Postglacial history of prairie, savanna, and forest in northwestern Minnesota

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Introduction

Northwestern Minnesota lies near the center of North America within an area outlined by the 46th and 49th parallels N. and 94th and 97th meridians W. Near the center of the area lie Itasca State Park and Lake Itasca, the source of the Mississippi River. The area was repeatedly glaciated during the Pleistocene and most recently became available for plant occupancy 12,000 to 13,000 years ago. Plant migration and succession has culminated in three major vegetational formations: Pine-Hardwood Forest, Deciduous Forest, and Prairie (Fig. 1). The transitions between these formations in general correspond to steep climatic gradients, although locally influenced by topographic, soil, and fire factors.

The Pine-Hardwood Forest is characterized by *Pinus strobus* and *P. resinosa*. The name is a contraction of the term Hemlock - White Pine - Northern Hardwoods Forest applied to the same unit by Braun (1950); her term is not suitable for Minnesota because of the absence of *Tsuga*. This formation contains in places typical elements of the Boreal Forest, such as *Abies* and *Picea*, as well as characteristic genera of the Deciduous Forest, such as *Quercus*, *Acer*, *Fłóra* and *Ulmus*. Conifers are generally absent from the Deciduous Forest. The Deciduous Forest in the broad sense of Braun (1950) is here divided into three formations, Aspen Parkland, Oak Savanna, and Mesic Deciduous Forest. The Aspen Parkland is characterized by almost pure groves of *Populus tremuloides* and has its most extensive development northward in Manitoba. The Oak Savanna lies in the southern part of the area between the Prairie and Mesic Deciduous Forest; it is characterized by open stands of *Quercus macrocarpa*. The Mesic Deciduous Forest is dominated by luxuriant closed stands of *Quercus*, *Acer*, *Fłóra*, and *Ulmus*. The Prairie or Grassland is usually treeless and is dominated by various genera of *Gramineae, Compositae*, and *Leguminosae* (Weaver, 1954).

Beginning about 1880, exploitation by settlers gradually destroyed or drastically altered the Prairie by cultivation and the Forest and Savanna

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by logging, reducing the fire frequency, and cultivation. Studies of relics of the natural vegetation indicate that the transitions or ecotones are unstable as a result of climatic change (Buell and Cantlon, 1951; Buell and Martin, 1961). Such studies are complementary to longer-term vegetational history, which can only be known through fossils.

The fossil evidence for postglacial vegetation in northwestern Minnesota is limited to three tree-pollen diagrams from the Pine-Hardwood Forest. The lower portion of two diagrams by Potzger (1946) shows high Picea pollen percentages, and the upper portions have high Pinus values. Quercus is strongly represented in the middle of the diagrams. He interpreted the lower Picea zone to represent an early boreal-type vegetation and the succeeding Pinus zone to represent the Pine-Hardwood Forest. He stated, "there is no evidence of replacement of coniferous forest by prairie... however, Quercus extended a controlling influence farther eastward than it has today, and was replaced again by Pinus." He apparently assumed Prairies would be represented by high percentages of Gramineae pollen to the near exclusion of tree pollen. Because he did not publish herb-pollen percentages, his evidence cannot be evaluated.

He also failed to describe the sediment stratigraphy, and the possibility of a hiatus in sedimentation during a Prairie invasion cannot be excluded.

Erdtman (1943, Fig. 11) published a pollen diagram from Twin Lakes Bog in Itasca Park, a site studied by the present writer. It is a truncated record because it lacks the early Picea zone of Potzger (1946). The lower portion contains high values of Quercus. The pollen succession upward is toward such deciduous genera as Betula, Ostrya, and Tilia, followed by a Pinus-dominated zone at the top. No discussion was given, as the diagram was presented only to illustrate diagram-drawing technique (G. Erdtman, oral communication), but the diagram suggests a succession from xeric oak forest to Mesic Deciduous Forest to the present Pine-Hardwood Forest.

No pollen diagrams have been available until now from the Deciduous Forest or Prairie areas, so their postglacial history has been quite unknown. However, pollen-analytical studies elsewhere in Minnesota show that the early boreal-type vegetation was widespread and was succeeded by a series of forest and prairie invasions, presumably as a result of climatic change (Fries, 1962; Wright, Winter, and Patten, 1964; Farnham, McAndrews and Wright, 1964).

Because it has strong contrasts in vegetation linked with climate and because it has many pond sites containing sediment, northwestern Minnesota provides an excellent opportunity to apply pollen analysis to the reconstruction of postglacial vegetation and climatic history.

The area chosen for field studies, here called the Itasca transect, is bounded by township lines 143N and 144N and range lines 34W and 45W; it lies in Hubbard, Clearwater, Mahnomen, and Norman Counties. This transect of eleven townships extends westward from the Pine-Hardwood Forest across a narrow belt of Mesic Deciduous Forest and Oak Savanna and ends in the Prairie. The transect was chosen because it contained most of the major landforms and plant communities of northwestern Minnesota, in fact all except the Aspen Parkland formation and the patterned bog of the Pine-Hardwood Forest. In addition, it contained many relict stands, notably in Itasca State Park, where the University of Minnesota Forestry and Biological Station is located. Ecologists connected with the Station have made many studies of the vegetation within the transect area.

The objective of this study is the reconstruction of post glacial vegetation and climatic history of northwestern Minnesota, based on the Itasca transect. This reconstruction involves study of 1) the qualitative and quantitative characteristics of the natural vegetation of the time just before settlement, and estimates of the climatic and other environmental factors that determined them, 2) the fossil pollen of this vegetation, and 3) the
pollen in postglacial sediment and its relation to the contemporary vegetation.

Plant nomenclature follows Fernald (1950). Species names and authors that do not appear in that manual are *Sarcobatus vermiculatus* (Hook.) Torr., *Juniperus scopulorum* Sarg. and *Iva azelaris* Pursh.

This paper is based on a dissertation submitted to the Graduate School of the University of Minnesota in partial fulfillment of the requirements of the degree of Doctor of Philosophy (McAndrews, 1964).

**Methods**

The field work, which was done between June 1958 and May 1963, involved 1) a survey and sampling of the relict vegetation along the formation boundaries, and 2) the collection of cores of sediment from ponds in each formation. The vegetation studies were carried on in the summer; the coring was done in the winter when ice provided a firm working surface.

The general cover-types of the transitional areas were mapped with the aid of air photographs. Field checks were made of critical boundaries. In transitional areas, relict stands of natural vegetation were identified and studied. Particular attention was paid to the structural characteristics of these stands and to their physiographic setting. Tree ages were obtained from counts of wood-growth layers on cut stumps and wood samples taken from living trees with a Swedish increment borer.

Short cores were collected from the upper meter of pond sediment for study of the pollen spectra of immediate pre- and post-settlement time. For this purpose, cores of loose, watery sediment were taken from seven ponds in the transect with a Rowley-Dahl sampler (1956). The core tubes were kept in an upright position until the sediment was frozen, then extruded after slight peripheral thawing, and wrapped in aluminum foil. Disks 1 cm thick were sawed from the frozen cores at each 5-cm interval. The outside of each disk was washed in running water to remove possible contamination, placed in a labeled jar, and refrigerated until prepared for analysis.

The sediment of four ponds was cored from the surface to the underlying glacial drift (long cores). The upper meter of loose sediment was sampled as described for the short cores. The lower sediments were cored with a modified Livingstone sampler by hand or with a chain hoist (Cushing and Wright, 1962). A 1" or 1½" diameter thin-walled steel coring tube designed to take meter-long core segments was used, and 100% recovery was usually obtained. In lower, more compact sediments, core recovery was most successful when ½ meter lengths were attempted. The core segments were extruded in the field, wrapped in aluminum foil, labeled, and refrigerated until sampled in the laboratory.

Sediment samples were prepared for pollen analysis with slight modification of the method of Faegri and Iverson (1950, p. 58). It usually included successive treatments with 10% HCl, 10% KOH, 40% HF, 10% HNO₃, and acetylation solution. The HNO₃ was used to remove pyrite crystals (Vallentine, 1963). The concentrate was stained with safranin and mounted in silicone oil (Anderson, 1960). Staining was most effective when the concentrate was brought to a circumneutral pH by three prior washings with water.

Pollen analysis was made with a Leitz 'Labolux' binocular microscope equipped with 10x oculars and fluorite objectives of 40x and 114x. Reference pollen from identified plant material was used for comparison in all fossil pollen identifications.

In selected samples a minimum of 50 *Pinus* pollen grains were determined as belonging to either the subgenus *Haploxylon* or the subgenus *Diplloxylon* with the criteria of Ueno (1958). The germinal furrow of *Haploxylon* grains are verrucate in contrast to the plicate furrows of *Diplloxylon* grains. Following Cushing (1963), the *Haploxylon* grains are called *Pinus strobus* type after the only species of this subgenus occurring naturally in eastern North America, and the *Diplloxylon* grains are called the *Pinus banksiana/roxburghii* type after the only two species of this subgenus that occur in Minnesota.

The core samples were generally spaced at 20-cm intervals, but in horizons of special interest analyses were made at 5 or 10 cm intervals. At least 300 pollen of trees, shrubs, and wind-pollinated herbs, other than aquatics, were counted per sample. The sediment of the long core from Martin Pond was sieved for leaves, wood fragments, fruits, and seeds, but only taxa of special importance in interpreting the pollen diagrams will be discussed.

The percentages shown in the pollen diagrams (Plates 2-6) are calculated from the sum of the determinable pollen of trees, shrubs, and anemophilous herbs other than aquatics. Excluded from the sum, but calculated as a percentage of the sum, were pollen of entomophilous herbs, aquatic herbs, Cretaceous types, unknown grains and spores of pteridophytes. Thus the pollen sum is intended to represent the upland vegetation. Although Cyperaceae may occur as a minor component of upland communities, aquatic Cyperaceae are considered the main source of this pollen type (Ritchie, 1964).
The pollen and spore counts are presented in an appendix, to provide data for different statistical manipulations. The pollen diagrams are all of a uniform type. The sediment symbols, omitted on the short-core diagrams, are adapted from Faegri and Iverson (1950). To the right of the lithology column is a summary diagram showing the pollen percentages of trees and shrubs (AP) plotted against anemophilous herbs (NAH); the curves for *Picea* and *Gramineae* are also shown. The solid curve indicates percentage directly from the scale at the bottom of the diagram; the stippled curve is exaggerated five times. The column labeled pollen sum separates the curves included in the pollen sum from those not included in the sum. The pollen zones are indicated at the extreme right.

For ease of discussion, the pollen diagrams were divided into several biostratigraphic units (zones), using a system similar to that of Cushing (1963). The main unit is the assemblage zone, which is defined as a body of strata characterized by a certain assemblage of fossils without regard to their stratigraphic range (American Commission on Stratigraphic Nomenclature, 1961). It is defined solely on the basis of the fossils it contains (pollen) without reference to lithology of the sediment, inferred environments, or concepts of time. However, in this study the fossil assemblages designated as zones have chronological and phytosociological implications. Some of the assemblages were divided into named subzones. Such subzones usually resemble assemblage zones at other sites, but at one site a subzone was designated without reference to other zones or sites.

A third kind of zone used is the peak zone, which according to the code is characterized by the exceptional abundance of some one taxon, for which it is named. The peak zone of this study occurs at two sites and implies a special condition for the proliferation and deposition of the fossil for which it was named. The zonation was drawn after consideration of all diagrams together, but it must be emphasized that the boundaries were defined solely from the fossil assemblages without regard to chronology.

