4.0	12.0	10.0	16.0
N	FRAXINUS PENNSYLVANICA-TYPE	0	3.0	5.0	4.0	2.0	4.0	0
O	OSTRYA-TYPE	10.0	11.0	26.0	16.0	24.0	22.0	2.0
P	PINUS UNDIFFERENTIATED	75.5	69.0	63.5	39.0	15.0	16.0	21.0
Q	QUERCUS	55.0	53.5	78.5	80.0	64.0	52.5	39.5
R	ARTEMISIA	9.5	21.0	34.5	19.0	24.0	45.5	32.5
S	SALIX	0	2.0	3.0	5.0	2.0	3.0	3.0
T	TILIA	0	2.0	1.0	1.0	2.0	0	0
U	ULMUS	8.0	4.0	9.0	12.0	12.0	3.0	2.0
V	TUBULIFLORAE UNDIFF.	13.0	5.0	10.0	9.0	9.5	12.0	9.0
W	UNKNOWN OR RARE	1.0	2.0	2.0	2.5	1.0	2.0	0
X	INDETERMINABLE POLLEN	12.0	17.5	16.5	10.0	19.0	26.0	8.5
Y	CYPERACEAE	16.0	11.0	11.0	16.5	9.5	22.0	16.5
AB	ABIES	1.0	0	0	0	0	1.0	.5
AC	ALNUS CF. CRISPA	2.0	1.0	2.0	1.0	2.0	2.0	0
AE	ANEMONE-TYPE	0	0	0	1.0	0	0	0
AI	ACER SACCHARINUM-TYPE	0	0	1.0	0	1.0	0	0
AM	AMORPHA	0	0	2.0	0	0	0	0
AN	ACER NEGUNDO-TYPE	1.0	0	1.0	1.0	0	0	0
AR	ACER RUBRUM	0	0	0	0	0	0	.5
AS	ACER SACCHARUM	1.0	0	0	0	2.0	0	0
CA	CARYA	0	0	0	0	0	2.0	0
CZ	CERREALIA CF. AVENA	0	0	0	0	0	0	0
DZ	ZIGADENUS	0	0	0	1.0	0	0	0

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[Peterson Slough pollen counts continued]

EQ	EQUISETUM	1.0	0	0	0	0	0	1.0
GA	GALIUM	0	0	0	1.0	0	0	0
HU	HUMULUS-TYPE	0	0	0	0	1.0	0	0
IC	IVA CILIATA-TYPE	0	0	1.0	0	0	0	0
IX	IVA XANTHIFOLIA-TYPE	0	0	1.0	1.0	1.0	1.0	1.0
JC	JUGLANS CINEREA-TYPE	0	0	0	0	0	0	1.0
LM	LEMNA	0	0	0	0	0	0	0
MO	MORUS	0	0	0	0	0	0	0
MR	MYRICA	0	0	0	1.0	0	0	0
MY	MYRIOPHYLLUM EXALBESCENS-TYPE	1.0	1.0	1.0	1.0	1.0	1.0	0
NS	NYSSA	0	0	0	1.0	0	0	0
NU	NUPHAR	0	6.0	1.0	0	0	1.0	0
NY	NYMPHAEA	0	0	0	0	0	0	1.0
OS	OSMUNDA CLAYTONIANA	0	0	0	0	0	0	0
PB	POPULUS BALSAMIFERA-TYPE	1.0	0	0	0	0	0	0
PL	PLATANUS	0	0	0	0	0	0	0
PS	PETALOSTEMUM CANDIDUM-TYPE	1.0	0	0	0	0	0	0
PT	POPULUS TREMULOIDES-TYPE	3.0	3.0	8.0	2.0	4.0	1.0	0
QN	XANTHIUM	0	0	0	0	1.0	0	0
RH	RHUS	0	0	0	0	0	0	1.0
RO	ROSACEAE	1.0	0	1.0	0	0	0	1.0
SF	SPHAGNUM	0	1.0	0	0	0	0	1.0
SL	SALSOLA KALI	0	0	0	0	0	0	0
SP	SPARGANIUM-TYPE	0	0	0	0	1.0	0	0
SR	SARCOBATUS	0	1.0	0	0	0	0	2.0
TH	THALICTRUM	2.0	0	0	0	0	0	0
TR	PTERIDIUM-TYPE	1.0	0	0	0	0	0	0
TS	TSUGA	0	0	0	0	0	0	0
TY	TYPHA LATIFOLIA	0	1.0	1.0	0	0	2.0	0
UM	UMBELLIFERAE	0	0	0	0	0	0	0
UP	POTAMOGETON (EUPOTAMOGETON)	1.0	1.0	3.0	0	0	3.0	3.0
UR	URTICA-TYPE	0	0	0	0	1.0	1.0	0
VL	VIBURNUM LENTAGO	0	0	0	0	0	0	0
VT	VITIS	1.0	0	0	0	0	1.0	0
WH	HYPERICUM	0	0	0	0	0	0	0

Wentzel's Pond, Hubbard County, Minnesota

COUNTS OF POLLEN AND SPORES

SYM	VARIABLE	DEPTH OF SAMPLE (CM)								
		0	25.	35.	45.	55.	70.	80.	90.	
.	EXOTIC	324.0	340.0	350.0	107.0	71.0	76.0	121.0	90.0	
A	ALNUS CF. RUGOSA	10.0	5.0	6.0	2.0	13.0	10.0	9.0	6.0	
B	BETULA	16.0	13.0	10.0	6.0	14.0	11.0	16.5	23.0	
C	CORYLUS	1.0	1.0	2.0	2.0	5.0	1.0	5.0	1.0	
E	PINUS BANKSIANA/RESINOSA	46.0	45.5	35.5	40.0	28.5	20.5	33.5	17.5	
F	FRAXINUS NIGRA-TYPE	2.0	0	0	2.0	2.0	2.0	0	4.0	
G	POACEAE	20.0	15.0	9.0	16.0	14.0	17.0	18.0	33.0	
H	PINUS STROBUS	4.0	17.0	8.5	3.0	9.0	14.0	9.0	17.0	
I	PICEA	.5	0	3.0	1.5	2.0	2.5	7.5	6.5	
J	THUJA-TYPE	1.0	0	2.0	0	0	0	0	3.0	
K	CHENOPODIUM-TYPE	3.0	9.0	5.0	0	2.0	0	4.0	1.0	
L	LARIX	0	1.0	0	1.0	0	1.0	0	0	
M	AMBROSIA	18.0	21.0	14.0	7.0	2.0	3.0	2.0	3.0	
N	FRAXINUS PENNSYLVANICA-TYPE	1.0	0	0	0	1.0	0	0	0	
O	OSTRYA-TYPE	1.0	1.0	4.0	4.0	3.0	6.0	4.0	3.0	
P	PINUS UNDIFFERENTIATED	98.5	45.0	71.0	84.0	121.0	108.0	120.5	85.5	
Q	QUERCUS	27.5	25.0	13.0	9.0	9.0	21.0	23.0	9.0	
R	ARTEMISIA	3.0	6.0	6.0	5.0	5.0	7.0	6.0	9.0	
S	SALIX	5.0	1.0	4.0	5.0	2.0	2.0	4.0	0	
T	TILIA	0	0	0	0	1.0	1.0	0	0	
U	ULMUS	3.0	3.0	2.0	2.0	0	2.0	3.0	1.0	
V	TUBULIFLORAE UNDIFF.	2.0	3.0	1.0	3.0	3.0	4.0	5.0	1.0	
W	UNKNOWN OR RARE	1.0	2.0	3.0	1.0	0	2.0	1.0	0	
X	INDETERMINABLE POLLEN	6.0	3.0	9.5	1.0	1.0	4.5	7.5	7.0	
Y	CYPERACEAE	44.0	36.0	27.0	33.0	27.0	22.0	34.5	21.5	
AB	ABIES	0	0	0	0	1.0	1.0	1.0	1.5	
AC	ALNUS CF. CRISPA	0	0	0	1.0	2.0	3.0	0	3.0	
AI	ACER SACCHARINUM-TYPE	1.0	0	0	0	0	0	0	0	
AM	AMORPHA	1.0	0	0	0	1.0	0	0	0	
AN	ACER NEGUNDO	0	0	0	1.0	0	2.0	0	1.0	
AS	ACER SACCHARUM	0	1.0	0	1.0	1.0	0	0	0	
BO	BOTRYCHIUM	0	0	0	0	0	0	1.0	0	
CR	CRUCIFERAE	0	0	0	0	0	0	0	0	
CZ	CEREBALIA	0	0	2.0	0	0	0	0	0	
EQ	EQUISETUM	0	3.0	1.0	0	0	0	3.0	1.0	
ET	EPHEDRA TRIFURCA-TYPE	0	0	1.0	0	0	0	0	0	

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[Wentzel's Pond pollen counts continued]

EV	EPHEDRA VIRIDIS-TYPE	0	0	0	1.0	0	0	0	0
GD	GENTIANA PUBERULA-TYPE	0	0	0	0	0	0	0	0
GZ	ZEA	1.0	1.0	0	0	0	0	0	0
IX	IVA XANTHIFOLIA-TYPE	1.0	0	0	0	2.0	0	1.0	0
LE	LILIUM	0	0	0	0	0	0	0	1.0
LG	LIGULIFLORAE	0	0	0	0	0	0	0	0
LL	MELILOTUS-TYPE	0	1.0	0	0	0	0	0	0
LM	LEMNA	4.0	0	2.0	1.0	0	0	1.0	0
LY	AGASTACHE-TYPE	0	0	0	0	0	0	1.0	0
MF	MYRIOPHYLLUM ALTERNIFLORUM-TYPE	0	0	0	0	0	0	0	0
MY	MYRIOPHYLLUM EXALBESCENS-TYPE	0	0	0	0	1.0	0	0	0
NU	NUPHAR	7.5	4.0	4.0	5.5	4.0	3.0	7.0	3.5
PF	POTENTILLA-TYPE	0	0	0	0	0	0	0	0
PL	PLATANUS	0	1.0	0	0	0	0	0	1.0
PO	POLYGONUM LAPATHIFOLIUM-TYPE	0	0	0	0	0	0	0	0
PP	PETALOSTEMUM PURPUREUM	0	0	1.0	0	0	0	0	0
PS	PETALOSTEMUM CANDIDUM-TYPE	0	0	0	0	0	0	0	0
PT	POPULUS TREMULOIDES-TYPE	12.0	4.0	6.0	5.0	0	3.0	1.0	2.0
RA	RANUNCULUS-TYPE	0	0	0	0	0	0	0	0
RO	ROSACEAE	0	0	0	0	1.0	0	0	0
RU	RUMEX	0	0	0	0	0	0	0	0
SF	SPHAGNUM	0	0	0	0	0	0	0	0
SG	SAGITTARIA	0	0	1.0	1.0	0	0	0	0
SP	SPARGANIUM-TYPE	1.0	1.0	1.0	0	1.0	2.0	0	1.0
SR	SARCOBATUS	0	0	0	0	1.0	0	0	0
TH	THALICTRUM	0	0	0	1.0	0	0	0	0
TR	PTERIDIUM-TYPE	0	1.0	0	0	2.0	0	0	0
TS	TSUGA	0	0	0	0	0	0	1.0	0
TY	TYPHA LATIFOLIA	0	0	1.0	0	0	0	0	0
UM	UMBELLIFERAE	0	0	0	0	0	0	0	1.0
UP	POTAMOGETON (EUPOTAMOGETON)	1.0	0	3.0	1.0	3.0	1.0	4.0	4.0
UR	URTICA-TYPE	0	1.0	0	0	0	0	0	0
UT	UTRICULARIA	0	0	0	0	0	0	0	0
VT	VITIS	1.0	0	0	0	0	0	0	0

Wentzel's Pond, Hubbard County, Minnesota

COUNTS OF POLLEN AND SPORES

DEPTH OF SAMPLE (CM)