**General considerations of northwestern Minnesota**

Because northwestern Minnesota lies in a prominent vegetational transition, local and regional physiographic and soil conditions play an important role in the patterns of the natural vegetation. Regional relief affects precipitation and temperature. Local physiographic variations create microhabitats with distinctive microclimates. Lakes provide fire-breaks. During the Wisconsin glaciation, a complex of materials was deposited on which are developed soils with widely varying moisture and nutrient characteristics.

**Physiographic setting**

Northwestern Minnesota may be divided into: 1) the nearly level Glacial Lake Agassiz lowland, which is situated in a drift-covered bedrock basin now overlain with till, in turn overlain with lacustrine deposits, and

![Physiographic map of northwestern Minnesota. The Itasca transect, the rectangle in the center, is 66 miles long and 6 miles wide.](image-url)
2) the hilly, glaciated upland to the east (Fig. 2). The surface of the lowland is the bed of Glacial Lake Agassiz and consequently has little local relief. Eastward it slopes gently upward from an altitude of about 900 feet along the Red River to 1,100-1,200 feet along the highest eastern beaches. Most of the streams tributary to the Red River arise in the glaciated upland, where they have moderately steep gradients in contrast to their low gradients on the bed of Lake Agassiz. Only a few lakes occur within the lowlands, and three of these are exceptionally large, namely Lake of the Woods and the two Red Lakes.

The surface of the glaciated upland was formed by late-Wisconsin ice movements and consists of several prominent end moraines and ground moraines with associated outwash plains. The end morainic areas rise eastward from the upper beaches of Lake Agassiz to about 1,600 feet. They have local relief of 200 to 400 feet and contain many undrained depressions occupied by lakes, ponds, and small peat bogs. Before settlement, the uplands were forested, except along the lower, western margin, which was occupied by Prairie (Upham 1884).

**Glacial geology**

Northwestern Minnesota is covered by three general kinds of glacial drift, originating from late-Wisconsin ice movements from the northwest, north, and northeast. These drifts reflect the type of bedrock over which the ice passed. The petrography of the source material and the mode of deposition of the drift have contributed to important differences in soil texture.

Extreme northwestern Minnesota and adjacent southeastern Manitoba are underlain by Paleozoic limestone and dolomite. Drift derived from this source is calcareous. The Cretaceous shale of western Minnesota imparts a prominent component of silt and clay to till derived from this source. Most of northern and northeastern Minnesota and adjacent Ontario is part of the Canadian Shield, composed of granitic and metamorphic rocks. Till derived from these sources is coarse-textured and noncalcareous.

Wright (1962) and Baker (1963) have summarized the ice movements and described the major geomorphic features of the area. Three discrete ice lobes deposited drift. The Wadena Lobe came from southern Manitoba, and at its terminus it contributed to the Alexandria Moraine complex. It formed a complex of ground moraine and outwash centering in Wadena County as well as the east-trending Itasca Moraine in central Hubbard and southern Clearwater counties (Fig. 3). In its advance this

lobe encountered both limestone and granite, and consequently the soil developed from this till is a calcareous sandy loam.

After the retreat of the Wadena Lobe, the Rainy Lobe advanced from the northeast and formed the St. Croix Moraine in Todd and Cass Counties.

**FIG. 3. Map of surficial geology of northwestern Minnesota (from Levee and Sardeson, 1932, and Wright, 1962). The Itasca transect, the rectangle in the center, is 66 miles long and 6 miles wide.**
On this till, a noncalcareous sandy-loam soil has developed. While the Wadena and Rainy Lobes were active, the Des Moines Lobe occupied the Red River Valley and contributed to the Alexandria Moraine and later formed the Big Stone Moraine. Its St. Louis Sublobe, advancing to the east, occupied the area north of the Itasca Moraine and left somewhat patchy till deposits. The Des Moines Lobe till is derived in part from limestone and shale bedrock, and thus a calcareous silt-loam soil has developed.

Following the retreat of the Des Moines Lobe, the large proglacial Lake Agassiz occupied the lowland. It is marked by a complex series of beach deposits and by various lacustrine deposits of sand, silt, and clay (Nikiforoff, 1939). Wright and Ruhe (1965) correlate the advances of the Wadena Lobe with the main Wisconsin ice advance and suggest that the still-stand of the Wadena Lobe at the Itasca Moraine and of the Rainy Lobe at the St. Croix Moraine occurred in the Cary Stade or before. The eastward extension of the St. Louis Sublobe is correlated with the Mankato Stade. Because an ice advance during the Valders Stade probably did not occur in northwestern Minnesota, Lake Agassiz very likely started its formation during the Two Creeks Intermadale following the Mankato Stade.

An absolute chronology for the various events in northwestern Minnesota is difficult to construct because of the lack of local radiocarbon dates. A general estimate places the Cary maximum as about 14,000 years ago, and Mankato about 13,000. Thus in northwestern Minnesota, some ice-free areas have been available for plant colonization since about 13,500 years ago, and all morainic areas about 12,000 years ago.

The series of parallel beaches of Lake Agassiz indicate the lake shrank in stages (Upham, 1896). The highest beach was formed before 11,700 years ago (Shay, 1965). The complete disappearance of this lake from northwestern Minnesota and colonization of its bed by terrestrial plants is estimated at about 8,000 to 9,000 years ago (Shay, 1965).

Soils

Arneson (1963) classified the soils of northwestern Minnesota on the nature of the soil parent-material and on the kind of vegetation important in their development. Prairie soils are found on the lacustrine sediments of the Lake Agassiz lowland, on the till of the lower margin of the glaciated upland, and on some of the outwash plains of the upland. The upper 6 to 12 inches of the profile is melanized with organic matter from the underground parts of prairie plants. On lake sediment and till, the soils are calcareous and have an accumulation of calcium within the upper 20 inches. The prairie soils on the Lake Agassiz sediments (except the gravelly or sandy beaches) and Des Moines Lobe till are relatively impermeable because of the fine texture of the soil parent-material; consequently, they have slow drainage, except in areas of the upland having strong relief. The prairie outwash soils on the upland have been leached of calcium. Because of their sandy to gravelly texture, they are well to excessively well drained and tend to be dry.

Forest soils are found on the upper part of the glaciated upland. They occur on both Des Moines Lobe and Wadena Lobe till and on outwash sand. In contrast to the prairie soils, the upper horizon is bleached. Forest soils are leached to a depth of 30 or more inches and have no horizon of calcium accumulation. They are usually well drained because of their silty to sandy-loam texture combined with moderate to strong relief.

Peat soils occur on areas of impeded drainage, especially in the northwestern patterned bog of the Agassiz lowland. For a discussion of their character and development, Heinselman (1963) may be consulted.

The prairie and forest soils intergrade along the western flank of the glaciated upland. These prairie-border soils have moderate development of the melanized and calcified horizons of a prairie soil, but they also have a slightly bleached horizon of a forest soil. They occur on well-drained silt-loam till.

The three types of soil correspond to three great soil groups (Nygard McMillen, and Hole, 1952): the prairie soils (except those on outwash) as chernozems, the prairie-border soil as degraded chernozems, and the forest soils as grey-wooded soils. According to Arneson (personal communication) and Nygard et al. (1952), the chernozems and grey-wooded soils show only the developmental influence of prairie and forest vegetation respectively; it is not clear whether the degraded chernozems have resulted from forest invading prairie or have developed exclusively from the influence of the Oak Savanna and Mesic Deciduous Forest that covered them at the time of settlement. However, Buell and Cauton (1951) attributed slight degradation of a chernozem under an Acer-Feld stand along the western margin of the Mesic Deciduous Forest to a 19th century forest invasion of prairie.

The melanized outwash soils in the Pine-Hardwood Forest are chiefly covered with Pinus banksiana. There is no discussion in the literature of the effect of this implied vegetation change upon soil development. It is interesting to note that most of the areas of prairie-outwash soils lie along
the western side of the Pine-Hardwood Forest, with forest-outwash soils farther eastward.

Climate

The general extent of the largest unit of vegetation, the formation, is commonly attributed to climatic control (Weaver and Clements, 1938), although in detail formation boundaries such as those in northwestern Minnesota may be more directly influenced by other factors. Borchert (1950) showed that the Prairie formation of central North America has a climate distinct from that of the Forest formations to the east.

The prairie-forest transition of central North America lies in the mid-latitude belt of prevailing westerly winds. Cyclonic disturbances with trajectories from the southwest, west, and northwest across the area. Air masses originating from three source regions are associated with the cyclones. Those from the south provide warm, moist, maritime-tropical air, while those from the north provide cold, dry, continental-polar air. The third source region, the western interior, provides dry continental air. The seasonal and annual frequency and trajectory of the cyclonic storms with different associated air masses determine the general character of the climate and the prairie-forest transition.

Temperature and precipitation

Borchert (1950) found that the northeastern boundary of the prairie area has a relatively steep mean gradient of both summer and winter precipitation. Relative to the prairie, the forest area has greater winter snowfall, more persistent snow cover, and a greater number of rainy days in summer, with an accompanying increase in cloud cover and relative humidity. The prairie and prairie-forest transition areas have more variability than the forest area; the prairie has a greater risk of a large summer-rainfall deficit and thus of droughts. During dry summers, the prairie also has larger positive departures from average temperatures. The probability of summer droughts decreases with increasing distance eastward from the transition.

The distinctive prairie climate reflects a relatively strong zonal circulation with a dominance of dry, continental air masses from the western interior. The transition and forest climates are more influenced by meridional circulation of moist, tropical-atlantic air and cold arctic air masses. Major summer droughts along the transition result from the failure of moist, tropical air masses to dominate the circulation during this season.
Regional elevations change rapidly, e.g., in Norman, Clay, and Wilkin Counties.

To compare further the climatic differences across the prairie-forest transition with regard to temperature and precipitation, published weather summaries (1931-1955) were examined for stations in northwestern Minnesota (Strube, 1959) and eastern North Dakota (Braunvandliek, 1959) in an area roughly outlined by 46° 50' to 47° 50' N. latitude and 97° to 99° W. longitude. Twenty-seven stations were available, nine from the pine-hardwood forest area, two from the deciduous forest area, and sixteen from the prairie area.

All mean July temperatures are lower in the pine-hardwood forest than in the prairie. The average of the pine-hardwood forest is 68.2°F and in the prairie 71.0°F. The two stations in the deciduous forest have an intermediate value of 69.8°F. Mean January temperatures failed to show any regular gradient across the transition.

Mean annual precipitation is lower for all stations in the prairie than for stations in the forest. The prairie stations average 18.3 inches, the deciduous forest stations 22.6 inches, and the pine-hardwood forest stations 24.8 inches. In Figure 6, precipitation values and altitudes for each station are plotted on a common latitude, but they are spaced at their approximate longitudinal distances. The positions of stations 17 and 18 were deliberately reversed so that the higher-altitude station is to the east. Precipitation in the prairie shows a gradual eastward increase from 16 to 20 inches and an
obtained by van Arsdale, Parmeter, and Riker (1957) in a comparable area of southwestern Wisconsin. Part of the difference lies in the relatively greater precipitation and cloud cover in Wisconsin. These authors also found a positive correlation between elevation and August precipitation. It is concluded that differences in regional elevation across the prairie-
forest transition steepen a climatic gradient that is already steep for other reasons.

**Droughts**

Borchert (1950) emphasized the variability of precipitation and temperature that leads to drought along the eastern prairie margin. The longest recorded series of widespread drought years occurred during the 1930's. These dry years were accompanied by high temperatures and high soil-moisture deficits. Figure 7 compares average calculated soil-moisture deficits for northwestern Minnesota for 1901-1955 and 1926-1955 (Baker, 1958). The average for the shorter period places more emphasis on the drought years of the 1930's. In general the isolines parallel contours with the greatest deficits in the lowland and show a steep gradient where the contours are most closely spaced. In the 1926-1955 period, the deficit values were displaced to the east, and the gradient was steepened. This was

![Map of soil-moisture deficit](image)

**Fig. 7.** Comparison of average calculated soil-moisture deficit in inches for 1901-1955 (left) and for more arid portion of the period 1926-1955 (right). The broken line indicates a change in scale. Adapted from Baker (1958).
definitely a period of stress for the more mesic forest species and a time of noticeable prairie expansion at the expense of forest; and in prairie areas of Minnesota, the short-grass plains species increased in importance in relation to tall-grass prairie plants (D. B. Lawrence, personal communication).

Is the drought of the 1930’s with high soil-moisture deficits a typical recurrent feature of the prairie-forest transition of northwestern Minnesota? Baker (1962), in a study of the long-term temperature and moisture trends in Minnesota, stated that for the period of the historical weather record 1840-1958 at St. Paul, Minnesota “... the feature of declining precipitation with rapidly rising summer temperatures of the late 1920’s and early 1930’s was a unique occurrence considering duration and intensity.” This is in accord with shorter records of other stations in the state.

Will (1946), in his study of tree-ring width of Quercus macrocarpa and Juncus scoparius in central North Dakota, attributed narrow rings to drought years. The drought of the 1930’s was reflected by a continuous series of 15 narrow rings from 1922 through 1937. Only three other such long series of narrow rings occurred in the period of his record from 1406 to 1940, namely 1596-1611, 1633-1649, and 1836-1851. Although he did not present a critical discussion of the causes of ring-width variation, his conclusion of the rarity of the protracted 1930’s-type drought agrees with Baker (1962) in the portion of the record that coincides. Will (1946) also noted that years of drought and abundant moisture ran in series but had no discernible cyclic pattern. Tree-ring patterns were correlative both in eastern and western North Dakota, but average moisture years in central North Dakota were often dry years in the west and moist years in the east. This agrees with Bercheri’s (1950) conclusion that dry years are less frequent and intense as the forest margin is approached.

Baker (1960, 1962) found that in Minnesota the period 1900-1958 was marked by an increase of 1.0°F in annual temperature. Winter temperatures increased more than those of summer. The long-term record at St. Paul shows the trend began in the 1860’s. The long-term record of precipitation shows no significant change.

In summary, the prairie and forest areas have distinctive climates, and the transition between them has steep gradients of precipitation and summer temperature. The gradients are enhanced by regional elevation differences of between 500 and 1,000 ft because of orography. Intense summer droughts with consequent depletion of soil moisture are relatively more frequent and prolonged in the prairie area.

In northwestern Minnesota, an increase of 3°F in mean July temperature and a decrease of 5 inches in mean annual precipitation, assuming the present pattern of seasonal distribution, would extend the prairie climate into the forest area. In this event, the degree to which prairie would replace forest would depend largely on local physiographic and soil conditions and the amount of increased fire frequency. An intermediate change in climate, affecting especially also winter temperature and snow cover, would favor dominance of deciduous forest.

Wind

Wind direction is of special importance in this study because of its influence on the dispersal of pollen. Because of its location in the belt of prevailing westerlies, the general drift of wind-borne pollen would be expected to be from the prairie to the forest. However, when prevailing wind directions for the pollination months are examined, another picture emerges. Crookston (Polk County, Minnesota) is the closest wind-recording prairie station to the Itasca transect. Although the records of no other station were examined, it is thought to be typical of northwestern Minnesota. Here the yearly prevailing wind is from the northwest. Table 2 (Soini, 1951) shows that the pollination months (April-October) are dominated by winds prevailing from either the northwest or the southeast. Thus it may be possible both for large amounts of tree pollen to be wind-borne from the forest into the prairie and for herb pollen to be carried from the prairie to the forest.

Vegetation

Historic records

The general boundaries and something of the communities of the natural vegetation of the late 19th century are known from maps drawn by

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early travelers. Upham (1884, 1896) recorded the prairie-forest boundary in northwestern Minnesota during the summer of 1881 when he traced the eastern beaches of Lake Agassiz. His maps clearly show the belt of Deciduous Forest between the Prairie and Pine-Hardwood Forest by noting the approximate western limit of conifer species. Ayers (1899), in a map entitled the Pine Region of Minnesota, showed the extent of the Pine-Hardwood Forest, Deciduous Forest, and Prairie, with the transition from Deciduous Forest to Prairie as a narrow band of "brush prairie." The brush prairie corresponds largely with the two lesser formations, Oak Savanna and Aspen Parkland. Ayers' map was constructed from "the earliest surveys," which probably include Upham's maps and the General Land Office Survey.

The land survey was conducted in northwestern Minnesota between 1870 and 1880 by the Federal Government prior to extensive land settlement. Surveying chiefly consisted in laying out section lines. The surveyors summarized qualitatively the vegetation along the section lines and noted the obvious boundaries, such as the forest margin. Marschner (1959) constructed a detailed vegetation map from the survey notes; a generalized version is given in Figure 8. Unfortunately, the maps of Upham, Ayers, and Marschner were not accompanied by detailed descriptions of the vegetation or of the criteria used for the map units. Curtis (1959) is useful in interpreting these maps, for many of the map units are similar to those known in detail from Wisconsin. More detailed consideration of the land-survey records and relic stands will be given in the discussion of the Itasca transect.

**Pine-Hardwood Forest**

In Figure 8 this formation was not subdivided because of the great variety and often small areas of community types present. However, a large area of patterned bog on peat that lies in the Agassiz lowland was separated from communities of the predominantly mineral soils of the glaciated upland. The two chief communities of the patterned bog area are fen (dominated by Carex and Phragmites) and bog forest (with Picea mariana, Larix laricina, and Thuja occidentalis). The fen and bog areas alternate in streamline and tassle pattern that are visible on air photos, and these patterns are related to drainage in the underlying peat. Peat accumulation and the bog communities basically result from impeded drainage in the underlying sediments of Lake Agassiz. Heinselman (1963) has prepared a detailed discussion of the patterned-bog area.
least, succeeded by *Pteridium* and prairie grasses (bracken grassland of Curtis, 1959; Bergman and Stallard, 1916).

The leading dominants of the widespread till soils are *Pinus strobus* and *P. resinosa*, not only with respect to their great numbers but also their size, longevity, and resistance to fire (Bergman and Stallard, 1916). *Pinus resinosa* occurs in pure stands or is mixed with *P. bankiana* on coarse-textured soils or *P. strobus* on finer-textured soils. *Populus tremuloides*, *P. balsamifera*, *Betula papyrifera*, and *Pinus banksiana* are pioneers on the many burned areas. On coarse-textured soils these species tend to be succeeded by *Pinus resinosa*; on finer-textured soils, especially areas of De Moines Lobe, they are succeeded by *P. strobus* and such hardwoods as *Quercus macrocarpa*, *Q. rubra*, *Populus grandidentata*, *Ulmus americana*, *U. thomasi*, *U. rubra*, *Fraxinus pennsylvanica*, *Ostrya virginiana*, *Tilia americana*, *Acer rubrum* and *A. saccharum* (Kittridge, 1938). *Abies balsamea* and *Picea glauca* are widespread but relatively uncommon in pine and hardwood stands.

Rare hardwoods found only adjacent to large lakes are *Celtis occidentalis* and *Acer saccharinum* (Buell and Bormann, 1955) and *Carya cordiformis* (Kittridge, 1934).

Common upland shrubs include species of *Corins*, *Cornus*, *Amelanchier*, *Prunus*, *Viburnum*, *Beroa*, and *Ribes*, whereas *Alnus crispa*, *Taxus canadensis*, *Juniperus communis* var. *depressa*, and *Carpinus caroliniana* are uncommon or rare.

Many former lakes and ponds have become partially or completely filled with peat. The deeper, wetter peats support a bog forest of *Larix laricina*, *Picea mariana*, and less commonly *Thuja occidentalis* (Conway, 1948). The shallower, drier, and more fertile peats have a forest of *Abies balsamea*, *Frasinus nigra*, and *Ulmus americana* (Kell, 1938). Uncommon trees limited to bog margins are *Pyrus americana*, *P. decora*, and *Betula lutea* (Christ, 1959). Large areas of peat support Carex fen or shrub carr dominated by *Alnus rugosa*, *Betula pumila* var. *glandalifera*, *Salix spp.*, *Chamaedaphne calyculata*, and *Ledum groenlandicum*. Pure stands of the grass *Zizia aquatica* occur in open water less than 4 feet deep.

The northern boundary of the Pine-Hardwood Forest is the general northward limit of *Pinus strobus*, *P. resinosa*, *Quercus*, *Acer*, and *Tilia*, but *Frasinus nigra*, *Ulmus americana* and *Thuja* extend somewhat farther north into the Boreal Forest. The characteristic trees of the Boreal Forest are *Pinus banksiana*, *Abies*, *Picea*, *Larix*, *Populus*, and *Betula*. The western boundary of the Pine-Hardwood Forest is the general limit of conifers, especially pine. However, all hardwoods extend westward into the Mesic Deciduous Forest, with the possible exception of *Acer rubrum*.

The Pine-Hardwood Forest, in contrast to the Mesic Deciduous Forest, occurs eastward on the glaciated upland, where summer temperatures are lower, the growing season shorter, and the winter snow cover greater. The characteristic pines are most abundant on the predominantly sandy soils.

**Mesic Deciduous Forest**

This formation is characterized by the *Acer-Tilia* and *Quercus-Populus* forest types (Fig. 8). The leading dominants on the most mesic sites are *Acer saccharinum* and *Tilia americana*, but on most sites *Ulmus americana* and *Quercus rubra* are more important than *Acer*. Also common in these stands are *Quercus macrocarpa*, *Populus*, *Betula*, *Fraxinus*, and *Ostrya*. Most of the dominants are fire-sensitive, and stands often occur on the eastern or leeward side of lakes or rivers (Daubenmire, 1936). The *Acer-Tilia* type is most extensive on the finer-textured soils of the upper parts of the Big Stone and Alexandria Moraines.

The *Quercus-Populus* types occupy less mesic sites, i.e., at lower altitudes, on coarser-textured soil, and on sites subject to frequent fire. The dominants *Quercus macrocarpa*, *Populus tremuloides*, and *P. balsamifera* reproduce vegetatively after fire, and *Quercus* has a fire-resistant bark. In the absence of fire, this type tends to be succeeded by the more mesic hardwoods of the *Acer-Tilia* type.

**Itasca transect**

**Physiographic setting**

A diagram of the main physiographic features of the transect is given in Plate 1. The altitudes were taken at 1-mile intervals from the Benidji and Grand Forks maps of the Army Map Service (scale 1:250,000, contour interval 50 feet). The westernmost township lies in the Glacial Lake Agassiz lowland. East of the uppermost beaches (1,050 feet elevation) is the glaciated upland, with three prominent end moraines.

The Erskine Moraine is a northwest-trending ridge rising to over 1,300 feet in elevation. It is less prominent north and south of the transect. Ten miles of undulating ground moraine separate it from the rolling, massive Big Stone Moraine to the east.