SYM	VARIABLE	105.	130.	150.	160.	180.	210.	229.
.	EXOTIC	90.0	74.0	48.0	46.0	64.0	35.0	54.0
A	ALNUS CF. RUGOSA	13.0	8.5	5.0	6.0	4.0	3.0	2.0
B	BETULA	29.0	16.0	13.0	12.0	12.0	8.0	5.0
C	CORYLUS	4.0	2.0	5.0	2.0	3.0	2.0	0
E	PINUS BANKSIANA/RESINOSA	14.5	3.0	5.5	2.8	1.8	.8	3.5
F	FRAXINUS NIGRA-TYPE	4.0	0	1.0	2.0	3.0	0	1.0
G	POACEAE	17.0	37.0	65.0	33.0	35.0	57.0	90.5
H	PINUS STROBUS	11.0	5.5	9.0	6.7	4.6	2.7	1.5
I	PICEA	1.5	3.5	0	0	1.0	1.5	0
J	THUJA-TYPE	2.0	0	0	0	2.0	0	0
K	CHENOPODIUM-TYPE	0	0	2.0	3.0	2.0	4.0	6.0
L	LARIX	0	0	0	0	2.0	0	0
M	AMBROSIA	2.0	4.0	2.0	2.0	7.0	4.0	3.0
N	FRAXINUS PENNSYLVANICA-TYPE	0	0	0	0	0	0	0
O	OSTRYA-TYPE	6.0	4.0	2.0	2.0	8.0	1.0	1.0
P	PINUS UNDIFFERENTIATED	52.0	49.0	40.5	25.0	21.0	25.5	20.0
Q	QUERCUS	25.0	12.0	10.0	13.5	17.0	17.0	13.0
R	ARTEMISIA	5.0	9.0	5.5	9.0	3.0	15.0	24.0
S	SALIX	1.0	3.0	3.0	2.0	2.0	4.0	5.0
T	TILIA	0	0	0	0	1.0	0	1.0
U	ULMUS	1.0	5.0	1.0	0	2.0	1.0	0
V	TUBULIFLORAE UNDIFF.	2.0	9.0	9.0	7.5	7.0	22.0	13.0
W	UNKNOWN OR RARE	0	1.0	1.0	2.0	0	5.0	0
X	INDETERMINABLE POLLEN	3.0	8.5	6.0	2.5	9.0	15.5	28.5
Y	CYPERACEAE	30.5	35.5	62.0	68.0	86.5	150.5	176.5
AB	ABIES	0	0	0	0	0	0	0
AC	ALNUS CF. CRISPA	0	0	1.0	1.0	1.0	1.0	1.0
AI	ACER SACCHARINUM-TYPE	0	0	0	0	0	0	0
AM	AMORPHA	2.0	1.0	0	2.0	1.0	1.0	0
AN	ACER NEGUNDO	0	0	0	0	0	0	0
AS	ACER SACCHARUM	2.0	0	0	0	0	0	0
BO	BOTRYCHIUM	0	0	0	1.0	0	0	0
CR	CRUCIFERAE	0	0	0	0	0	0	1.0
CZ	CEREALIA	0	0	0	0	0	0	0
EQ	EQUISETUM	1.0	0	0	0	1.0	0	0

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[Wentzel's Pond pollen counts continued]

ET	EPHEDRA TRIFURCA-TYPE	0	0	0	0	1.0	1.0	0
EV	EPHEDRA VIRIDIS-TYPE	0	0	0	0	0	1.0	0
GD	GENTIANA PUBERULA-TYPE	0	2.0	0	0	0	0	0
GZ	ZEA	0	0	0	0	0	0	0
IX	IVA XANTHIFOLIA-TYPE	0	0	0	2.0	0	0	0
LE	LILIUM	0	0	0	0	0	0	0
LG	LIGULIFLORAE	0	0	0	0	0	0	2.0
LL	MELILOTUS-TYPE	0	0	0	0	0	0	0
LM	LEMNA	0	0	0	2.0	0	1.0	2.0
LY	AGASTACHE-TYPE	0	0	0	0	0	0	0
MF	MYRIOPHYLLUM ALTERNIFLORUM-TYP	0	0	0	0	1.0	0E	0
MY	MYRIOPHYLLUM EXALBESCENS-TYPE	0	0	0	0	0	0	0
NU	NUPHAR	8.0	0	0	2.0	0	0	0
PF	POTENTILLA-TYPE	0	0	0	0	0	0	1.0
PL	PLATANUS	0	0	0	0	0	0	0
PO	POLYGONUM LAPATHIFOLIUM-TYPE	0	0	2.5	0	1.0	0	1.0
PP	PETALOSTEMUM PURPUREUM	0	0	0	0	0	0	1.0
PS	PETALOSTEMUM CANDIDUM-TYPE	0	0	0	0	0	3.0	0
PT	POPULUS TREMULOIDES-TYPE	0	2.0	2.0	1.0	0	1.0	5.0
RA	RANUNCULUS-TYPE	0	2.0	0	0	1.0	0	1.0
RO	ROSACEAE	1.0	0	0	0	0	0	0
RU	RUMEX	0	4.0	0	0	0	0	0
SF	SPHAGNUM	0	0	0	0	1.0	0	0
SG	SAGITTARIA	0	1.0	0	0	1.0	6.0	3.0
SP	SPARGANIUM-TYPE	0	0	1.0	0	0	2.0	2.0
SR	SARCOBATUS	0	0	2.0	1.0	0	0	0
TH	THALICTRUM	0	0	0	0	1.0	1.0	0
TR	PTERIDIUM-TYPE	0	1.0	0	0	0	0	0
TS	TSUGA	0	0	0	0	0	0	0
TY	TYPHA LATIFOLIA	0	0	1.0	0	0	0	0
UM	UMBELLIFERAE	0	0	0	0	0	0	0
UP	POTAMOGETON (EUPOTAMOGETON)	3.0	1.0	1.0	6.0	3.0	9.0	6.0
UR	URTICA-TYPE	0	0	0	0	0	0	0
UT	UTRICULARIA	0	1.0	0	0	0	0	0
VT	VITIS	0	0	0	0	0	0	0

Hostage Lake, Crow Wing County, Minnesota

COUNTS OF POLLEN AND SPORES

SYM	VARIABLE	DEPTH OF SAMPLE (CM)						
		0	25.	40.	100.	180.	200.	225.
.	MICROSPHERE	270.0	217.0	114.0	147.0	143.0	206.0	126.0
A	ALNUS CF. RUGOSA	5.0	10.0	13.0	17.0	19.0	22.0	7.0
B	BETULA	66.5	18.0	25.0	41.0	20.5	42.5	20.0
C	CORYLUS	2.0	2.0	1.0	2.0	2.0	1.0	2.0
D	DRYOPTERIS-TYPE	0	0	0	0	0	0	1.0
E	PINUS BANKSIANA/RESINOSA	12.3	57.0	64.0	12.6	35.0	5.9	42.0
F	FRAXINUS NIGRA-TYPE	2.0	3.0	3.0	1.0	1.0	2.0	3.0
G	POACEAE	6.0	8.0	11.0	8.0	7.0	11.0	20.0
H	PINUS STROBUS	3.7	22.5	35.5	16.9	23.0	5.1	83.5
I	PICEA	1.0	4.0	1.5	8.5	3.5	5.5	2.0
J	THUJA-TYPE	1.0	2.0	3.0	0	2.0	1.0	1.0
K	CHENOPODIUM-TYPE	8.0	4.0	3.0	2.0	0	1.0	3.0
L	LARIX	0	1.0	3.5	0	1.0	0	1.0
M	AMBROSIA	25.0	16.0	4.0	11.5	3.0	7.0	7.0
N	FRAXINUS PENNSYLVANICA-TYPE	5.0	1.0	0	1.0	2.0	3.0	0
O	OSTRYA-TYPE	5.0	5.0	7.0	6.0	7.0	1.0	6.0
P	PINUS UNDIFFERENTIATED	96.5	149.0	113.5	220.0	175.0	161.0	200.0
Q	QUERCUS	37.5	19.0	21.0	20.5	46.0	68.0	58.0
R	ARTEMISIA	9.5	4.0	3.0	4.5	11.5	8.5	7.0
S	SALIX	1.0	4.0	1.0	3.0	0	2.0	0
T	TILIA	1.0	1.0	0	2.0	0	0	0
U	ULMUS	3.0	4.0	3.0	1.0	1.0	6.0	9.0
V	TUBULIFLORAE UNDIFF.	2.0	1.0	1.0	1.0	7.0	2.0	4.0
W	UNKNOWN OR RARE	1.0	0	0	3.0	0	0	2.0
X	INDETERMINABLE POLLEN	6.5	4.0	7.5	5.0	9.5	6.0	3.0
Y	CYPERACEAE	2.0	8.5	7.5	6.0	9.5	5.0	12.5
AB	ABIES	0	0	0	1.5	.5	1.0	1.0
AC	ALNUS CF. CRISPA	2.0	2.0	0	0	1.0	0	1.0
AI	ACER SACCHARINUM-TYPE	0	2.0	1.0	0	0	1.0	1.0
AM	AMORPHA	0	0	0	0	0	0	0
AN	ACER NEGUNDO-TYPE	0	1.0	0	0	0	0	0
AR	ACER RUBRUM	1.0	0	2.0	1.0	0	0	1.0
AS	ACER SACCHARUM	0	0	0	0	.5	0	0
AT	ATHYRIUM	0	0	0	0	0	0	1.0
BR	BRASENIA	2.0	2.0	2.0	1.0	0	0	0
CA	CARYA	0	0	0	0	0	1.0	0

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[Hostage Lake pollen counts continued]

CE	CF. CEANOTHUS	0	0	0	0	0	0	1.0
CY	CARYOPHYLLACEAE	0	0	0	0	0	0	0
EQ	EQUISETUM	3.0	1.0	0	1.0	0	0	0
HU	HUMULUS-TYPE	0	1.0	0	0	0	0	0
IC	IVA CILIATA-TYPE	0	0	0	0	1.0	0	1.0
IX	IVA XANTHIFOLIA-TYPE	0	0	0	0	0	0	1.0
JC	JUGLANS CINEREA-TYPE	0	0	0	1.0	1.0	1.0	1.0
LD	MEDICAGO SATIVA	0	1.0	2.0	0	0	0	0
LE	LILIACEAE	0	0	0	0	0	0	0
LY	MENTHA-TYPE	0	0	0	0	0	0	0
NU	NUPHAR	1.0	1.0	0	0	0	0	0
OS	OSMUNDA CINNAMOMEA	0	0	1.0	0	0	0	0
PL	PLATANUS	1.0	0	0	0	0	0	1.0
PO	POLYGONUM LAPATHIFOLIUM-TYPE	0	0	0	1.0	0	0	1.0
PP	PETALOSTEMUM PURPUREUM	0	0	0	0	0	1.0	0
PS	PETALOSTEMUM CANDIDUM-TYPE	0	0	0	0	0	1.0	0
PT	POPULUS TREMULOIDES-TYPE	10.0	3.0	3.0	3.0	2.0	1.0	6.0
QN	XANTHIUM	0	0	0	1.0	0	0	0
RH	RHUS	0	0	0	1.0	0	0	0
RO	ROSACEAE	0	0	0	0	0	0	0
RU	RUMEX	0	1.0	0	0	0	0	0
SP	SPARGANIUM-TYPE	0	1.0	0	1.0	1.0	1.0	0
SR	SAROBATUS	0	0	0	0	0	0	0
TH	THALICTRUM	1.0	2.0	1.0	0	1.0	1.0	0
TR	PTERIDIUM-TYPE	1.0	1.0	1.0	1.0	2.0	1.0	1.0
TS	TSUGA	0	0	0	0	1.0	1.0	0
TY	TYPHA LATIFOLIA	1.0	0	0	0	0	0	0
UP	POTAMOGETON (EUPOTAMOGETON)	0	1.0	0	0	3.0	0	1.0
WV	VERBENA	0	0	0	0	0	0	0