The Big Stone Moraine trends northeast and rises to a general altitude of 1,500 feet. The White Earth River crosses it from the southeast. Both the summit and the western flank have many lakes and ponds, in contrast to the almost lakeless terrain westward. This moraine is well marked north...
and south of the transect; the eastern boundary is the Twin Lakes glacial drainageway, a valley three miles broad containing outwash and large lakes.

East of the drainage way the transect is situated upon the massive Itasca Moraine, which has strong local relief up to 200 feet, a general altitude of 1,600 feet, and one hill over 2,000 feet. It is crossed by several north-south drainage ways that terminate in outwash plains. The Lake George outwash plain is a southern extension of a large outwash area north of the transect. Similar outwash plains occur just south of the transect in Becker County. The rolling terrain of the Itasca Moraine contains many lakes and ponds. The Mississippi River has its source in Lake Itasca and flows to the north and east.

**Glacial Geology**

There are no bedrock exposures in the transect, and the surface (except for local alluvium and peat) is the result of late-Wisconsin glaciation. The Itasca Moraine was formed by a stillstand of the Wadena Lobe, which deposited sandy till. During the wastage of the ice, meltwater formed many local, sandy outwash deposits in addition to those in drainage ways and outwash plains. Most of the smaller lake and pond basins originated from the melting of buried ice blocks, although, as will be shown later, the ice blocks probably persisted for some time after the disappearance of active surface ice.

The area including the Big Stone Moraine west to the Lake Agassiz beach was last covered by the ice of the Des Moines Lobe. It deposited a silty till. In the transect the main outwash deposit of this moraine lies in the Twin Lakes drainage way. Another drainage way lies on the western side of the moraine, and although it does not contain extensive outwash deposits it is marked by a series of small lakes and ponds, of which Horse Pond is an example.

The Erskine Moraine has few ponds and relatively subdued topography. The highest point of the moraine, Frenchman’s Bluff, is a kettle-like deposit of sand and gravel. At the west base of this moraine, the upper beaches of Lake Agassiz rise about 5 feet above the surrounding surface. These sand and gravel deposits are rather indistinct on the ground but can readily be traced on air photographs. This set of beaches was formed prior to 11,700 years ago (Shay, 1965) before the lake retreated to form new beaches. The northern half of R 43 and the adjacent township to the north contain a glacial drainage way and delta complex formed when Lake Agassiz stood at its highest levels.

**Soils**

The glacial drift composing most of the soil parent-material contains limestone and thus is calcareous. However, the soils developed from the two types of till have quite different textural and drainage characteristics. Soils derived from Wadena Lobe till are usually well-drained sandy loams leached to a depth of 5 or 6 feet and have a typical forest-soil profile. Interspersed with the till soils and more extensively on outwash plains are the loamy-sand outwash soils. They are similar to till soils in having good drainage, but commonly they have lower nitrogen content, higher acidity, and lower moisture equivalent (Alway and McMiller, 1938). The Lake George outwash plain is a large area of these relatively infertile and dry soils.

Soils derived from Des Moines Lobe till differ from those of the Wadena Lobe till in texture, internal drainage, and profile development. They have a loam to silt-loam texture. Soils on the Erskine and Big Stone Moraines are well drained, but those on the ground moraine tend to be poorly drained. Soils on the crest of the Big Stone Moraine are leached to a depth of 2 or 3 feet while those to the west on the ground moraine are leached to a lesser depth and have limestone pebbles within a few inches of the surface (Buell and Facey, 1960). Soils on the poorly-drained ground moraine are solonchaks and have lime accumulations at or near the surface (Brekenridge and Tester, 1961; Nikiforoff 1938).

The prairie soils west of the Big Stone Moraine have an accumulation of organic matter in the upper 6 to 12 inches and a horizon of limy accumulation at 12 to 20 inches. The soils of the crest of the Big Stone Moraine are forest soils without a thick accumulation of organic matter near the surface but with pronounced leaching of carbonates and clay from the upper horizons and an accumulation of clay in a lower horizon. The soils of the western flank are intermediate: accumulations of organic matter and carbonate are present to a lesser extent than in the prairie soils, and some leaching of clay and organic matter typical of forest soils is present (Buell and Canton, 1961). Because of their finer texture, the soils of the Des Moines Lobe till are more fertile and less dry than those of the coarser-textured Wadena Lobe till.

Peat soils are common, especially on the Itasca and Big Stone Moraines, although they cover a much smaller area than mineral soils. Most of them originated by centripetal filling of ponds and small lakes by partially decayed bog vegetation (Conway, 1949). They are usually less than 10 feet deep and overlie gyttja or marl or both. At Bog D (Itasca Park) herb,
moss, and wood peat occur, and peat accumulation began about 4,000 years ago.

**Natural vegetation immediately prior to settlement**

The modern plant communities of the transect have limited use in the interpretation of the fossil evidence of the natural vegetation of most of postglacial time. Since settlement in the late 19th century, man has become the dominant ecological factor, with his axe, plow, and cow. The Indian inhabitants did not practice agriculture and probably had little effect on the vegetation, except by setting fires. For reconstruction of the natural vegetation, community types were distinguished from the land-survey notes and were compared with data from relic stands.

**Land-survey notes**

The smallest unit of the presettlement land survey was the section, a mile square. Thirty-six sections, six on a side, formed a township. Posts were placed at each section corner; in forested areas, they were witnessed by four inscribed “bearing-trees.” Quarter-section corners (and sixteenth-section corners where sections were subdivided) were witnessed by two bearing-trees. The bearing-trees were usually over 5 inches in diameter; they were the closest living trees to the corners and were located in different quadrants. The direction and distance from the corner-post, the diameter, and species of each bearing-tree was recorded. The vegetation along each section line was summarized usually as a list of trees, presumably in their order of abundance. Various other vegetation features were also recorded, e.g. burned areas, blowdowns, bogs, and prairies. Plat maps of each township were drawn from the survey notes. These maps showed the principal landscape features, such as rivers, lakes, bogs, hills, and the forest boundary.

Bourdo (1956) reviewed the survey method and its application to the quantitative study of former forests. It has been used in mapping and characterizing the prairie-forest transition in the central states by Transue (1935) and locally in Indiana (Potzger, Potzger and McCormick, 1956), Illinois (Kilburn, 1959), Wisconsin (Cottam, 1948), Iowa (Dieck-Peddie, 1953; McCoomb and Loomis, 1944), and Missouri (Howell and Kuehler, 1956).

In the present study, land-survey data were obtained from the eleven townships of the Itasca transect from notebooks examined in the Office of the Secretary of State, State Capital Building, St. Paul, Minnesota. Bearing-tree data were taken from section, quarter-section, and, where available, from sixteenth-section corners. These data included the common name of the tree, its diameter, and its distance from the corner post. The qualitative descriptions of the vegetation along the survey lines were also copied, as were the notations of fires and blowdowns. Photostatic copies were obtained of plat maps where prairie-forest contacts were indicated.

Different parts of the transect were surveyed between 1871 and 1879 by eight parties of surveyors. Bearing-trees were identified by common names, and in many cases the names used by different parties were not the same. Most names are interpretable only to genus (Table 3), and the only consistently useful specific distinctions are within *Pinus* and *Acer*. Because many of the genera are represented in the transect by only one species, all generic identifications may be referred to these particular species.

To map the vegetation of the transect (Plate 1), I first transferred the prairie-forest contacts from the township plats to a prepared base map. A symbol for each taxon of bearing-tree was placed at its proper corner on the

<table>
<thead>
<tr>
<th>Common names applied by surveyors to bearing trees</th>
<th>Botanical name</th>
<th>Rare species probably not used as bearing trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>pine</td>
<td><em>Pinus app.</em></td>
<td></td>
</tr>
<tr>
<td>Norway, yellow pine</td>
<td><em>P. resinosa</em></td>
<td></td>
</tr>
<tr>
<td>white pine</td>
<td><em>P. strobus</em></td>
<td></td>
</tr>
<tr>
<td>jack pine, black pine</td>
<td><em>P. balsamena</em></td>
<td></td>
</tr>
<tr>
<td>spruce</td>
<td><em>Picea glauca, P. mariana</em></td>
<td></td>
</tr>
<tr>
<td>fir, balsam</td>
<td><em>Abies balsamea</em></td>
<td></td>
</tr>
<tr>
<td>tamarack</td>
<td><em>Larix laricina</em></td>
<td></td>
</tr>
<tr>
<td>white cedar</td>
<td><em>Thuja occidentalis</em></td>
<td></td>
</tr>
<tr>
<td>aspen</td>
<td><em>Populus tremuloides, P. grandidentata</em></td>
<td></td>
</tr>
<tr>
<td>balsam, Balsam of Gilroy</td>
<td><em>Betula papyrifera</em></td>
<td></td>
</tr>
<tr>
<td>birch, white birch, paper birch</td>
<td><em>Quercus app.</em></td>
<td></td>
</tr>
<tr>
<td>oak</td>
<td><em>Q. rubra, Q. alba</em></td>
<td></td>
</tr>
<tr>
<td>red oak, black oak</td>
<td><em>Q. macrocarpa</em></td>
<td></td>
</tr>
<tr>
<td>bur oak, white oak</td>
<td><em>Acer rubrum, A. saccharum</em></td>
<td></td>
</tr>
<tr>
<td>maple</td>
<td><em>A. negundo</em></td>
<td></td>
</tr>
<tr>
<td>sugar</td>
<td><em>Tilia americana</em></td>
<td></td>
</tr>
<tr>
<td>box elder</td>
<td><em>Fraxinus pennsylvanica, P. nigra</em></td>
<td></td>
</tr>
<tr>
<td>linden</td>
<td><em>Ulmus americana</em></td>
<td></td>
</tr>
<tr>
<td>elm</td>
<td><em>U. rubra, U. thomasi</em></td>
<td></td>
</tr>
<tr>
<td>ironwood</td>
<td><em>Ostrya virginiana</em></td>
<td></td>
</tr>
<tr>
<td>willow</td>
<td><em>Salix amygdaloides</em></td>
<td></td>
</tr>
</tbody>
</table>

**Table 3. Common names of bearing trees and their botanical equivalents. The bearing tree names were taken from the land survey notes of the Itasca transect. The list includes all tree species native to the transect.**
The Pine-Hardwood Forest is easily recognized in ranges 34 through 39 by the prevalence of bearing-trees of pine mixed with hardwoods such as *Populus*, *Betula*, and *Quercus*. The western boundary is placed at the limit of pines in R 40.

The Pine-Hardwood Forest is divided into three sharply defined types based on the prevalence among the bearing-trees of different pine species. The *Pinus banksiana* type (largely R 34-35) had mostly *P. banksiana* and *P. resinosa* to the near exclusion of *P. strobus* and hardwoods. The *Pinus strobus*-hardwood type (R 38-40) in contrast had mostly *P. strobus* and hardwoods and very few *P. banksiana* and *P. resinosa*. The mixed pine-hardwood type (R 34-38) had a mixture of hardwoods and pine, with *P. resinosa* the most common.

Between the Pine-Hardwood Forest and the forest boundary, the Mesic Deciduous Forest is characterized by the absence of pine rather than the occurrence of any species not found in the eastern townships. In the Mesic Deciduous Forest, the number of taxa recorded as bearing-trees decreases westward toward the forest edge in R 41. Thus, it is divided into areas of *Acer-Tilia* type, a *Tilia-Ulma* type, and a *Quercus-Populus* type. The *Acer-Tilia* type lies between the Pine-Hardwood Forest and the western limit of *Acer saccharum* bearing-trees. Westward the *Tilia-Ulma* type extends to the western limit of *Tilia*, *Ulma*, *Frazins*, *Ostrya*, and *Betula* bearing-trees. The *Quercus-Populus* type (chiefly *Q. macrocarpa* and *P. tremuloides*) lies between the *Ulma-Tilia* type and the forest boundary.