Hostage Lake, Crow Wing County, Minnesota

COUNTS OF POLLEN AND SPORES

DEPTH OF SAMPLE (CM)

SYM	VARIABLE	250.	300.	350.	375.	400.	485.
.	MICROSPHERE	142.0	126.0	174.0	138.0	101.0	306.0
A	ALNUS CF. RUGOSA	26.0	22.5	19.0	18.0	10.0	7.0
B	BETULA	38.5	44.5	38.0	24.0	23.5	6.0
C	CORYLUS	2.0	2.0	3.0	2.0	0	2.0
D	DRYOPTERIS-TYPE	0	1.0	0	0	0	0
E	PINUS BANKSIANA/RESINOSA	3.6	3.2	1.0	.7	.6	4.5
F	FRAXINUS NIGRA-TYPE	2.0	7.0	1.0	0	4.0	5.0
G	POACEAE	23.0	16.0	19.0	23.0	27.0	52.0
H	PINUS STROBUS	7.9	17.8	1.0	1.8	.9	14.0
I	PICEA	5.0	3.5	4.5	2.5	8.0	3.0
J	THUJA-TYPE	0	1.0	3.0	2.0	3.0	7.0
K	CHENOPODIUM-TYPE	2.0	0	6.5	2.0	5.5	8.0
L	LARIX	0	2.0	1.0	2.0	1.0	0
M	AMBROSIA	6.0	10.0	6.0	17.0	18.0	27.0
N	FRAXINUS PENNSYLVANICA-TYPE	1.0	3.0	1.0	3.0	0	1.0
O	OSTRYA-TYPE	5.5	6.5	17.5	2.0	3.0	6.0
P	PINUS UNDIFFERENTIATED	105.0	69.0	37.0	36.0	19.5	21.0
Q	QUERCUS	59.0	71.0	86.0	68.0	57.5	91.0
R	ARTEMISIA	10.0	13.0	14.0	19.0	31.0	53.0
S	SALIX	1.0	0	1.0	0	2.0	2.0
T	TILIA	0	1.0	1.0	1.0	0	1.0
U	ULMUS	2.0	2.0	6.0	3.0	6.0	8.0
V	TUBULIFLORAE UNDIFF.	3.0	6.0	5.0	8.0	10.0	10.0
W	UNKNOWN OR RARE	1.0	1.0	1.5	1.0	0	2.0
X	INDETERMINABLE POLLEN	4.0	8.0	16.0	15.0	5.5	7.0
Y	CYPERACEAE	9.0	8.5	3.0	8.0	10.0	15.5
AB	ABIES	1.0	0	0	1.0	1.0	0
AC	ALNUS CF. CRISPA	0	0	2.0	0	1.0	2.0
AI	ACER SACCHARINUM-TYPE	.5	2.0	0	0	0	0
AM	AMORPHA	0	0	0	0	0	1.0
AN	ACER NEGUNDO-TYPE	0	0	0	0	0	1.0
AR	ACER RUBRUM	0	1.0	.5	1.0	1.0	0
AS	ACER SACCHARUM	1.0	0	0	0	0	2.0
AT	ATHYRIUM	0	0	0	0	0	0
BR	BRASENIA	0	0	0	0	0	0
CA	CARYA	0	0	0	0	0	0
CE	CF. CEANOTHUS	0	0	0	0	0	0

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[Hostage Lake pollen counts continued]

CY	CARYOPHYLLACEAE	0	1.0	0	0	0	0
EQ	EQUISETUM	0	3.0	3.0	0	0	2.0
HU	HUMULUS-TYPE	0	0	0	0	0	0
IC	IVA CILIATA-TYPE	1.0	0	0	2.0	0	0
IX	IVA XANTHIFOLIA-TYPE	1.0	1.0	1.0	0	0	0
JC	JUGLANS CINEREA-TYPE	2.0	1.0	0	0	0	0
LD	MEDICAGO SATIVA	0	0	0	0	0	0
LE	LILIACEAE	0	0	1.0	0	0	0
LY	MENTHA-TYPE	0	0	1.0	0	0	0
NU	NUPHAR	0	0	0	0	0	0
OS	OSMUNDA CINNAMOMEA	0	0	0	0	0	0
PL	PLATANUS	0	0	2.0	0	1.0	1.0
PO	POLYGONUM LAPATHIFOLIUM-TYPE	0	0	0	0	0	0
PP	PETALOSTEMUM PURPUREUM	0	0	0	0	1.0	0
PS	PETALOSTEMUM CANDIDUM-TYPE	0	0	0	0	0	1.0
PT	POPULUS TREMULOIDES-TYPE	0	1.0	0	0	1.0	2.0
QN	XANTHIUM	0	0	0	0	0	0
RH	RHUS	0	1.0	0	0	0	0
RO	ROSACEAE	0	1.0	0	0	0	0
RU	RUMEX	0	0	0	0	0	0
SP	SPARGANIUM-TYPE	0	0	2.0	0	1.0	1.0
SR	SAROBATUS	2.0	0	0	0	0	0
TH	THALICTRUM	0	1.0	0	0	0	0
TR	PTERIDIUM-TYPE	2.0	1.0	1.0	0	0	0
TS	TSUGA	0	0	0	0	0	0
TY	TYPHA LATIFOLIA	0	0	0	0	0	1.0
UP	POTAMOGETON (EUPOTAMOGETON)	1.0	1.0	8.0	3.0	2.0	3.0
WV	VERBENA	0	0	1.0	0	0	0

Big John Pond, Beltrami County, Minnesota

COUNTS OF POLLEN AND SPORES

DEPTH OF SAMPLES (CM)

SYM	VARIABLE	0	15.	20.	40.	50.	65.	90.
.	MICROSPHERE	254.0	67.0	61.0	50.0	94.0	116.0	197.0
A	ALNUS CF. RUGOSA	2.0	6.0	6.0	7.0	5.0	5.0	11.0
B	BETULA	5.0	12.0	11.0	10.0	19.0	15.0	26.0
C	CORYLUS	4.0	0	4.0	0	6.0	2.0	5.0
D	DRYOPTERIS-TYPE	0	0	0	0	0	0	0
E	PINUS BANKSIANA/RESINOSA	18.0	32.5	24.5	15.4	37.0	19.5	21.5
F	FRAXINUS NIGRA-TYPE	1.0	0	1.0	0	2.0	0	6.0
G	POACEAE	9.0	4.0	2.0	9.0	12.0	15.0	26.0
H	PINUS STROBUS	13.0	10.5	9.5	9.6	20.0	11.0	21.0
I	PICEA	3.5	8.0	7.0	6.0	9.5	12.5	7.5
J	THUJA-TYPE	1.0	1.0	0	0	1.0	2.0	1.0
K	CHENOPODIUM-TYPE	2.0	4.0	3.0	2.0	0	1.0	4.0
L	LARIX	1.0	0	2.0	1.0	1.0	4.0	1.0
M	AMBROSIA	7.0	13.0	6.0	0	3.0	0	4.0
N	FRAXINUS PENNSYLVANICA-TYPE	0	0	0	0	0	0	0
O	OSTRYA-TYPE	2.0	1.0	1.0	1.0	1.0	4.0	11.0
P	PINUS UNDIFFERENTIATED	92.0	112.0	158.5	139.5	178.0	113.0	109.0
Q	QUERCUS	3.0	5.0	8.0	3.0	6.0	11.0	23.0
R	ARTEMISIA	5.0	4.0	1.0	6.0	3.0	7.0	8.0
S	SALIX	1.0	3.0	2.0	3.0	0	2.0	2.0
U	ULMUS	0	2.0	3.0	1.0	2.0	0	1.0
V	TUBULIFLORAE UNDIFF.	0	4.0	2.0	0	2.0	2.0	5.0
W	UNKNOWN OR RARE	1.0	0	1.0	0	1.0	1.0	0
X	INDETERMINABLE POLLEN	11.0	16.0	6.5	10.0	8.0	16.5	19.5
Y	CYPERACEAE	47.0	59.5	53.0	40.5	60.0	74.0	85.0
AB	ABIES	1.0	4.5	0	1.0	3.5	.5	1.5
AC	ALNUS CF. CRISPA	0	1.0	3.0	3.0	4.0	3.0	2.0
AM	AMORPHA	0	0	0	0	0	0	0
AN	ACER NEGUNDO	1.0	0	0	0	0	0	0
AR	ACER RUBRUM	0	0	1.0	0	0	0	0
AS	ACER SACCHARUM	0	0	0	0	0	1.0	0
AT	ATHYRIUM	0	0	1.0	1.0	0	0	0
CA	CARYA	1.0	0	0	0	0	0	0
CE	CF. CEANOTHUS	0	0	0	0	0	0	0
CY	CARYOPHYLLACEAE	0	0	1.0	0	0	0	0
CZ	ZEA	1.0	0	0	0	0	0	0

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[Big John Pond pollen counts continued]

EH	EPHEDRA UNDIFF.	0	0	0	0	0	0	0
EQ	EQUISETUM	1.0	0	0	1.0	0	0	0
GA	GALIUM	0	0	0	0	0	0	0
HU	HUMULUS-TYPE	0	0	0	0	0	1.0	0
IC	IVA CILIATA-TYPE	0	0	0	0	2.0	1.0	0
IX	IVA XANTHIFOLIA-TYPE	1.0	0	0	0	1.0	0	0
JC	JUGLANS CINEREA-TYPE	0	0	0	0	0	0	0
LG	LIGULIFLORAE	0	0	0	0	0	0	0
LR	TRIFOLIUM REPENS-TYPE	1.0	0	0	0	0	0	0
LY	AGASTACHE-TYPE	0	0	0	0	0	0	0
MY	MYRIOPHYLLUM EXALBESCENS-TYPE	0	0	0	1.0	0	0	0
NU	NUPHAR	2.0	2.0	4.5	0	2.0	0	0
NY	NYMPHAEA	0	0	0	1.0	0	0	0
PE	PARIETARIA-TYPE	0	0	0	0	0	0	0
PL	PLATANUS	0	0	1.0	0	0	0	0
PO	POLYGONUM LAPATHIFOLIUM-TYPE	0	0	0	0	2.0	0	0
PS	PETALOSTEMUM CANDIDUM-TYPE	0	0	0	0	0	0	0
PT	POPULUS TREMULOIDES-TYPE	3.0	2.0	1.0	2.0	1.0	3.0	9.0
QN	XANTHIUM	0	1.0	0	1.0	0	0	0
RH	RHUS	1.0	0	0	0	0	0	0
RO	ROSACEAE	0	1.0	0	0	0	0	0
SF	SPHAGNUM	0	1.0	0	0	0	1.0	0
SP	SPARGANIUM-TYPE	0	0	0	0	0	0	0
SR	SARCOBATUS	0	0	1.0	0	1.0	0	0
TH	THALICTRUM	0	1.0	0	0	0	1.0	1.0
TR	PTERIDIUM-TYPE	0	1.0	0	0	0	0	0
TY	TYPHA LATIFOLIA	0	0	0	0	1.0	0	0
UP	POTAMOGETON (EUPOTAMOGETON)	1.0	1.0	3.0	2.0	0	2.0	6.0
UT	UTRICULARIA	0	0	0	0	0	0	0
WM	MYRIOPHYLLUM ALTERNIFLORUM-TYPE	0	0	0	0	0	0	0
YL	LYCOPODIUM LUCIDULUM-TYPE	0	0	0	0	0	0	0

Big John Pond, Beltrami County, Minnesota

COUNTS OF POLLEN AND SPORES

DEPTH OF SAMPLE (CM)

SYM	VARIABLE	105.	115.	125.	145.	200.
.	MICROSPHERE	79.0	227.0	261.0	233.0	326.0
A	ALNUS CF. RUGOSA	7.0	16.0	10.0	7.0	3.0
B	BETULA	24.0	36.0	24.0	10.0	7.0
C	CORYLUS	1.0	1.0	3.0	0	2.0
D	DRYOPTERIS-TYPE	0	0	2.0	1.0	0
E	PINUS BANKSIANA/RESINOSA	7.2	5.6	6.0	3.0	.5
F	FRAXINUS NIGRA-TYPE	6.0	6.0	2.0	2.0	2.0
G	POACEAE	15.0	21.0	43.0	59.0	51.0
H	PINUS STROBUS	8.8	22.4	7.0	7.5	2.0
I	PICEA	6.0	3.0	2.5	4.0	2.5
J	THUJA-TYPE	2.0	0	0	0	0
K	CHENOPODIUM-TYPE	3.0	0	9.0	4.0	6.0
L	LARIX	2.0	1.0	0	1.0	0
M	AMBROSIA	5.0	4.0	9.0	5.0	9.0
N	FRAXINUS PENNSYLVANICA-TYPE	1.0	0	0	1.0	0
O	OSTRYA-TYPE	7.0	11.0	3.0	3.0	5.0
P	PINUS UNDIFFERENTIATED	56.5	72.5	40.5	31.0	38.5
Q	QUERCUS	37.0	40.0	23.0	10.0	28.0
R	ARTEMISIA	13.0	22.5	23.0	28.0	43.0
S	SALIX	2.0	6.0	3.0	0	2.0
U	ULMUS	1.0	4.0	1.0	4.0	1.0
V	TUBULIFLORAE UNDIFF.	3.0	6.0	13.0	20.0	10.0
W	UNKNOWN OR RARE	4.0	0	0	1.0	0
X	INDETERMINABLE POLLEN	28.0	21.0	20.5	20.0	29.0
Y	CYPERACEAE	67.0	92.0	172.0	162.0	170.0
AB	ABIES	2.0	0	1.5	0	.5
AC	ALNUS CF. CRISPA	4.0	2.0	1.0	2.0	1.0
AM	AMORPHA	0	0	0	0	4.0
AN	ACER NEGUNDO	0	0	0	0	0
AR	ACER RUBRUM	0	0	0	0	0
AS	ACER SACCHARUM	0	0	0	0	0
AT	ATHYRIUM	0	0	0	0	0
CA	CARYA	0	0	0	0	0
CE	CF. CEANOTHUS	0	1.0	0	0	0
CY	CARYOPHYLLACEAE	0	0	0	1.0	1.0
CZ	ZEA	0	0	0	0	0
EH	EPHEDRA UNDIFF.	0	0	0	0	1.0

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[Big John Pond pollen counts continued]

EQ	EQUISETUM	1.0	1.0	6.0	1.0	2.0
GA	GALIUM	0	0	1.0	0	0
HU	HUMULUS-TYPE	0	0	0	0	0
IC	IVA CILIATA-TYPE	0	0	0	0	1.0
IX	IVA XANTHIFOLIA-TYPE	0	0	2.0	1.0	0
JC	JUGLANS CINEREA-TYPE	0	1.0	0	0	0
LG	LIGULIFLORAE	0	0	0	0	1.0
LR	TRIFOLIUM REPENS-TYPE	0	0	0	0	0
LY	AGASTACHE-TYPE	1.0	0	1.0	0	2.0
MY	MYRIOPHYLLUM EXALBESCENS-TYPE	1.0	0	1.0	7.0	2.0
NU	NUPHAR	0	0	0	0	0
NY	NYMPHAEA	1.0	0	0	0	0
PE	PARIETARIA-TYPE	0	1.0	0	0	0
PL	PLATANUS	0	0	0	0	0
PO	POLYGONUM LAPATHIFOLIUM-TYPE	0	1.0	0	2.0	0
PS	PETALOSTEMUM CANDIDUM-TYPE	0	0	0	0	1.0
PT	POPULUS TREMULOIDES-TYPE	6.0	6.0	9.0	2.0	7.0
QN	XANTHIUM	0	1.0	0	0	1.0
RH	RHUS	0	1.0	0	0	0
RO	ROSACEAE	0	0	0	0	0
SF	SPHAGNUM	0	0	0	0	0
SP	SPARGANIUM-TYPE	0	0	0	2.0	11.0
SR	SARCOBATUS	1.0	0	0	0	0
TH	THALICTRUM	0	0	0	1.0	0
TR	PTERIDIUM-TYPE	0	0	0	0	0
TY	TYPHA LATIFOLIA	0	0	0	1.0	1.0
UP	POTAMOGETON (EUPOTAMOGETON)	4.0	5.0	3.0	6.0	1.0
UT	UTRICULARIA	0	0	1.0	0	0
WM	MYRIOPHYLLUM ALTERNIFLORUM-TYPE	0	1.0	1.0	1.0	0
YL	LYCOPODIUM LUCIDULUM-TYPE	0	1.0	0	0	0

Mud Lake, Hubbard County, Minnesota

COUNTS OF POLLEN AND SPORES

DEPTH OF SAMPLE (CM)

SYM	VARIABLE	0	50.	100.	200.	300.	335.	350.	360.
.	MICROSPHERE	510.0	162.0	185.0	74.0	87.0	351.0	72.0	339.0
A	ALNUS CF. RUGOSA	8.0	22.0	23.0	9.0	29.0	27.0	30.0	31.0
B	BETULA	52.0	31.5	39.0	12.0	29.0	35.0	37.0	40.0
C	CORYLUS	4.0	6.0	6.0	2.0	4.0	5.0	1.0	15.0
D	DRYOPTERIS-TYPE	0	0	1.0	0	1.0	1.0	0	0
E	PINUS BANKSIANA/RESINOSA	56.5	153.0	114.0	71.5	106.0	31.5	39.5	28.0
F	FRAXINUS NIGRA-TYPE	3.0	1.0	7.0	0	1.0	4.0	3.0	4.0
G	POACEAE	19.0	13.0	8.0	7.0	12.0	17.0	12.0	21.0
H	PINUS STROBUS	7.0	41.5	27.0	28.0	50.0	71.0	42.5	32.5
I	PICEA	4.0	10.5	9.5	3.5	1.5	2.5	2.0	5.0
J	THUJA-TYPE	4.0	1.0	7.0	1.0	3.0	4.0	1.0	5.0
K	CHENOPODIUM-TYPE	3.0	0	2.5	2.0	5.0	1.0	3.0	4.0
L	LARIX	2.0	2.0	1.0	2.0	0	0	3.0	1.0
M	AMBROSIA	18.0	7.0	9.0	2.0	1.0	4.0	1.0	6.0
N	FRAXINUS PENNSYLVANICA-TYPE	2.0	0	0	1.0	0	0	0	1.0
O	OSTRYA-TYPE	0	5.0	3.0	7.0	8.0	9.0	13.0	11.0
P	PINUS UNDIFFERENTIATED	46.5	165.0	96.0	72.0	96.0	98.0	62.0	45.5
Q	QUERCUS	55.0	23.0	25.0	13.0	40.0	35.0	26.0	47.0
R	ARTEMISIA	6.5	10.0	13.0	4.0	10.0	14.5	9.0	18.0
S	SALIX	3.0	5.0	1.0	0	0	2.0	3.0	2.0
T	TILIA	0	0	0	0	0	0	0	1.0
U	ULMUS	4.0	10.0	4.0	1.0	8.0	4.0	6.0	4.0
V	TUBULIFLORAE UNDIFF.	3.0	0	5.0	0	2.0	10.0	3.0	7.0
W	UNKNOWN OR RARE	1.0	2.0	2.0	1.0	4.0	1.0	1.0	1.0
X	INDETERMINABLE POLLEN	2.0	3.5	2.5	0	2.5	10.0	2.0	13.0
Y	CYPERACEAE	7.0	24.5	12.0	9.0	7.0	16.0	14.0	15.0
AB	ABIES	0	4.0	1.0	1.0	.5	0	0	0
AC	ALNUS CF. CRISPA	1.0	2.0	2.0	1.0	4.0	3.0	0	0
AE	ANEMONE-TYPE	0	0	0	0	0	1.0	0	0
AI	ACER SACCHARINUM-TYPE	1.0	0	0	0	0	0	0	0
AM	AMORPHA	1.0	1.0	0	0	1.0	1.0	3.0	0
AN	ACER NEGUNDO-TYPE	1.0	0	0	0	0	0	0	0
AR	ACER RUBRUM	0	0	0	0	0	0	0	1.0
AS	ACER SACCHARUM	0	1.0	0	1.0	3.0	1.0	0	1.0
AT	ATHYRIUM	0	0	0	2.0	0	0	2.0	0
CA	CARYA	0	0	0	0	0	0	0	0
CL	CELTIS	1.0	0	0	0	0	0	0	0

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[Mud Lake pollen counts continued]

CY	CARYOPHYLLACEAE	3.0	0	0	0	0	0	0	0
DT	DRYOPTERIS THELYPTERIS-TYPE	0	1.0	0	0	0	0	0	0
EQ	EQUISETUM	0	0	0	0	0	0	0	2.0
GA	GALIUM	0	0	0	0	0	1.0	0	0
HU	HUMULUS-TYPE	0	1.0	0	0	0	0	0	0
IC	IVA CILIATA-TYPE	0	0	1.0	0	0	0	0	0
IX	IVA XANTHIFOLIA-TYPE	1.0	1.0	1.0	0	0	1.0	0	0
JC	JUGLANS CINEREA-TYPE	0	0	0	0	0	0	0	0
JN	JUGLANS NIGRA-TYPE	0	0	0	0	0	0	0	0
LG	LIGULIFLORAE	0	0	0	0	0	0	0	0
MO	MORUS	2.0	0	2.0	2.0	0	0	0	0
NU	NUPHAR	1.0	0	0	0	0	0	1.0	0
NY	NYMPHAEA	1.0	0	0	0	0	0	0	0
PB	POPULUS BALSAMIFERA-TYPE	4.0	0	1.0	0	1.0	0	5.0	0
PL	PLATANUS	0	1.0	0	1.0	0	0	1.0	2.0
PP	PETALOSTEMUM PURPUREUM	0	0	0	0	0	1.0	0	0
PS	PETALOSTEMUM CANDIDUM-TYPE	0	0	0	0	0	0	0	0
PT	POPULUS TREMULOIDES-TYPE	20.0	6.0	6.0	1.0	6.0	7.0	6.0	9.0
QN	XANTHIUM	1.0	0	0	1.0	2.0	0	0	0
RO	ROSACEAE	1.0	0	1.0	1.0	0	0	0	0
RU	RUMEX	2.0	0	0	0	0	0	0	0
SF	SPHAGNUM	0	2.0	0	0	0	0	0	0
SG	SAGITTARIA	0	0	0	0	0	0	0	0
SP	SPARGANIUM-TYPE	1.0	0	0	0	0	0	0	0
SR	SARCOBATUS	0	0	1.0	0	0	0	1.0	2.0
TH	THALICTRUM	0	0	1.0	1.0	0	0	1.0	0
TR	PTERIDIUM-TYPE	0	0	0	0	0	1.0	2.0	0
TS	TSUGA	0	0	0	1.0	0	0	0	0
TX	TAXUS	0	0	0	1.0	0	0	0	0
TY	TYPHA LATIFOLIA	0	0	0	0	0	1.0	0	0
UM	UMBELLIFERAE	0	0	0	0	0	0	0	0
UP	POTAMOGETON (EUPOTAMOGETON)	0	3.0	2.0	2.0	3.0	2.0	0	0
UR	URTICA-TYPE	1.0	0	1.0	0	1.0	0	0	0
VT	VITIS	0	0	0	0	0	0	1.0	0

Mud Lake, Hubbard County, Minnesota

COUNTS OF POLLEN AND SPORES

DEPTH OF SAMPLE (CM)