West of the forest boundary the surveyors recorded "prairie," which is mapped as prairie type; "brush prairie" and "aspen groves," which are mapped as *Populus* scrub type; and "oak openings," which are mapped as oak-savanna type. The oak-savanna type was more or less continuous just west of the forest boundary; and farther westward and the *Populus* scrub type occurred in groves in a matrix of prairie. The area in R 41 characterized by oak-savanna type is designated the Oak Savannah formation, and the nearly treeless area westward is called the Prairie formation.

**Quantitative aspects**

The bearing-trees are at the corners of a regular grid and may be considered a low-intensity, quantitative sample of the natural arboral vegetation. Although not an unbiased sample, they provide rough data for comparison with regional topography and soils. In addition, the relative importance of each genus may be compared with its relative pollen value, and over- and under-representation in the pollen spectra may be noted.

Because the vegetation boundaries trend north-south all the bearing trees in two columns of sections were treated as a population sample. In Range 40, however, each section had been surveyed in sixteenths, so because of the larger number of bearing-trees available only those of a single column of sections were used as a population sample. Only genera that occurred on the upland were considered; bog genera (*Larix*, *Thuja* and *Salix*) were omitted.

Calculation of density in stems per acre was attempted but abandoned because of unrealistic results. Instead, an important percentage (I. P.) for each genus was calculated. The I. P. was the sum of the relative density (percent of bearing-trees) and the relative dominance (percent of basal area bearing-trees) divided by two. Thus, not only the relative number but also the relative size of each taxon was included.

In R 34 through R 39 the number of trees in each sample of 12 sections ranged between 54 and 84. In R 40 the number was between 120 and 114. The I. P.'s were plotted in Figure 9, and a smooth curve was fitted by inspection. As expected, the pine values are high in the Pine-Hardwood Forest, while deciduous species such as *Ulma*, *Quercus*, *Ostrya*, *Acer*, and *Tilia* are highest in the Mesic Deciduous Forest. *Populus* and *Betula* have moderate values but no distinct trend in either formation. *Abies*, *Picea*, and *Frazins* have insignificant values. In R 40 the pine species was not usually designated in the notes, but the large diameter of the trees implies *P. strobus*. The prevalence of *P. strobus* over other pine species in ranges 38, 39, and 40 is clearly shown.

How valid are the bearing-tree data as a quantitative measure of the vegetation? Certainly bias in diameter selection was present because the survey instructions call for trees over 5 inches in diameter. In practice, however, trees as small as 2 inches diameter were occasionally used. Burdo (1956) found trees 8 to 14 inches in diameter most desired. Thus species that do not commonly reach this size would be underrepresented.

Burdo pointed out that another source of bias may be for trees with a smooth, easily-scribbled bark. He showed how bias in species and diameter selection could be detected by comparing mean distances and diameters for each species. This method was unworkable for the Itasca transect, as mean distances were often unrealistically large because many corners occurred in openings such as marshes, burns, and blowdowns.

A subjective estimate of bias suggests that *Ostrya* is underrepresented because it seldom reaches 6 in. dia. *Populus* may be overrepresented because
of its smooth, easily-scribable bark. In burned areas *Pinus strobus*, *P. resinosa*, and *Quercus* may be overrepresented because the larger trees of these species are fire-resistant. No trees with multiple stems were recorded, but *Tilia*, *Betula*, and to a lesser extent *Quercus* commonly have multiple stems. Thus the bearing-tree values for *Populus* and *Pinus* may be too high, whereas *Ostrya* and *Betula* are certainly too low, perhaps by a factor of 2 or 3.

**Pine-Hardwood Forest**

The *Pinus banksiana* type is mapped as occurring only on the Lake George outwash plain, although smaller areas, somewhat poorly resolved in the survey notes, also occurred in the Twin Lakes drainageway. The bearing-tree data indicate that these dry, sterile soils had even-aged stands of *Pinus banksiana* mixed with small amounts of *P. resinosa*. Trees such as *Pinus strobus* and hardwoods that require better soil conditions were virtually absent. The forest was not completely uniform, as local peaty areas supported *Picea-Larix* bog forest.

Little disturbed stands on this and other outwash areas indicate this type has persisted since the survey time. Although not well represented as a bearing-tree, small *Quercus macrocarpa* trees are locally present. These stands are somewhat open, with a ground cover notably of *Pteridium* and lichens. The even ages reflect reproduction after fires. *Pinus banksiana* has serotinous cones that open and spread large amounts of seed after the parent tree has been killed by fire. *Pinus resinosa*, especially larger trees, may survive fires that kill the smaller *Pinus banksiana*. *Quercus macrocarpa* is also adapted to frequent fires in that it can reproduce from stump sprouts.

The herb flora of the *Pinus banksiana* type is of interest because it contains many grasses and forbs common to the prairie, such as *Atriplex gerardii*, *A. scoparia*, *Stipa spartea*, *Sorghastrum nutans*, *Artemisia campestris*, *Zizia aurea*, *Aster spp.*, *Lithospermum canescens*, and *Elymus philadelphicum*. These remain inconspicuous in the shade of the trees. During all but a very mild surface fire, *Pinus banksiana* trees are killed. The release from shading stimulates a luxuriant growth of the prairie

*Itasca transect*. The bearing-tree values are the importance %/2 (relative density plus relative dominance) of all herb taxa in two adjacent columns of sections. The bearing-tree data were taken from notes of the land survey conducted 1871-1879. The transect sites from west to east are: Terrell Pond, Birchwood Pond, McGrawe Pond, Bad Medicine Pond, Bog A Pond, Bog D Pond, Martin Pond, and Chicky Pond. The transect is 6 miles wide and the forest portion is 42 miles long.
species, which dominate the site of the burn for several years. Meanwhile, Pinus banksiana seeds have germinated, and upon growth to sapling size they shade and suppress the prairie species, which then become inconspicuous until another fire repeats the cycle. However, if the site is burned during the prairie stage, the immature pine are killed before they can produce seed, and succession to pine is delayed for several decades. This maintenance of prairie by fire on outwash plains in the Pine-Hardwood Forest apparently occurred in southern Hubbard County in the late 19th century. According to Alway and McMiller (1935), the land survey recorded Pinus banksiana type in 1860, but in the same area in 1871 the survey recorded prairie, and it was still prairie when the area was settled in 1879. It is not improbable that if the climate were somewhat drier and fires more frequent, the outwash soils would be dominated by the prairie type together with fire-stunted Quercus macrocarpa, even though the surrounding till soils continued to support forest types.

On the till soils, the most striking feature of the survey notes was the many large Pinus strobus and P. resinosa. Bearing-trees were up to 34 inches in diameter, with trees 20-30 inches not uncommon. Trees of this diameter are usually between 100 and 120 feet high, well above the usual 80 feet maximum of hardwoods. Pines of this size may reach an age of 300-500 years and are usually scarred by fire once or more times (Ayers, 1899; Spurr, 1954). These pines, especially P. resinosa, tend to occur naturally in small, even-aged stands of a few acres under a variety of soil conditions. Pinus strobus usually occupied the better soils and occurred as scattered individuals of uneven ages. In addition to the large pines, there were scattered stands of younger pines that would eventually replace the larger, older trees.

In contrast to the large pines were the widespread, even-aged stands of P. banksiana and hardwoods dominated by Populus tremuloides, P. balsamifera, and Betula populifera. The larger trees of these species were 12-14 inches in diameter and perhaps 40-70 years old. The hardwoods are fast-growing pioneers, especially adapted to repeated fires. They are killed by fire but reproduce vegetatively, Betula by stump sprouts and Populus by root suckers. All produce abundant, wind-dispersed seed. Because these species are relatively intolerant of shade, in the absence of repeated fires they are succeeded by more shade-tolerant species such as Abies balsamea, Picea glauca, Acer saccharum, and Tilia americana, although Betula may persist from stump sprouts. These shade-tolerant species were relatively uncommon in the survey notes.

The survey notes recorded numerous burned areas, and R 39 and the eastern third of R 40 had almost been completely burned over at the time of the survey. Spurr (1951) summarized the 19th century fire history of Itasca Park from fire scars on large Pinus resinosa and from ages of stands that developed immediately following fire. He showed that major fires occurred in 1772, 1803, 1811, 1820, 1865, and 1886. Evidence for minor, less extensive fires was also found, and there is evidence for such a small fire in 1894 (McAndrews, unpublished). Ground cleared by fire provides a suitable seed bed for pine and results in even-aged stands. The oldest even-aged trees were the long-lived, fire-resistant Pinus resinosa and P. strobus, while the extensive younger stands of the shorter-lived Populus, Betula, and Pinus banksiana originated, for the most part, immediately after fires of the late 19th century. Probably fires of the early 19th century also were followed by these species, but they have either largely been destroyed by subsequent fires and replaced by pine or have been succeeded by more shade-tolerant species. Since the advent of 20th century fire protection in the Park the succession has been toward the relatively more shade-tolerant Acer saccharum or Abies balsamea (Buell and Cantlon, 1951).

The ecological basis for the prevalence of Pinus strobus over the other pine species in the Pinus strobus-hardwood type area is not clear. This type occupies the same Wadena Lobe sandy till as the mixed-pine-hardwood type eastward. Both types were subject to fire, in fact much of the Pinus strobus-hardwood type had been extensively burned at the time of the survey. Thus there appears to be no fire or soils difference to explain the shift in pine species. According to modern observations and land-survey notes from elsewhere in Minnesota (McAndrews, unpublished), Pinus strobus is as was the most important pine on the Deciduous Forest margin of the Pine-Hardwood Forest. A possible explanation might lie in a climatic gradient across the transition, a hypothesis requiring further investigation.

In general, the western boundary of the Pine-Hardwood Forest follows the western limit of sandy soils along the western margin of the Twin Lakes drainageway. However, a few pines, probably P. strobus, were present on the eastern margin of the Des Moines Lobe silty till.

**Mesic Deciduous Forest**

This formation occupies the crest and the upper part of the west flank of the Big Stone Moraine. The soil parent-material is Des Moines Lobe silty till. The boundaries of the three community types correspond to contours and thus also to the postulated climatic gradient of mean July temperature and mean annual precipitation. Examination of relief stands
indicates that the community types have undergone succession since the
survey time. These successions provide an insight into the pollen success-
sions of postglacial time.

The western boundary of the Quercus- Populus type follows the 1,400-ft
contour; the Ulmus-Tilia type lies between 1,450 and 1,500 ft and the
Acer-Tilia type above 1,500 ft. The greatest concentration of Acer bear-
trees was above 1,550 ft. The Acer bearing-trees were usually designated as
"sugar," indicating Acer saccharum, and those noted as "maple" were
probably also this species; Acer rubrum did not occur in the stands
examined on the Big Stone Moraines in 1962.

The Quercus-Populus type was dominated by close-grown Quercus
macrocarpa and Populus tremuloides, with a small amount of P. balsami-
fera. The bearing-trees ranged from 3 to 15 inches in diameter; trees at
the same corner were usually about the same size, indicating a mosaic of
even-aged stands. A burned area was recorded in sec. 7 and 18 of R 40 and
the stands probably originated after such fires. At lower altitudes, this type
was bounded by prairie and oak savanna; at higher altitudes, it graded
into Ulmus-Tilia or Acer-Tilia types.