SYM	VARIABLE	385.	400.	424.	460.	502.	524.	580.
.	MICROSPHERE	363.0	62.0	115.0	132.0	80.0	138.0	155.0
A	ALNUS CF. RUGOSA	44.0	26.0	23.0	26.0	18.0	34.0	22.0
B	BETULA	37.5	31.0	28.0	15.0	18.0	16.0	9.0
C	CORYLUS	2.0	11.0	9.0	3.0	3.0	2.0	5.0
D	DRYOPTERIS-TYPE	3.0	0	0	1.0	0	1.0	2.0
E	PINUS BANKSIANA/RESINOSA	10.0	13.0	12.4	7.0	15.0	23.5	1.5
F	FRAXINUS NIGRA-TYPE	3.0	8.0	4.0	4.0	3.0	3.0	2.0
G	POACEAE	23.0	15.0	34.0	35.0	34.0	64.0	48.0
H	PINUS STROBUS	36.0	22.0	12.1	9.0	3.5	10.0	3.5
I	PICEA	.5	3.5	4.0	2.5	0	0	4.5
J	THUJA-TYPE	1.0	0	1.0	1.0	1.0	3.0	1.0
K	CHENOPODIUM-TYPE	3.0	3.0	2.0	2.0	2.0	2.5	6.0
L	LARIX	5.0	1.0	1.0	1.0	0	0	2.0
M	AMBROSIA	5.0	6.0	4.0	11.0	12.0	15.0	10.0
N	FRAXINUS PENNSYLVANICA-TYPE	1.0	1.0	4.0	1.0	0	1.0	0
O	OSTRYA-TYPE	17.0	6.0	6.0	13.0	1.0	2.0	2.0
P	PINUS UNDIFFERENTIATED	28.5	21.5	16.0	15.5	16.0	22.0	13.0
Q	QUERCUS	51.0	35.5	39.0	41.0	28.0	32.0	23.0
R	ARTEMISIA	16.0	10.0	13.0	31.0	33.0	58.5	41.0
S	SALIX	6.0	4.0	1.0	10.0	5.0	5.0	5.0
T	TILIA	0	0	2.0	0	0	0	0
U	ULMUS	11.0	4.0	5.0	5.0	1.0	10.0	3.0
V	TUBULIFLORAE UNDIFF.	8.5	6.5	4.0	10.0	6.0	8.0	3.0
W	UNKNOWN OR RARE	2.0	1.0	1.0	0	0	2.0	0
X	INDETERMINABLE POLLEN	10.5	3.0	3.0	4.0	3.0	4.0	4.5
Y	CYPERACEAE	24.0	14.0	15.0	15.0	9.5	20.0	19.0
AB	ABIES	4.5	2.0	0	0	1.0	1.0	0
AC	ALNUS CF. CRISPA	2.0	0	2.0	1.0	0	4.0	2.0
AE	ANEMONE-TYPE	0	0	0	0	0	0	0
AI	ACER SACCHARINUM-TYPE	0	0	0	0	1.0	0	0
AM	AMORPHA	0	1.0	0	3.0	2.0	3.0	0
AN	ACER NEGUNDO-TYPE	0	1.0	0	1.0	0	1.0	0
AR	ACER RUBRUM	0	0	0	0	0	0	0
AS	ACER SACCHARUM	1.0	0	0	2.0	0	2.0	0
AT	ATHYRIUM	0	1.0	1.0	0	0	0	0
CA	CARYA	0	0	0	0	1.0	0	0
CL	CELTIS	2.0	0	0	0	0	0	0

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[Mud Lake pollen counts continued]

CY	CARYOPHYLLACEAE	0	0	0	0	0	0	0
DT	DRYOPTERIS THELYPTERIS-TYPE	0	0	0	1.0	0	0	0
EQ	EQUISETUM	2.0	0	0	0	0	0	2.0
GA	GALIUM	0	0	0	1.0	0	0	1.0
HU	HUMULUS-TYPE	0	0	0	0	0	0	0
IC	IVA CILIATA-TYPE	1.0	0	0	0	0	0	0
IX	IVA XANTHIFOLIA-TYPE	0	0	1.0	0	1.0	0	0
JC	JUGLANS CINEREA-TYPE	0	0	0	0	0	0	1.0
JN	JUGLANS NIGRA-TYPE	0	1.0	0	0	0	0	0
LG	LIGULIFLORAE	0	0	0	1.0	2.0	0	0
MO	MORUS	0	0	1.0	0	0	0	1.0
NU	NUPHAR	0	0	0	1.0	1.0	0	0
NY	NYMPHAEA	0	0	0	0	0	0	0
PB	POPULUS BALSAMIFERA-TYPE	0	1.0	0	3.0	0	2.0	1.0
PL	PLATANUS	1.0	0	0	1.0	1.0	1.0	0
PP	PETALOSTEMUM PURPUREUM	0	0	1.0	0	0	0	0
PS	PETALOSTEMUM CANDIDUM-TYPE	0	0	0	1.0	0	0	0
PT	POPULUS TREMULOIDES-TYPE	9.0	10.0	10.0	3.0	2.0	2.0	2.0
QN	XANTHIUM	0	0	1.0	0	1.0	0	0
RO	ROSACEAE	0	0	0	2.0	0	0	0
RU	RUMEX	0	0	0	0	0	0	0
SF	SPHAGNUM	0	0	0	0	1.0	0	0
SG	SAGITTARIA	0	0	0	0	0	1.0	0
SP	SPARGANIUM-TYPE	0	0	0	0	1.0	0	0
SR	SARCOBATUS	0	1.0	0	0	1.0	0	0
TH	THALICTRUM	2.0	0	0	0	0	1.0	2.0
TR	PTERIDIUM-TYPE	0	0	0	1.0	2.0	0	0
TS	TSUGA	0	0	0	0	0	0	0
TX	TAXUS	0	0	0	0	0	0	0
TY	TYPHA LATIFOLIA	0	0	0	0	1.0	1.0	1.0
UM	UMBELLIFERAE	0	0	0	0	0	0	1.0
UP	POTAMOGETON (EUPOTAMOGETON)	0	0	0	1.0	2.0	3.0	4.0
UR	URTICA-TYPE	0	1.0	0	0	0	0	0
VT	VITIS	0	0	0	0	1.0	0	0

APPENDIX 3.A
RELEVÉ LOCATIONS

RELEVE DATES AND LOCATIONS

Township numbers over 100 are relative to the fifth principal meridian, and those less than 100 are relative to the fourth principal meridian.

RELEVE	DATE	LOCATION	REMARKS
001	31 Aug. 1979	NE of NW of S. 6, T.134 N, R.27 W	Age classes 1935,36
002	31 Aug. 1979	S of S. 9, T.136 N, R.27 W	Age class 1944
003	1 Sep. 1979	SW of NW of S.26, T. 55 N, R.25 W	Age classes 1928,41
004	4 Sep. 1979	NE of S. 6, T.148 N, R.29 W	Age classes 1922,17
005	6 Sep. 1979	SE of NW of S.30, T.150 N, R.35 W	Age classes 1943,39
006	6 Sep. 1979	SW of NE of S.35, T.148 N, R.35 W	Age class 1924
007	7 Sep. 1979	S of S.17, T.147 N, R.34 W	Age class 1924
008	7 Sep. 1979	SW of SW of S.35, T.146 N, R.32 W	Age classes 1917-41
009	8 Sep. 1979	SW of SW of S.22, T.142 N, R.39 W	Age classes 1917,26
010	9 Sep. 1979	NW of NE of S.25, T.140 N, R.38 W	Age class 1938
011	9 Sep. 1979	SE of NW of S. 1, T.138 N, R.35 W	Age classes 1937-53
012	10 Sep. 1979	SW of NE of S.21, T.135 N, R.34 W	Age classes 1917-33
013	19 Oct. 1979	SW of S.33, T.130 N, R.36 W	Age classes 1915-50
014	20 Oct. 1979	NE of S.24, T.139 N, R.36 W	Age classes 1911-46
015	23 Jul. 1980	NE of SE of S.14, T.139 N, R.35 W	Age classes 1902-14
016	24 Jul. 1980	SE of SW of S.11, T.140 N, R.34 W	Age classes 1907,08
017	24 Jul. 1980	NE of NW of S.10, T.139 N, R.35 W	Age classes 1919-53
018	25 Jul. 1980	NW of NW of S.16, T.139 N, R.32 W	Age classes 1909-41
019	25 Jul. 1980	SW of SW of S.10, T.139 N, R.32 W	Age class 1919
020	27 Jul. 1980	SW of NW of S.31, T.140 N, R.33 W	Age class 1900,01
021	20 Sep. 1980	NE of NE of S.11, T. 44 N, R.31 W	Age class 1932-34
022	20 Sep. 1980	NE of NE of S.11, T. 44 N, R.31 W	Age classes 1897-1932
023	21 Sep. 1980	SW of SW of S. 1, T.138 N, R.35 W	Age class 1927
024	21 Sep. 1980	SE of SW of S. 7, T.138 N, R.34 W	Age classes 1938-48
025	22 Sep. 1980	SE of SW of S.13, T.139 N, R.35 W	Age classes 1925-46
026	22 Sep. 1980	SW of SW of S.13, T.139 N, R.35 W	Age classes 1928-39
027	23 Sep. 1980	SW of SW of S.11, T.140 N, R.34 W	Age classes 1901-09
028	23 Sep. 1980	SE of NE of S.15, T.140 N, R.33 W	Age classes 1930-47
029	24 Sep. 1980	SW of NE of S.27, T.144 N, R.34 W	Age classes 1919-29
030	24 Sep. 1980	NE of NW of S.22, T.144 N, R.34 W	Age class 1925-28
031	25 Sep. 1980	NW of NW of S.14, T.138 N, R.34 W	Age class 1922
032	28 Sep. 1980	SW of NE of S.31, T.144 N, R.34 W	
033	18 Aug. 1981	NW of SW of S.11, T.147 N, R.34 W	Age class 1933
034	19 Aug. 1981	SW of NW of S.15, T.147 N, R.34 W	Age class 1928
035	19 Aug. 1981	SE of SE of S.15, T.147 N, R.34 W	Age class 1933
036	19 Aug. 1981	SW of NW of S.10, T.147 N, R.34 W	Age class 1928
037	19 Aug. 1981	SW of NE of S.17, T.147 N, R.34 W	Age class 1927

[continued on next page]

[Releve Dates and Locations continued]

038	20 Aug. 1981	NE of NW of S. 5, T.145 N, R.29 W	Age classes 1923,28
039	20 Aug. 1981	NW of SE of S. 3, T.145 N, R.29 W	Age class 1928
040	9 Oct. 1981	SW of NW of S.31, T.136 N, R.27 W	Age classes 1917,27
041	10 Oct. 1981	SW of NE of S. 9, T.136 N, R.27 W	Age class 1937,41
042	10 Oct. 1981	SW of NW of S.11, T.136 N, R.27 W	Age classes 1921,41
043	10 Oct. 1981	NE of NE of S.15, T.136 N, R.27 W	Age classes 1919-31
044	11 Oct. 1981	SW of NW of S.31, T.136 N, R.27 W	Age classes 1914-26
045	11 Oct. 1981	NE of NW of S.16, T.137 N, R.26 W	Age classes 1914,32
046	6 Aug. 1982	SW of NE of S. 9, T.143 N, R.34 W	Mosses collected
047	13 Aug. 1982	NW of NE of S.22, T.140 N, R.34 W	
048	13 Aug. 1982	SW of NE of S.15, T.140 N, R.34 W	
049	13 Aug. 1982	NE of SE of S. 9, T.139 N, R.32 W	
050	14 Aug. 1982	SE of NW of S.12, T.140 N, R.34 W	
051	14 Aug. 1982	SW of NW of S.12, T.140 N, R.34 W	
052	14 Aug. 1982	SE of NW of S.12, T.140 N, R.37 W	
053	14 Aug. 1982	SW of NE of S. 2, T.140 N, R.37 W	
054	14 Aug. 1982	SW of NE of S.18, T.140 N, R.36 W	
055	15 Aug. 1982	SE of NW of S.30, T.139 N, R.32 W	Adj. Badoura fire
056	15 Aug. 1982	NE of SE of S.13, T.139 N, R.33 W	
057	15 Aug. 1982	NW of SE of S.33, T.144 N, R.34 W	
058	16 Aug. 1982	NW of NE of S.34, T.144 N, R.34 W	
059	15 Sep. 1982	SE of NW of S.15, T.136 N, R.27 W	

APPENDIX 3.B

VOUCHER SPECIMENS AND ADDITIONAL TAXA

VOUCHER SPECIMENS

231 different species or species complexes were encountered in the study.

152 species have corresponding voucher specimens.

387 voucher specimens were collected and submitted to the herbarium.

The numbers above pertain to vascular species only.

SPECIES	COLLECTION NUMBER
<i>Actea rubra</i> (Ait.) Willd.	4703
<i>Agastache foeniculum</i> (Pursh) Ktze.	3,2003,2702,3909,5107,5201
<i>Agropyron trachycaulum</i> (Link) Malte.	3209,3410,3411,3507,3610,3708,4006
<i>Agrostis scabra</i> Willd.	52
<i>Allium stellatum</i> Fraser	4702,5003,5303
<i>Alnus rugosa</i> (Du Roi) Spreng.	4000
<i>Anaphalis margaritacea</i> (L.) C.B.Clarke	3213
<i>Anemone patens</i> L.	2202
<i>Anemone riparia</i> Fern.	3312,3400,3515,3702,4701,4808,5300
<i>Apocynum androsaemifolium</i> L.	2200,2603
<i>Arabis divaricarpa</i> Nels.	1708
<i>Arabis lyrata</i> L.	2212
<i>Artemisia absinthium</i> L.	2512
<i>Artemisia ludoviciana</i> Nutt.	2211
<i>Asclepias ovalifolia</i> Dcne.	10,1710,2102,2802,3313
<i>Aster azureus</i> Lindl.	13,1807,1815,4106,4204b,4302
<i>Aster ciliolatus</i> Lindl.	42,1712,3403,3504,3803,4502
<i>Aster laevis</i> L.	28,1804,1902
<i>Aster lateriflorus</i> (L.) Britt.	43
<i>Aster macrophyllus</i> L.	1500
<i>Aster ptarmicoides</i> (Nees) T. & G.	11,2404,4208,5503
<i>Aster sagittifolius</i> Willd.	4,4102,4213
<i>Astragalus canadensis</i> L.	2900
<i>Athyrium filix-femina</i> (L.) Roth	3805
<i>Botrychium multifidum</i> (S.G. Gmel.) Rupr.	3615
<i>Bromus ciliatus</i> L.	9,3612
<i>Bromus kalmii</i> A. Gray	18
<i>Campanula rotundifolia</i> L.	1810,2703,3003
<i>Campanula rotundifolia</i> forma <i>albiflora</i> Rand & Redf.	5801
<i>Carex pennsylvanica</i> Lam.	3409,3609,3809,4004,4113,4211,4312 4508
<i>Ceanothus ovatus</i> Desf.	1800

[continued on next page]

[Voucher Specimens continued

<i>Celastrus scandens</i> L.	3907
<i>Chenopodium hybridum</i> v. <i>gigantospermum</i> (Aellen)Rouleau	5104
<i>Chimaphila umbellata</i> v. <i>cistatlantica</i> Blake	2907
<i>Cirsium arvense</i> (L.) Scop.	2301,4607,5005,5302
<i>Convolvulus spithameus</i> L.	40,4304
<i>Cornus racemosa</i> Lam.	1600,2500,3214,3405,4700,4800,5100
<i>Cornus stolonifera</i> Michx.	26,4616,4904
<i>Corydalis aurea</i> Willd.	1705
<i>Crepis tectorum</i> L.	5009
<i>Cynoglossum boreale</i> Fern.	3914
<i>Danthonia spicata</i> (L.) Beauv.	53,1715,1907
<i>Dryopteris spinulosa</i> (O.F. Muell.) Watt	47,1908,2001,2300,3509,3802
<i>Elymus canadensis</i> L.	51,1608,4803,5400
<i>Epigea repens</i> L.	2910
<i>Equisetum hyemale</i> L.	1814,2909,3617,3811
<i>Equisetum pratense</i> Ehrh.	3808
<i>Erigeron canadensis</i> L.	2509
<i>Erigeron glabellus</i> v. <i>pubescens</i> Hook.	5313
<i>Erigeron strigosus</i> v. <i>septentrionalis</i> (Fern.& Wieg.) Fern.	3308,3404
<i>Fragaria vesca</i> Duchesne	5314
<i>Fragaria vesca</i> v. <i>americana</i> Porter	1711
<i>Fragaria virginiana</i> Duchesne	3207
<i>Galium triflorum</i> Michx.	45
<i>Geranium maculatum</i> L.	57,4805
<i>Geum triflorum</i> Pursh	2402
<i>Goodyera pubescens</i> (Willd.) R. Br.	1808
<i>Goodyera repens</i> (L.) R. Br.	4310
<i>Goodyera tessellata</i> Lodd.	24,4108,4219,4311,4403,4404,5008,5601 5703,5705
<i>Hackelia americana</i> (Gray) Fern.	5108,5301,5310,5404
<i>Helianthemum Bicknellii</i> Fern.	1702,2508
<i>Helianthus giganteus</i> L.	3514,4804,5200
<i>Helianthus laetiflorus</i> Pers.	2414,4205,5600
<i>Helianthus strumosus</i> L.	55
<i>Heliopsis helianthoides</i> (L.) Sweet	5001
<i>Hepatica americana</i> (DC.) Ker.	4501
<i>Hieracium scabrum</i> Michx.	2913,3006,4207
<i>Hieracium umbellatum</i> L.	3008,3302
<i>Koeleria cristata</i> (L.) Pers.	3512,3613
<i>Krigia biflora</i> (Walt.) Blake	4901,5504
<i>Lactuca canadensis</i> L.	4608,5304,5402,5701

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[Voucher Specimens continued]

<i>Lathyrus ochroleucus</i> Hook.	1706,3402
<i>Lathyrus venosus</i> Muhl.	3301,3401
<i>Lechea stricta</i> Leggett	1709
<i>Liatris aspera</i> Michx.	4215,5506
<i>Liatris ligulistylis</i> (Nels.) K. Schum.	17,3502,3607,3710
<i>Lilium philadelphicum</i> L.	4202
<i>Lithospermum canescens</i> (Michx.) Lehm.	1809
<i>Lonicera canadensis</i> Bartr.	33
<i>Lonicera dioica</i> L.	1502,2002,2513,1602,2700,3606
<i>Lychnis alba</i> Mill.	60,2403
<i>Lysimachia ciliata</i> L.	80,5700
<i>Maianthemum canadense</i> v. <i>interius</i> Fern.	2906
<i>Melampyrum linneare</i> Desr.	1805
<i>Monotropa uniflora</i> L.	32
<i>Muhlenbergia glomerata</i> (Willd.) Trin.	1903,3614,3707,4005,4111,4209,4307, 4407,4506,5010
<i>Muhlenbergia mexicana</i> (L.) Trin.	2302,3009,4507
<i>Oryzopsis asperifolia</i> Michx.	38
<i>Oryzopsis pungens</i> (Torr.) Hitchc.	54,1716,4110,4212,4610,4704,4902,5510 5704
<i>Osmorhiza Claytoni</i> (Michx.)C.B. Clarke	3901,3903
<i>Panicum columbianum</i> Scribn.	2412
<i>Panicum Leibergeri</i> (Vasey) Scribn.	2511,2704
<i>Parietaria pensylvanica</i> Muhl.	5308
<i>Parthenocissus inserta</i> (Kerner)K.Fritsch	5,1820,3904
<i>Pedicularis canadensis</i> L.	21,3711
<i>Phlox pilosa</i> L.	78,1821,5505,5602
<i>Physalis virginiana</i> Mill.	1813,2101,2203,5502
<i>Poa pratensis</i> L.	3510
<i>Polygala paucifolia</i> Willd.	4611
<i>Polygala Senega</i> L.	14
<i>Polygonatum biflorum</i> (Walt.) Ell.	5007
<i>Polygonatum pubescens</i> (Willd.) Pursh	3506,4218
<i>Polygonum Convolvulus</i> L.	59,2604,5106,5202,5307,5409
<i>Potentilla argentea</i> L.	2504
<i>Prenanthes alba</i> L.	2501,3503,3703
<i>Prunus pensylvanica</i> L.	5205
<i>Prunus pumila</i> L.	1812,1900,3000,3212,3407,3501,3601,3705 3801,4303,4614,4900
<i>Pyrola asarifolia</i> Michx.	2208,3806
<i>Pyrola rotundifolia</i> L.	37b,1901,4002,4007,4309,4406
<i>Pyrola secunda</i> L.	37a,1811,1909,3807
<i>Pyrola virens</i> Schweigger	3208,5507,5803
<i>Rhus glabra</i> L.	1601
<i>Ribes cynosbati</i> L.	3007,3201

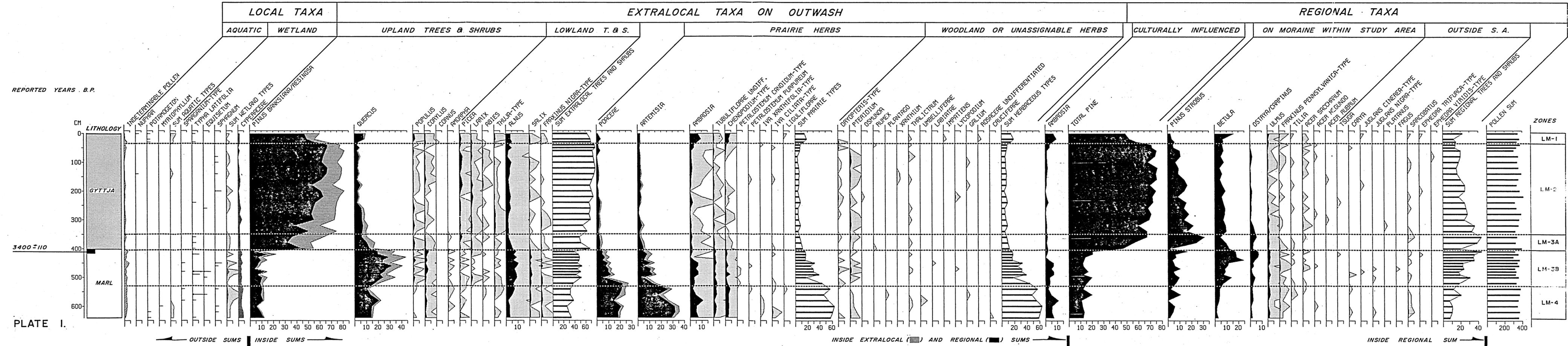
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[Voucher Specimens continued]