The Ulmus-Tilia type was a mixture of all the dominants of the Mesic
Deciduous Forest except Acer saccharum. The main bearing-trees were
Ulmus and Tilia, together with Populus and Quercus (Q. rubra as well as
Q. macrocarpa). In addition, Betula, Fraxinus, and Ostrya were present.
This type occurred north of the White Earth River and also as a gallery
forest along the river. Modern Quercus-Populus stands have a more xeric
aspect than Ulmus-Tilia stands. The relatively thin canopy of the Quercus-
Populus type allows enough light to reach the ground for the development
of a dense shrub layer of Coriaria. The denser Ulmus-Tilia stands have less
shrub cover but a dense herb cover. In contrast, Acer-Tilia stands have
little cover beneath the dense canopy, except for Acer seedlings and
saplings. In 1962, the Quercus-Populus type area had many mesic hard-
woods and could be classified as Ulmus-Tilia type. A similar mesophytic
succession has occurred in the Ulmus-Tilia type area, for here Acer sac-
charum has become a major dominant.

The modern western boundary of Acer-dominated stands was deter-
mined from 1958 air photos and checked in the field in 1962. It corre-
sponds closely with the western boundary of the Ulmus-Tilia type determined
from the 1973 survey.

The Acer-dominated Waubun Acer-Tilia stand of Buell and Cantlon
(1951) occurs within the Ulmus-Tilia type. These investigators postulated a
succession at this site from prairie to Acer-Tilia about 1810. The survey

notes indicate the succession occurred after 1873 from a mesic Ulmus-
Tilia forest. The section containing the stand was dominated by Quercus,
Populus, Ulmus and Tilia. Maximum diameter of bearing-trees in inches
were Quercus 18, Ulmus 14, Tilia 12, Populus 12, and Betula 10. Acer
saccharum was not mentioned. However, it must have been present locally
but have-gone unnoticed because Buell and Cantlon (1961) found stumps
that would have been 60-year-old trees at the time of the survey.

When the Waubun stand was re-examined in 1962, several old cut oak
stumps were found, suggesting that oak trees were important in the past
vegetation. Oak has the most durable and easily identified stumps in the
local vegetation. Because the Waubun stand had been damaged since 1950,
an analysis of the vegetation and stumps in a contiguous undamaged stand
was undertaken. This stand, the Reichow stand, is in the N 1/4 of Sec. 20
and SE 1/4 of Sec. 17. Four canopy trees at each of 40 stations were
sampled according to the method of Morisita (1954). In addition, the
distance and diameter of the nearest oak stump within 100 feet of the
station was recorded.

Although the criteria for tree selection was different, the two stands (Table 4)
show a remarkable similarity. Acer saccharum and Tilia americana are clearly dominant. The reason for the sizable contribution of
Populus tremuloides in the Reichow stand in contrast to the Waubun stand is
unknown.

<table>
<thead>
<tr>
<th>Density (trees/acre)</th>
<th>Dominance (stand area ft²/ acre)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Reichow</td>
</tr>
<tr>
<td>Acer saccharum</td>
<td>135.8</td>
</tr>
<tr>
<td>Tilia americana</td>
<td>48.6</td>
</tr>
<tr>
<td>Populus tremuloides</td>
<td>56.6</td>
</tr>
<tr>
<td>Ulmus spp.</td>
<td>20.4</td>
</tr>
<tr>
<td>Betula papyrifera</td>
<td>16.2</td>
</tr>
<tr>
<td>Fraxinus nigra</td>
<td>30.3</td>
</tr>
<tr>
<td>F. pennsylvanica</td>
<td>8.1</td>
</tr>
<tr>
<td>Populus balsamifera</td>
<td>2.0</td>
</tr>
<tr>
<td>Ostrya virginiana</td>
<td>12.2</td>
</tr>
<tr>
<td>Quercus macrocarpa</td>
<td>4.1</td>
</tr>
<tr>
<td>total</td>
<td>314.3</td>
</tr>
<tr>
<td>Quercus spp. stumps</td>
<td>17.4</td>
</tr>
</tbody>
</table>
Oak stumps of 12 to 26 inches in diameter were located at 36 stations. One *Quercus macrocarpa* stump had a 30-year-old sprout indicating at least some of the oak had been logged about 1930. The former density and dominance indicated by the oak stumps (Table 4) are a minimum because the nearest stumps may not have been recorded. No stumps of other species were identifiable, although a few large rotten *Betula* logs were noted on the ground. More than half the *Tilia* trees had multiple stems originating from stump sprouts, indicating vegetative reproduction from an older generation—perhaps after logging.

The Waubun and Reichow stands are similar enough to suggest they have had a similar history, and both formed part of a larger stand in the past as is also suggested by the survey notes. The former density and dominance of oak shown by stumps and survey notes indicate that sometime after 1873 *Acer* succeeded a community partly dominated by oak. Perhaps the logging of the oak encouraged the succession. Forest does not invade prairie directly by an *Acer*-dominated community, but rather *Acer* appears at the terminus of a succession initiated by a *Quercus-Populus* community followed by the more mesic *Ulmus-Tilia* community.

The *Acer-Tilia* type on the crest of the Big Stone Moraine had the same dominants as the *Ulmus-Tilia* type but was characterized by a moderate amount of *Acer saccharum*. The relatively small number of *Acer* bearing-trees suggests that few stands in the type area were dominated by *Acer*. The impression gained from relict stands in 1962 was of a large recent increase in the number of stands dominated by *Acer*, and that it has become the predominant species since 1873.

Part of the reason for the expansion of *Acer* and other mesic hardwoods may be the decreased fire frequency since settlement. Prairie fires were common along the forest boundary (Buell and Facey, 1960). However, burns were not recorded in the survey notes from any part of the area now dominated by *Acer*, i.e. *Acer-Tilia* and *Ulmus-Tilia* types. In contrast, burns were recorded in the adjacent *Quercus-Populus* and *Pinus strobus*-hardwoods types. Thus, the *Acer-Tilia* and *Ulmus-Tilia* types apparently had a lower fire frequency before settlement, although settlement may have lowered the frequency still further. The extension of these mesic hardwoods may also reflect the increasing mean annual temperature (Baker, 1962).

**Oak Savannah**

This formation lies on the west flank of the Big Stone Moraine in R 41 between the Mesic Deciduous Forest and the Prairie. It consisted of three principal community types—oak savanna, *Populus* scrub, and prairie. The area is now largely cultivated fields, but enough relict stands existed in 1962 so that with additional use of the survey notes the natural vegetation could be reconstructed.

In the survey notes the oak-savanna type was called "oak openings"; according to Curtis (1959), these consisted of oak trees that bore low-spreading branches and were spaced so that the crowns did not touch. Beneath and between the trees was a luxuriant growth of Prairie grasses and forbs. This type has not been described in northwestern Minnesota, although Buell and Facey (1960) referred to open-grown oaks in this part of the transect. Many of the "openings" have succeeded to closed forest.

An "oak opening" recorded in the survey notes (N 1/2 Sec. 14) was visited in 1962 and found to be a forest dominated by *Quercus macrocarpa* in the part of the stand that was little disturbed by logging or pasturing. Most of the trees were close-grown, multiple-stemmed *Quercus macrocarpa* about 6 inches in diameter and 60 years old. Scattered about in the stand were larger, open-grown *Quercus macrocarpa* of 12-20 inches in diameter and well over 60 years old. The lowest branches on these large specimens were 6-10 feet above the ground and 3-11 inches in diameter. Maximum tree height was about 50 feet. Other trees present included *Quercus ellipsoidalis, Populus tremuloides, Acer negundo*, and *Fraxinus pennsylvanica*; these species were unimportant and appeared to be less than 60 years old. No typical prairie herbs were present. The stem density of the close-grown, younger-aged oaks was estimated between 200 and 300 per acre and the older, open-grown oaks at about 5 per acre.

The large, open-grown oaks are relics of the savanna vegetation recorded by the survey, and the younger, close-grown oaks represent the succession to forest beginning at the time of settlement. The latter group originated from oak shrubs or "grubs" that were present in the savanna but were suppressed by pre-settlement fires (Curtis, 1959). The savanna was easily burned, because the prairie ground-cover provided abundant fuel. The oak trees were not easily killed, for the bark is fire-resistant. Fire frequency lessened at the time of settlement because of the fire-breaking effect of roads and fields, and the grubs grew into multiple-stemmed trees and shaded out the holophyious prairie herbs; 12-15 years without fire is long enough for a grub to develop into a tree with fire-resistant bark (Curtis, 1959).

Oak-savanna stands commonly occurred as groves beside ponds that served as natural fire breaks. Such a stand occurred on the east side of Horse Pond (W 1/2, Sec. 22). The survey recorded oaks up to 16 inches in
diameter in this “oak opening.” One *Fraxinus* of 6 inches diameter was also recorded. In 1962 the stand was severely disturbed by logging and cattle grazing; the herb flora was of pasture grasses and weeds. It was dominated by *Quercus macrocarpa*, although *Q. ellipsoidalis*, *Fragilis pennsylvanica*, *Acer negundo*, *Populus tremuloides*, *Betula papyrifera*, and *Ulmus americana* were present. Many trees had been cut in 1961, and ring counts were made on 22 stumps, whose ages fell into three groups. The youngest group was from stump sprouts of trees cut in 1930. The second group had multiple stems and originated from grubs about 1903. As in the stand previously discussed, these trees were close-grown and lacked the spreading crown of the oldest trees in the stand. The oldest group was of open-grown, 13-18-inch-diameter *Quercus macrocarpa* dating from about 1884, and some of them had multiple stems indicating a grub origin. The oldest tree was an *Ulmus* that grew on the shore of the pond and had over 100 growth rings. Except for this tree, species other than *Quercus macrocarpa* appear to have originated after settlement. The 16-inch-diameter oak recorded in the 1871 survey indicates trees had occupied the site for at least the preceding 100 years.

The largest and probably oldest tree seen in the Oak Savanna is an open-grown *Quercus macrocarpa* in NW 1/4 NE 1/4 Sec. 26. It is about 40 ft tall and has three stems of 30, 25, and 15-inch diameters. The maximum number of growth rings obtained from the bark to the rotten interior was 135 and the stems are estimated to be between 200 and 300 years old. The multiple stems indicate a sprout origin, and the root system may be much older. Thus the oaks of the Oak Savanna have ages comparable to the older pines of the Pine-Hardwood Forest.

Not all oaks-savanna stands have succeeded to oak forest. In 1962 the NW 1/4 Sec. 27 and the W 1/2 Sec. 26 was rather undisturbed prairie containing individual oak trees in the open and groups of trees in stands up to 5 acres. These stands were not recorded in the survey notes, probably because of their small size. An example occurred on a knoll and west-facing slope on the east side of a pond (SW 1/4 NW 1/4 Sec. 27). This stand of 2 acres contained 72 *Quercus macrocarpa* and 2 *Populus tremuloides* trees. The oaks were open-grown, up to 25 ft high and 5-17 inches in diameter. A 7-inch-diameter tree was 59 years old; a 17-inch-diameter tree was 109 years old. The ground cover beneath and between the trees was dominated by *Sisyr spartes*, *Andropogon scoparius*, and other prairie herbs. The several grubs present were not vigorously growing into trees. Fire did not appear to be maintaining the grub habit; instead, cattle browsing may have been a factor. Some of the lower sprouts had been pruned by rabbits.