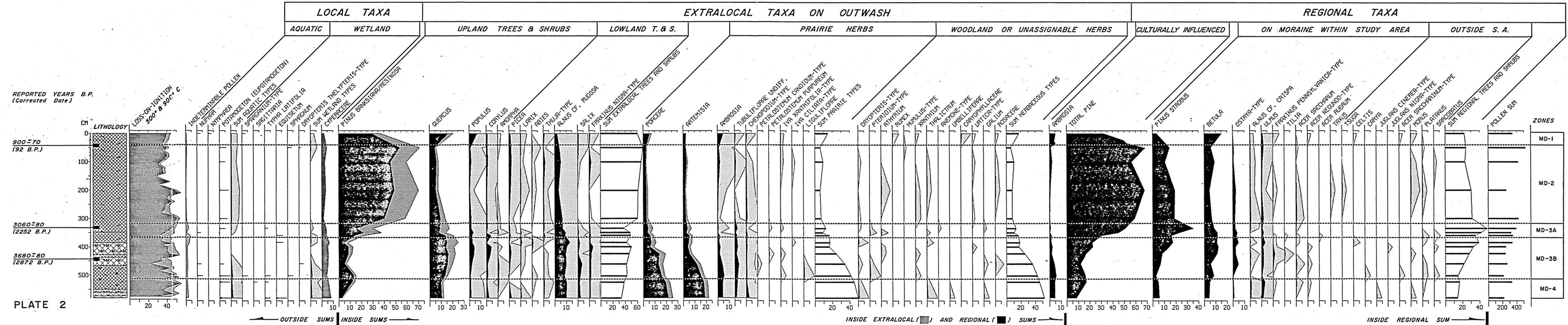
<i>Ribes hirtellum</i> Michx.	5312
<i>Rosa acicularis</i> Lindl.	4001,4100,4201
<i>Rosa blanda</i> Ait.	48,1821,3800
<i>Rubus idaeus</i> v. <i>strigosus</i> (Michx.)Maxim.	1809
<i>Rubus pubescens</i> Raf.	4801
<i>Salix discolor</i> Muhl.	25
<i>Salix humilis</i> Marsh.	15,16,34,2008
<i>Sambucus canadensis</i> L.	3906,5406
<i>Sanicula marilandica</i> L.	2006,4903
<i>Senecio pauperculus</i> Michx.	1713,1714,1801
<i>Smilacina stellata</i> (L.) Desf.	1819,3902
<i>Smilax herbacea</i> L.	7
<i>Solidago gigantea</i> Ait.	4104
<i>Solidago hispida</i> Muhl.	2,36,1701,1803,2503,4107,4216,4301 4308,4401
<i>Solidago juncea</i> Ait.	4217,4603,5509,5702,5900
<i>Solidago nemoralis</i> Ait.	12,2207,2415,2905,3005,3304,3511,4605
<i>Solidago speciosa</i> Nutt.	2908,3300,3603,3604,3611,4103
<i>Solidago speciosa</i> v. <i>rigidsulcata</i> T.&G.	5508
<i>Sorbus americana</i> Marsh.	4511
<i>Spiraea alba</i> Du Roi	56,2105,2406
<i>Spiranthes lacera</i> Raf.	1911,4600,5800
<i>Stachys palustris</i> L.	58,3908
<i>Symphoricarpos occidentalis</i> Hook.	1605,3406,3607,3704,4101
<i>Thalictrum dasycarpum</i> Fisch.	1606,3804
<i>Trientalis borealis</i> Raf.	4003
<i>Trifolium repens</i> L.	3310
<i>Urtica dioica</i> Ait.	5309
<i>Uvularia sessilifolia</i>	44
<i>Vaccinium angustifolium</i> Ait.	2902
<i>Vaccinium myrtilloides</i> Michx.	4405
<i>Veronicastrum virginianum</i> (L.) Farw.	72
<i>Viburnum Rafinesquianum</i> Schultes	1607,4400,4510
<i>Vicia americana</i> Muhl.	1501,1700
<i>Viola adunca</i> Sm.	2204,4105,4306,4410,4504,4612
<i>Viola conspersa</i> Reichenb.	31
<i>Viola pedatifida</i> G. Don	5407
<i>Viola sororia</i> Willd.	2601,3900
<i>Zizia aptera</i> (Gray) Fern.	22,4602

The occurrence of species not in Table 3.2 are given in Table 3.B.1 (back pocket).

LAKE MINNIE, FULL DIAGRAM
 HUBBARD COUNTY, MINNESOTA
 ANALYST: J.H. MCANDREWS, 1970



MUD LAKE, FULL DIAGRAM
 HUBBARD COUNTY, MINNESOTA
 ANALYST: J. C. ALMENDINGER, 1983



BIG JOHN POND, FULL DIAGRAM

BELTRAMI COUNTY, MINNESOTA
ANALYST: J.C. ALMENDINGER, 1984

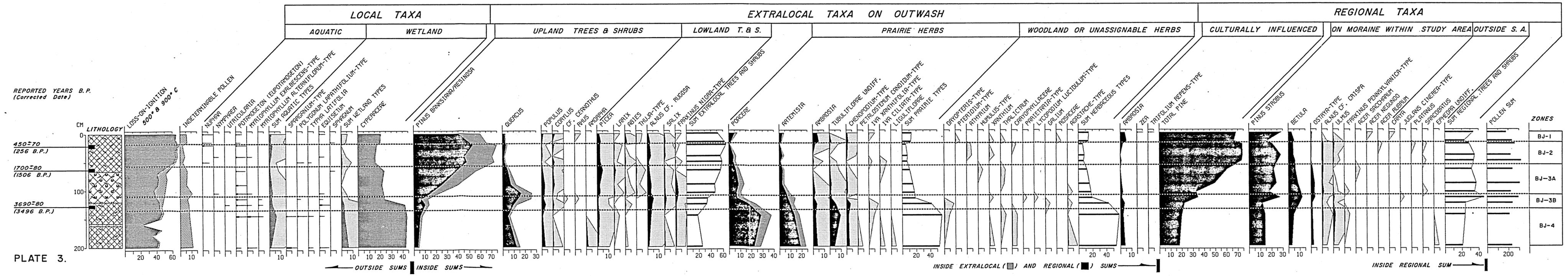


PLATE 3.

HOSTAGE LAKE, FULL DIAGRAM

CROW WING COUNTY, MINNESOTA
ANALYST: J.C. ALMENDINGER, 1984

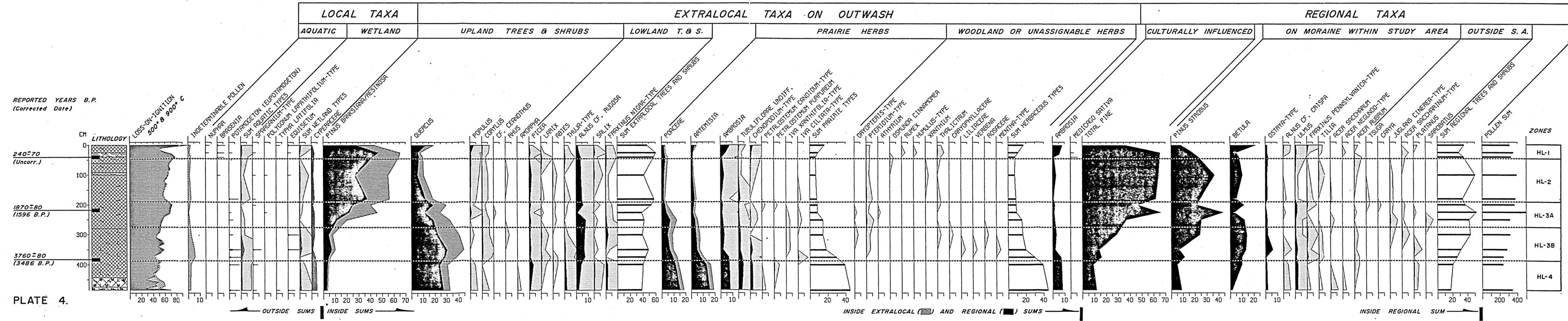


PLATE 4.

WENTZEL'S POND, FULL DIAGRAM
 HUBBARD COUNTY, MINNESOTA
 ANALYST: J.C. ALMENDINGER, 1983

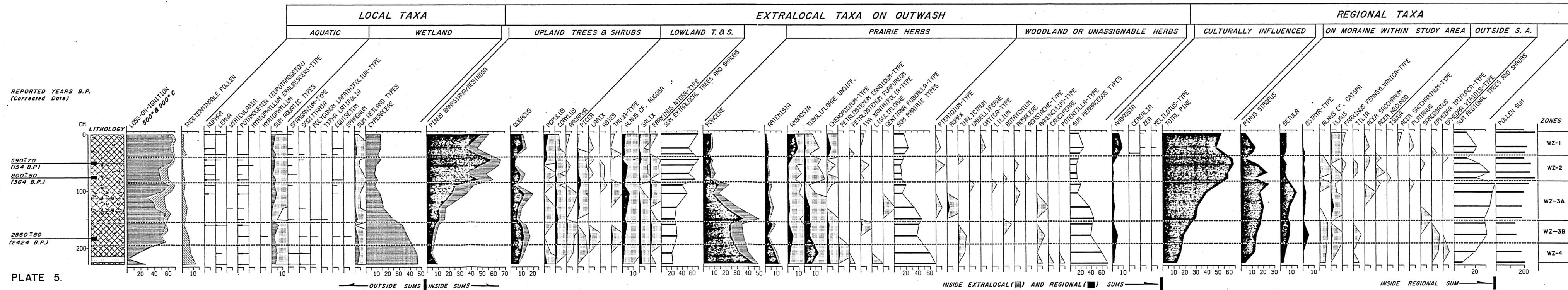


PLATE 5.

PETERSON SLOUGH, FULL DIAGRAM

BECKER COUNTY, MINNESOTA
ANALYST: J.C. ALMENDINGER, 1984

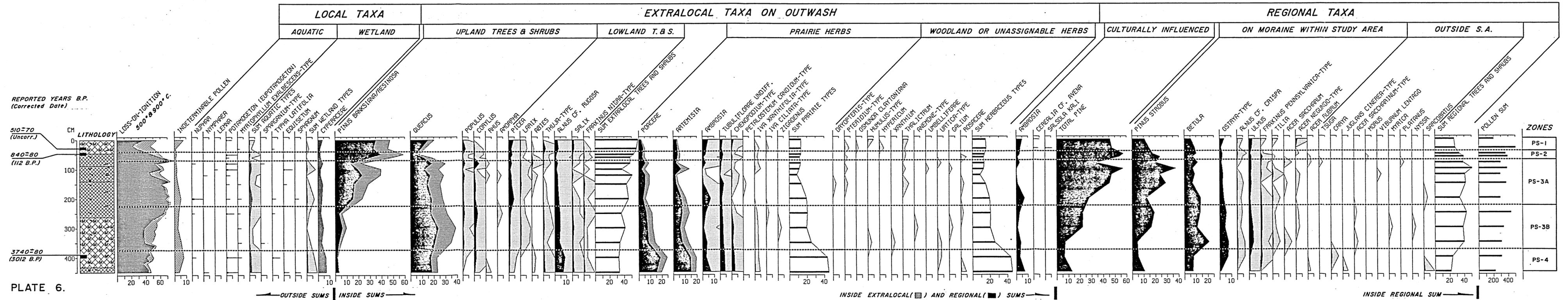


PLATE 6.

Table 3.2. Phytosociological table of relevés from *Pinus banksiana* forests in north-central Minnesota. Relevé order was fixed by (1) assignment to one of four soil-based units (Table 3.1) and by (2) the classification ranking from Figure 3.3. Table values are for species cover-abundance: 1, cover 0-1%; 2, cover 2-4%; 3, cover 5-9%; 4, cover 10-19%; 5, cover 20-100%. Species included occur in > 20% of the relevés in one of the seven combinations (Groups A-G) of soil-based units. Tree and shrub strata are: S=seedling or low shrub (0-2 m), U=sapling or tall shrub (2-10 m), T=tree (>10 m).

Soil-Based Unit	-LAKE- GEORGE	-----OTHER----- -----LIGHT SOILS-----							---SANDY--- DARK SOILS	---LOAMY--- DARK SOILS		
Relevé Number	253345 980267	235 46556	1 78901	444 34045	1144 28912	44552 39693	33333 34578	132 198	31121 14217	21221 23565	25455 70712	55124 34608
GROUP A												
<i>Hieracium scabrum</i>	12221.1.1	...1.
<i>Equisetum hyemale</i>	2.1.2.	.1...1...	...1.1
<i>Agrostis scabra</i>	1..22.	.1...	...2.2..1..
<i>Epigaea repens</i>	222...	2....	.2....
<i>Polygala paucifolia</i>	.22222
<i>Picea glauca</i> S	.211.112.
<i>Pyrola virens</i>	.212..	..2..
<i>Spiranthes lacera</i>	.1..2.2..
<i>Zizia aptera</i>	.21.1.	.2...	2....2..
<i>Ribes cynosbati</i>	..11..2..1..
<i>Cypripedium acaule</i>	..12..2..2..	1....
<i>Solidago juncea</i>11	..1..	..2..	1....1
GROUP B												
<i>Pinus resinosa</i> U	.2.22.1...	2.1.2	..2..	.1...
<i>Abies balsamea</i> S	..3211	.1.21	22...	2..22..1.2..1..
<i>Melampyrum lineare</i>	.2..22	..2.11	212.2	.1.2.	2..2.	..2..
<i>Pinus resinosa</i> S	11.12.	..21	111.1	2....	1....	2....
<i>Solidago nemoralis</i>	222211	1.2..2.	2....	..222	2.2..	2....
<i>Prunus pumila</i>	.22222	.2...12..	1221.	1221
<i>Ptilium crista-castrensis</i>22	..2..	..2..2	2222.2	..2.	..2..
<i>Pteridium aquilinum</i>	..25..	...53	23333	.5255	3..23	5.232	.22.2	32.	5....3
GROUP C												
<i>Linnaea borealis</i>2	...22	2.22.	.21.2	..2..	..2..22
<i>Betula papyrifera</i> S2.	...32	.22.1	2..2.	.2.21	1..2.	2....
<i>Acer rubrum</i> S3.	.23.2	2.221	2..1.	1....
<i>Acer rubrum</i> U22.	1.211	1....
<i>Betula papyrifera</i> T3	..1..	..3.11	..2..1.
<i>Trientalis borealis</i>2	..2..	2....	2.2222..2	.1.
<i>Monotropa uniflora</i>2	..2.2	22.1.1	2....1	.1.
<i>Betula papyrifera</i> U2..	2..1.1	112211.
<i>Pyrola rotundifolia</i>	2....1222	..22.	2.222	.1...	...	21...
<i>Goodyera tessellata</i>12.	..22	2222.2..
<i>Epilobium angustifolium</i>	..2...2..2	11.2.2	2..
<i>Ceanothus ovatus</i>2..	22.22	..2..	2.121
GROUP D												
<i>Vaccinium angustifolium</i>	552335	23222	22232	22222	22325	23332	22322	222	2222.	22222	222.2	...12
<i>Arctostaphylos uva-ursi</i>	553233	2.22.	..2..	22221	22322	22.22	222..2	2....	..2..
<i>Oryzopsis pungens</i>	232222	.21..	..2..	2322.	.12.2	22.2.2	2....	..1..
<i>Pinus banksiana</i> S	222222	.12..	..2..	2322.	.12.2	22.2.	..22..	...	1....	2.1..
<i>Gaultheria procumbens</i>	222222	..2.2	22..2	..222	22223	22.32	..2.22	...	2....	..22.
<i>Viola adunca</i>	222222	..22.	..22.	2..22	..2.22	..2..	222.2	2.2..
<i>Chimaphila umbellata</i>	2.2.22	..212	..2.22	2222.	22222	22222	212.1	..2	22.22	2....
<i>Corylus cornuta</i> S	..2.22	..2225	53332	3..12	..2..1	..2.1.	..2232	..22	..2..52
<i>Pinus banksiana</i> U	21....	..2..	211..2..	2..	..2.2	11...
<i>Bromus kalmii</i>	..2.1..	..12.	2.2..	2.22.	2.2..	2..	..2..	12...
<i>Rubus allegheniensis</i> ²	...2..	..2..	..2.2	..213	..22.	21.2.	..232	3..	3.22.2
<i>Aster azureus</i>	2.2..2.	22222	2.22.	22.2.	..22.
GROUP E												
<i>Corylus americana</i> S	...22.	3.322	22.33	32222	32232	32325	23221	425	22334	55533	55.55	55343
<i>Corylus americana</i> U2	2.1122	1.2..	1..2.	.1.42	.2555	55243
<i>Rhus radicans</i>22	22232	1.333	..2.22	22222	..2	1.222	2.222	22222	..2222
<i>Thalictrum dioicum</i>	...1..	..22	2.3..22.	..2.1	22222	..22	..2..	..2222	22222	22222
<i>Uvularia sessilifolia</i>22	2.2..	..222.2	2.2	..2..	..2.2	222.1	..222
<i>Aralia nudicaulis</i>	..2...	..2.	1.22.	..222.3	.32..2.1	2..2	..232	32523
<i>Pyrola secunda</i>22.2	..222.	2222	..22.	1.2.2	22..2	..22	22222	2.2..	222..	2.121
<i>Quercus macrocarpa</i> U	1....	1.112	..1..	2..21	1.1.1	..22.	323	22222	22222	332.5	..3232
<i>Symphoricarpos albus</i> S	22.12	22.2.1.	..222.2	22222	2.2	..2..3	..232	2.2..	..222
<i>Populus tremuloides</i> U	231..3	..1..	23...	...	1.21.	..2.2.	22....	2.122
<i>Prunus virginiana</i> U	22....	..22.2	..1..	1...1	..2..	2222.2.2	..2..	22.23	221.2
<i>Physalis virginiana</i>	212..	2....	..2..12	..2.1.	..2	..1..	2..2.	..22..	..2...
<i>Heuchera richardsonii</i>	2....	..2..	2..11	2.1..	..2..11..	..222.	22....	..1...
<i>Prunus pensylvanica</i> S223	222..	..12.	..22.1	..2.22	2....	..2	2.12.	..2..1	..1.2
<i>Prunus pensylvanica</i> U2	2222.	..21.	..21	..2..221.	..12.	..22.	1.2.2
<i>Parthenocissus inserta</i>2.22..	..2.222	..22.2	..2..	..2212
<i>Sanicula marilandica</i>2	2.2..	1....1.	..1..2	2.222	..2.	..2..	..2.2.	1212.	...12
<i>Agastache foeniculum</i>2	..2.	..2..	..22	..22	..2.	..2..	2....	22.11	..2..
<i>Smilacina stellata</i>2	..22.	..2.22	..2222.	..2..	2....	121..	..2..
<i>Asclepias ovalifolia</i>2	12.2.	11222	2....	1.2	..112	1.2..	2.1..	2....
GROUP F												
<i>Smilax herbacea</i>1..	1....1	1..1.	.1.	12...	21.21	12.21	2.11.
<i>Populus tremuloides</i> T3..3	1.21.	..3.2.	..32..	2...2
<i>Quercus borealis</i> ³ T2..	..1..	1.21.	1.1.2	..1..	..21..
<i>Quercus macrocarpa</i> T1.	2..2.	..2.222	..52..
<i>Amorpha canescens</i>	2....1.1.	2...1	2....	..22..	..21..
<i>Circium arvense</i>1.	1....2	1....	..22.	11...	2....
<i>Prunus serotina</i> S1..122..22.	2.11.
<i>Spiraea alba</i>	2....1..	2....2221.1..
<i>Crataegus spp.</i>2..	221..1	..2..	212.2	21..1
<i>Cornus racemosa</i> S	...2..	..1..2..2..	..22..	..2222	..22..
<i>Aquilegia canadensis</i>2	..2..12	..2..	22..2	22...
<i>Viburnum rafinesquianum</i> S1.	..2..	..11	..1.	..1..2	..22.2	..1221	..2322
<i>Veronicastrum virginianum</i>	1.1..2..2.	22122
GROUP G												
<i>Prunus serotina</i> U	1.1..2..2.	22122
<i>Cornus racemosa</i> U22.	..2.2
<i>Viburnum rafinesquianum</i> U1..	..1..1	..22.	..2212
<i>Pyrola asarifolia</i>	..2....2.	2....	..22.	..21
<i>Viola sororia</i>2.2.	..222.	2....
<i>Polygonum convolvulus</i>1.11	22...
<i>Plagiomnium cuspidatum</i>2..2..2	22..2
<i>Thalicttrum dasycarpum</i>11.	2....	2.1..
<i>Petalostemum candidum</i>	2....1..	..2..
<i>Populus grandidentata</i> U2	..21.	1....1..2
<i>Elymus canadensis</i>2..	2..21.2
<i>Helianthus giganteus</i>2..21
<i>Symphoricarpos occidentalis</i> U	1....	22...

1. includes *Viola conspersa*

2. includes all members of the subgenus Eubatus

3. includes *Quercus ellipsoidalis* and *Q. borealis* x *ellipsoidalis* hybrids

Table 3.4. Phytosociological table of relevés from Pinus banksiana forests in north-central Minnesota. Relevé order is the same as in Table 2. Table values are for species cover-abundance: 1, cover 0-1%; 2, cover 2-4%; 3, cover 5-9%; 4, cover 10-19%; 5, cover 20-100%. Height strata are: S=seedling (0-2 m), U=sapling (2-10 m), T=tree (> 10 m). Species showing similar presence-abundance patterns were grouped (A-D) to facilitate discussion.

Soil-based unit	-LAKE- GEORGE	-----OTHER----- -----LIGHT SOILS-----							---SANDY--- DARK SOILS	---LOAMY--- DARK SOILS		
Relevé number	253345 980267	235 46556	1 78901	444 34045	1144 28912	44552 39693	33333 34578	132 198	31121 14217	21221 23565	25455 70712	55124 34608
GROUP A												
<u>Picea glauca</u> U	.1....2
<u>Picea glauca</u> S	.211.112.
<u>Picea mariana</u> U	.1....	1....
<u>Abies balsamea</u> U22..12...1..
<u>Abies balsamea</u> S	..3211	.1.21	22...	.2..22..	...1.2..1..
<u>Pinus resinosa</u> T111..	3..2.2.2	..2.1
<u>Pinus resinosa</u> U	11.12.	...21	111.1	2....	1....	2....
<u>Pinus resinosa</u> S	.2.22.1...	2.1.2	.2..	.1...
<u>Pinus banksiana</u> T	555555	55555	55555	55555	55555	55555	55555	555	55555	55555	55555	55555
<u>Pinus banksiana</u> U	21....	..2..	211..2... 2..2.2	11...
<u>Pinus banksiana</u> S	222222	.12..	.2...	2322.	.12.2	22.2.	.22..	...	1....	2.1..
GROUP B												
<u>Pinus strobus</u> U1..1
<u>Pinus strobus</u> S2.	12..2	1....
<u>Fraxinus pensylvanica</u> U	1....22
<u>Fraxinus pensylvanica</u> S1.	...2.2..22
<u>Populus grandidentata</u> T2	...1.	1....
<u>Populus grandidentata</u> U2	..21.	1....1..2
<u>Populus grandidentata</u> S2.2	..12.	...1.	2....1..
<u>Acer rubrum</u> T1..
<u>Acer rubrum</u> U22..	1.211	1....
<u>Acer rubrum</u> S3.	.23.2	2.221	2..1.	1....2.
<u>Betula papyrifera</u> T3	..1..	..3.11	...2.1.
<u>Betula papyrifera</u> U2..	2..1.1	112211.
<u>Betula papyrifera</u> S2.	...32	.22.1	2..2.	.2.21	1..2.	2....
GROUP C												
<u>Populus tremuloides</u> T3...3	1.21.	.3.2.	.32..	2...2
<u>Populus tremuloides</u> U	231..3	..1..	23...	...	1.21.	.2.2.	22...	2.122
<u>Populus tremuloides</u> S21	221..	...22	..2..	.2...	.2...	22..2	...	2222.	1212.	.22..	2.112
<u>Quercus borealis</u> T2..	.1...	1.21.	1.1.2	..1..	.21..
<u>Quercus borealis</u> U1.1111	2..22	222212	.12	2.211	1.1.2	2.1..	..122
<u>Quercus borealis</u> S	.12211	..223	.3323	..221	22122	32223	2.1.2	322	.2322	32222	212..	..122
<u>Quercus macrocarpa</u> T1.	2..2.	..2.2	...22	.52..
<u>Quercus macrocarpa</u> U	1....	1.112	..1..	2..21	1.1.1	..22.	323	22222	22222	332.5	.232
<u>Quercus macrocarpa</u> S	..222.	22.12	2222.	311..	22.21	122.3	.32.	322	22332	33221	232.2	.2232
GROUP D												
<u>Prunus serotina</u> U	1.1..2..2.	22122
<u>Prunus serotina</u> S1..122..22.	2.11.