The trees were relatively small for their age, so here oak may be at its climatic limit, and the growth of grubs into trees may be favored only during exceptional growing seasons.

Differences in the structure and composition of vegetation associated with differences in elevation on the west flank of the Big Stone Moraine.
parallel the variation found locally on slopes of different aspect. A small-scale example of the effects of different slope direction in almost diagrammatic clarity was available for study around the west end of Sedivy Lake (SW 1/4 SW 1/4 Sec. 11). Here the nearly level upland supports oak savanna, whereas the north-facing slope has a dense, mesic forest and the south-facing slope supports prairie.

The vegetation was sampled in August, 1962, from the edge of the lake upslope to the surrounding cultivated fields along transsects of 220°, 270°, 315°, and 360° true direction. The slope was measured with a protractor and the distances were paced. Estimates of cover were made in the tree, shrub, and herb layers. The growth, habit, height, and diameter of trees were estimated.

Figure 10 shows the approximate size and spacing of tree crowns on a 1958 air photo. The dashed line representing the crest of the slope is not a contour; the upland is lower in the east than in the west. The closed-canopy forest is chiefly below the crest on the northeast-facing slope; the trees on the upland upland have a savanna spacing. Surrounding the stand on the upland are cultivated fields that had been prairie. Between the stand and the lake is a hydrophytic mat about 50 ft broad dominated by Phragmites, Carex, and Scirpus. The lake is permanent and about 6 ft deep.

Mesic forest occupies the nearly level, slightly peaty soil between the mat and the slope; it also occupies the lower half of the northeast-facing slope, which is inclined 10°. The 8-14-inch-diameter trees have 80% cover and are close-grown, with narrow crowns up to 70 ft tall. The chief species are Quercus macrocarpa, Fraxinus pennsylvanica, and Populus tremuloides; also present are Ulmus americana and Betula papyrifera. The 80% shrub cover was chiefly contributed by Corylus corvalis, Cornus stolonifera, C. racemosa, C. alnifolia, Xanthocyprium americanum, Viburnum rafinesquianum, and V. lentago. Saplings of Populus tremuloides, P. balsamifera, Acer negundo, and Ulmus americana form part of the shrub layer. Herb cover is a relatively low 50% and includes such mesic forest species as Sanguinaria canadensis, Uvularia grandiflora, Causophyllum thalictroides, Atriplex nudicaulis, Botrychium virginianum, and Solidago flexicaulis.

Xeric forest occupies the upper part of the northeast-facing slope and the east-facing slope. The trees are moderately open-grown, providing 50% cover. They are Quercus macrocarpa, with a few Fraxinus pennsylvanica. A typical sak is 50 ft tall and 14 inches in diameter, with a 5-inch-diameter living branch 15 ft above the ground and similar but dead branches 5 ft above the ground. The low, dead branches indicate the trees grew in a more open situation in the past, although not necessarily with savanna spacing. The 50% shrub cover is composed mainly of Corylus americana, Symphoricarpos occidentalis, Cornus racemosa, Prunus virginiana, and Rhus radicans. A common liana is Vitus riparia. The 75% herb cover is dominated by Carex pennsylvanica, Desmodium glutinosum, and Symphoricarpos occidentalis. The xeric forest grades into mesic forest on the lower part of the northeast-facing slope and into shrubby savanna along the crest of the slope.

Shrubby savanna occupies the flat area above the crest of the slope. Here open-grown Quercus macrocarpa up to 40 ft tall are widely spaced and have low, spreading crowns. Occasional Populus tremuloides contribute to a 20% tree cover. A rank growth of shrubs covers 90% of the surface. The chief dominant is Corylus americana, but also prominent are Cornus racemosa, Rhus glabra, and Symphoricarpos occidentalis. Herbs have 60% cover, and species composition is similar to that of the xeric forest. In addition, Vicia americana, Elymus canadensis, Monarda fistulosa, and Artemisia ludoviciana are present.

Prairie savanna occupies the southeastern slope. Open-grown Quercus macrocarpa 10-30 ft tall provide 30% tree cover. Shrub cover of 70% is contributed by the same species as in the shrubby savanna. However, the shrub cover is not continuous, and openings are occupied by such typical prairie species as Andropogon gerardii, Agropyron sp., Glycyrrhiza lepidoides, Monarda fistulosa, and Artemisia ludoviciana.

Prairie of grasses and forbs occupies the south-facing slope. A dense zone of Solidago canadensis occupies the moist area between the hydrophytic mat and the slope. The slope is dominated by grasses such as Andropogon gerardii, Stipa spartea, Sorgastrum nutans, and Bouteloua curtipendula. Common forbs are Amorpha canescens, Petalostemon parvum, Psoralia argophylla, Solidago rigida, Liatris spp., Artemisia ludoviciana, Aster sericus, A. ericoides, and A. partnicooides. Present on the disturbed soil of a gopher mound is Artemisia glauca. Several Quercus macrocarpa grubs occur but do not appear to be vigorous.

The division into communities is arbitrary; they grade into one another with lateral and vertical differences in slope and elevation. Adjacent communities have many species in common. The two most contrasting communities, mesic forest and prairie, have only two species in common—Quercus macrocarpa and Galium boreale, the former with different growth habits. The sharpest boundary is between the hydrophytic mat and the communities on mineral soil.

Some postsettlement human influence is evident. A wagon road, prob-
ably abandoned before 1930, follows the crest of the slope and has been invaded by shrubs. Several oak stumps in the xeric forest indicate selective logging in the past 50 years. Pasture weeds are absent, and thus grazing has not been a recent factor. According to the owner, the stand has seldom been burned. Several 8-inch-diameter oaks on the crest adjacent to the prairie had been cut in 1952, and ring counts indicate grub origin about 1910. They also had scars from a fire about 1938. Thus logging, grazing, and fire were not important recent factors in determining the general character of the vegetation at the time it was sampled.

No investigation of the soil was undertaken, but the soil parent-material is silty-loam till and is probably the same in each community of the stand.

The changes in the communities since the cessation of presettlement fires have been a stepwise mesic succession with discrete stages. The mesic forest has changed from a xeric forest through the addition or increase of the mesic Betula, Ulmus, Populus, and Fraxinus. The xeric oak forest has become more closed. The savanna communities have acquired a fire-sensitive shrub cover that has all but eliminated heliophils prairie herbs. In the area bordering the prairie, oak grubs have grown into small trees, and the former prairie area has been limited to the most xeric slope. Most of these successions probably occurred in the first decade of this century, and further succession is progressing more slowly or has halted.

In both the presettlement and modern communities, topography, as it influences insolation and soil moisture, is the master factor. It controls soil drainage, exposure to wind, and the duration and intensity of solar radiation. Soil drainage is most extreme on the upper part of the slopes, while the lower slopes are less well drained, and the water table is closer to the surface. Thus the greater stature of the trees of the lower slopes and the close-grown tree habit on the northeast-facing slope.

Intensity of solar radiation is highest on the south-facing slope and progressively less around to the northeast-facing slope. On the level surface above the crest, the intensity is between these extremes, although the duration is greater. Insolation influences temperature and rate of evaporation and transpiration from soil and plants, and thus the greatest deficiency of soil moisture occurs where insolation is greatest. Exposure to desiccating winds may be a factor contributing to the decreased stature and increased spacing of the trees above the crest. Thus, each community is related to a microclimatic soil-moisture gradient.

A macroclimatic change toward decreased precipitation and cloud cover and increased insolation and evaporation, resulting in decreased soil moisture, would expand the prairie to the east-facing slope and above the crest. Xeric forest would shift to the northeast-facing slope, and such mesic trees as Ulmus, Betula, and Fraxinus would be eliminated. Scrubby Populus would probably persist on the peaty soils at the foot of the northeast-facing slope. On the other hand, a climatic change toward higher soil moisture would eliminate the prairie and expand the mesic forest. Under these conditions of increased mesophytism, Ostrya virginiana, Quercus rubra, Fila americana, and finally Acer saccharum would be expected to migrate into the stand and come to dominate the most mesic sites.

Fire tends to decrease soil moisture by removing a shading canopy and to expand the more xeric vegetation at the expense of the more mesic. It decreases soil moisture by removing plant cover and exposing the soil to insolation and wind. It readily kills the aerial shoots of shrubs and trees, except Quercus macrocarpa. Prairie herbs are adapted to fire and vigorously grow from underground parts. After the death of their shoots, many woody species resprout from underground parts, but with reduced vigor. If fires are frequent and intense enough, woody species are eliminated, and the vegetation changes to prairie.

Fires are most frequent and intense when there is an abundance of dry fuel. The availability of such fuel is a function of both vegetation and climate. Prairie plants, because of their annual shoots, produce drier fuel than mesic-forest dominants, which have green perennial stems. Forest litter is also more moist than prairie litter, because it is shielded from the drying effects of sun and wind. A low-intensity fire in a prairie would be unlikely to burn much of an adjacent forest. However, if a fire occurred in a drought period, the forest would be more combustible and the death of many forest trees would be more likely. If there were a series of drought years accompanied by fire, then the forest might be eliminated and be succeeded by prairie. However, if the site is on an island or on the leeward side of a fire break, such as the side of a pond or lake or even a topographic feature such as a downslope slope, drought might provide fuel for a potentially damaging fire, but the frequency of fire would be low because of the protected nature of the site.

Prairie

This formation lies west of R 41 on the Des Moines Lobe till and farther westward on Lake Agassiz sediments. The three community types of the Oak Savanna formation are present, but the prairie type is most extensive, and oak savanna and Populus scrub occur as groves. The prairie type was identified by name in the survey notes and on
plat maps. As no bearing-trees were available, the corners were identified by posts placed in mounds of earth.

Buell and Facey (1960) located and described many of the relict stands in the transect. Common to most sites were grasses such as Andropogon scoparius and Koeleria cristata and legumes such as Amorpha canescens, Psoralea esculenta, Petalectea purpurea, and P. candelabrum. On dry, exposed sites, e.g., at Frenchman's Bluff on the Erskine Moraine, western grasses such as Bouteloua hirsuta, B. gracilis, and Stipa comata were prominent. Stipa spartea and Bouteloua curtipendula dominated mosic sites, while on moist sites, tall grasses such as Andropogon gerardi and Sorghastrum nutans were prominent. Also characteristic of the prairie were anemophilous Compositae such as Artemisia ludoviciana, A. glauca, and A. frigida, as well as entomophilous Compositae ("Tubuliflorae") such as Aster spp., Helianthus helianthoides, Ratibida columnifera, and Helianthus spp. The prairie commonly had widely-spaced shrubs of Rosa blanda and Salix humilis as well as colonies of Corylus americana and Symphoricarpos occidentalis.

The Populus scrub type was identified in the survey notes as "aspen" or "brush prairie." According to Ewing (1924) the scrub communities occurred as groves around marshes or in moist swales and were dominated by Populus tremuloides 10-25 ft tall. On drier sites, Quercus macrocarpa and on moist sites Populus balsamifera were common associates. Corylus americana and Prunus virginiana were common shrubs especially around the margins of the groves. The groves originated from Populus seedlings on moist soil and spread to the adjacent prairie by root suckers (Buell and Buell, 1959). Prairie plants were eliminated from the scrub, because they were shade-intolerant. However, prairie species may reappear when the Populus is killed by fires. Repeated fires are needed to eliminate the trees because of persistent root suckers.

The Populus-scrub groves on the Erskine Moraine apparently had a strong oak component, for they have succeeded to oak forest (Buell and Facey, 1960). The two oak-savanna groves on the Erskine Moraine were on the east side of ponds. In the northern half of R 43, the groves are associated with a glacial drainageway, but their relation to soil and topography has not been investigated.

Buell and Facey (1960) emphasized that prairie groves occupied sites with a favorable moisture balance. Oak savanna was found on well-drained sites protected from the desiccating effects of frequent prairie fires. Populus scrub occurred where ground water was near the surface. Both occurred on the finer soils and north-facing slopes of the Erskine Moraine, where increased altitude probably had a favorable effect on temperature and precipitation.

Large herds of bison were present in the Prairie and Oak Savanna until the mid-19th century; the last ones in Minnesota were seen in 1880 (Gunderson and Beer, 1933). They modified the vegetation especially where they congregated and trampled the soils around ponds and around trees and boulders on which they could rub their hides. Citations of early travelers (Bird, 1961) described the destruction of grass, shrubs, and small trees in prairie groves. Such disturbed soils form suitable habitat for the anemophilous Ambrosia artemisiifolia and for Chenopodiaceae such as Amaranthus hybridus, A. retroflexus, and Chenopodium hybridum (Steiger, 1930). The effect of grazing is hard to evaluate, but, judging from prairie relics moderately grazed by cattle, the weedy perennials Ambrosia psilostachya and Artemisia frigida thrived.

Another disturbed place in the prairie are mounds of fresh soil created by gophers and toads (Breckenridge and Tester, 1961). These mounds support a weedy flora including Ambrosia artemisiifolia and Chenopodium spp.

The interrelationship of vegetation, fire, topography, and climate is well illustrated on the Big Stone Moraine. Fire, whether started by lightning or Indians, was almost an annual event in the Prairie and Oak Savanna (Upham, 1896; Buell and Facey, 1960). The dry grass burned easily late in autumn and in spring, and fire spread rapidly sometimes as much as 50 or 100 miles in a few days. These fires burned eastward onto the Big Stone Moraine, where they commonly died out because of reduced windiness and because of topographic breaks in the hilly topography, moister fuel, and in the case of spring fires, persistent snow cover (Buell and Facey, 1960). The snow persisted because of lower temperatures in this area. If there were a climatic change toward warmer and drier winters, then the spring fires could burn more easily eastward into the Forest and perhaps change the Forest to Oak Savanna. Such a sequence of events, initiated by a climatic change, is presumed to have caused the vegetation changes in postglacial time, as described below in detail.

**Pollen assemblies and vegetation**

**Location and character of sites**

Eleven cores of sediment were collected from the centers of ponds within the transect or adjacent to it, four long cores and seven short cores. The ponds were chosen for their 1) location within a vegetation formation, 2) uniformity of basin diameter (600-1,000 ft) (by basin di-
ameter is meant the area occupied at highest water levels by open water or bog vegetation), 3) permanence of water during the drought of the 1930's as judged from 1939 air photos, and 4) proximity to stands described in the ecological literature.

Sites of one or more long cores and two or more short cores are located in each formation except the Oak Savanna. Pond sites in the Pine-Hardwood Forest are Martin, Cindy, Bog D, Bog A, Bad Medicine, and McCraney; in the Mesic Deciduous Forest are Reichow and Terhell; in the Oak Savanna is Horse, and in the Prairie are Faith and Thompson. All are in townships 143 N except Bad Medicine in T 142 and Faith in T 144.

Ponds of medium size were chosen instead of small ponds or peat bogs to reduce possible pollen over-representation from pond-side or bog-forest trees. Ponds of larger dimensions and lakes were not used because of their relative scarcity. Sites that did not dry up during the drought of the 1930's are assumed to have had continuous pollen sedimentation and preservation since the formation of the basin. Pond and basin dimensions were estimated from 1958 air photos.

The vegetation of Bogs A and D in Itasca Park is described in Conway (1949) and Marshall and Buell (1955). Erdtman (1943, Figure 11) presented a pollen diagram from this bog complex. Reichow and Terhell Ponds are adjacent to the Waubun Acer-Tilia forest stand which, according to Buell and Cantlon (1951), invaded prairie about 1810. The cores were examined for pollen-analytical evidence of this succession.

Martin Pond (NE 1/4 SW 1/4 Sec. 20, R 34) has a 600-ft-diameter basin occupied by treeless bog, except for the 150-ft-diameter pond in the center. The chief bog plants are Sphagnum and Chamaedaphne calyculata. The upland is densely forested with Populus tremuloides, Betula papyrifera, Quercus rubra, Q. macrocarpa, and Ulmus americana. Conifers were essentially absent from the surrounding upland, but pine stumps over 30 inches in diameter were found. A long core of 635 cm was collected below 75 cm of water.

Cindy Pond (NW 1/4 Sec. 25, R 34) is 1/2 mile southeast of Martin Pond. The 600-ft-diameter basin was occupied by open water, except for a marginal shrub zone dominated by Alnus rugosa, Betula pumila, and Salix. A 90-cm short core of non-calcareous detritus gyttja was collected below 75 cm of water.

Bog D Pond (NW 1/4 NW 1/4 Sec. 30, R 35) lies in the Twin Lakes Bog complex (Conway, 1949) just south of Lake Itasca in the Lake Itasca drainage way. The basin of the bog is linear and 675 ft wide at the pond. The 225-ft-diameter pond is surrounded by concentric zones of Carex mat, Larix forest, and Picea mariana forest. The upland is dominated by large Pinus resinosa and P. strobus. A long core of 800 cm was collected below 190 cm of water.

Bog A Pond (NW 1/4 SW 1/4 Sec. 30, R 35) is 1/4 mile west of Bog D Pond and has similar vegetation and dimensions. A 60-cm short core of non-calcareous detritus gyttja was collected below 400 cm of water.

Bad Medicine Pond (NW 1/4 SW 1/4 Sec. 4, R 37) has a 750-ft-diameter basin occupied by open water except for a shrub border zone. The upland around the pond was dominated by Pinus banksiana, Populus, and Betula, with a few Pinus resinosa and P. strobus. A 45-cm short core of gyttja was collected below 540 cm of water.

McCraney Pond (NW 1/4 NW 1/4 Sec. 25, R 40) has a 900-ft-diameter basin and lies within the Twin Lakes drainage way. It is one mile east of the boundary between Pine-Hardwood and Mesic Deciduous Forest. The open water is surrounded by a Carex-Typha mat 30 feet wide, and Larix bog forest is found in one end of the basin. The upland had a mixed forest of Populus, Betula, Quercus, and Abies with a few large Pinus strobus. An 80-cm short core of shell-rich gyttja was collected below 40 cm of water.

Reichow Pond (NW 1/4 NW 1/4 Sec. 25, R 40) lies in a 700-ft-diameter basin. It has a 600-ft-diameter pond surrounded by a dense zone of Alnus rugosa shrub with a Larix bog forest along one side. A few Picea mariana are mixed with the Larix. The upland has a forest of Acer saccharum, Tilia, Populus, and Ostrya. A 100-cm short core of shell-rich gyttja was collected below 50 cm of water.

Terhell Pond (NE 1/4 SE 1/4 Sec. 18, R 40) has a 1,000-ft-diameter basin filled with open water, except for a Typha marsh at the north end. The pond is 1/2 mile west of Reichow Pond and has a similar upland vegetation interspersed with cultivated fields. A long core of 1,100 cm was collected below 265 cm of water.

Horse Pond (NW 1/4 NE 1/4 Sec. 21, R 41) lies in a north-south basin about one mile long and 600 ft broad. Open water fills the basin; there is no marginal bog. The surroundings are cultivated fields and pasture. A former oak-savanna grove on the east side of the pond was at the time of this study a pasture dominated by Quercus macrocarpa. The stand also includes Quercus ellipsoidalis, Populus tremuloides, Ulmus americana, Betula papyrifera, Fraxinus pennsylvanica, and Acer negundo. This pond is on the western margin of the Oak Savanna, and the terrain was treeless for six miles to the west.

Faith Pond (NW 1/4 SW 1/4 Sec. 24, R 43) has a 750-ft-diameter basin that lies within a broad glacial drainage way. The 225-ft-diameter pond
is surrounded by a Carex-Typha marsh. The higher land is cultivated, but Populus scrub occurs in the drainageway. Populus tremuloides is dominant, and P. balsamifera, Quercus macrocarpa, Ulmus americana, and Acer negundo also occur. Common shrubs include Betula pumila, Cornus stolonifera and Salix discolor. This pond is 3/4 mile across the transect and was chosen because only one suitable pond was in the Prairie portion of the transect. A 90-cm short core of calcareous gyttja was collected below 440 cm of water.

Thompson Pond (NE 1/4 NE 1/4 Sec. 23, R 43) has a 750-ft-diameter basin filled with open water. Dead Salix amygdaloides trees of about 8-inch-diameter project above the water 30 feet from the present shoreline and probably mark the shoreline during the low-water drought years of the 1930's. A dense stand of Myriophyllum covered the shallower parts of the pond. The upland around the pond is cultivated, and part of the slope toward the shore has a stand of Populus tremuloides, P. balsamifera, and Acer negundo. A long core of 1135 cm was collected below 150 cm of water.

Short cores (plate 2)

The pollen analyses at 5 or 10 cm intervals are graphed together with a summary spectrum from the top of the pre-settlement portions of the long core diagrams (pl. 3, 4, 5, 6). The sites are arranged in their east-west order. In general, there is a greater variation between sites or groups of sites in a formation than in succeeding spectra of a single site. AP (arboreal pollen) is greater than NAP (non-arboreal pollen), and NAP is highest at western sites. Shrub pollen is not very important, although Corylus is slightly higher in the west. Pine is the dominant type, highest in the east. Deciduous tree pollen such as Quercus, Ulmus, Ostrya, Carpinus, Fraxinus, and Tilia are most important in the middle of the transect. The anemophilous herbs Gramineae, Artemisia, Ambrosia, and Chenopodiaceae are highest in the west, as are the entomophilous Tubuliflorae. Of the aquatics Myriophyllum is restricted to the west and Brasenia and Nymphaea to the east; Cyperaceae is relatively higher in the west. Thus the abundance of pollen types reflects the general nature of the formations in the transect.

The pollen of these two genera were not differentiated, but is reason to believe that most of the fossil pollen was derived from Ostrya, which has a broader ecological amplitude than Carpinus (Curtis, 1959) and is much more abundant in the transect than Carpinus. For these reasons and for the sake of brevity, only the word Ostrya is used in zone names.

Ambrosia assemblage zone. This assemblage, characterized by relatively high values of Ambrosia and Chenopodiaceae occurs in the upper 10-30 cm and represents the very recent and continuing sedimentation. Various species of Ambrosia and Chenopodiaceae are weeds in fields and along roadsides, and both the weeds and their pollen are most abundant in the cultivated, western part of the transect. Because these weeds largely grow on disturbed soil, this assemblage represents deposition since settlement, whereas the assemblage just below represents the natural pre-settlement vegetation.

Pinus strobus assemblage zone. This assemblage occurs at Cindy, Martin, Bog D, Bog A, Bad Medicine, and McCrane Pond and corresponds to the Pine-Hardwood Forest. Pine is the dominant pollen type, ranging between 35% and 55%. NAP is below 15%, except at Bog D. Betula, the second most important type, is 10-20%. Other deciduous tree types are lower: Quercus 6-10%, Ostrya/Carpinus 1-5%, and Ulmus 1-4%. Paired sites, Cindy-Martin, and Bog A-Bog D, resemble each other closely with respect to the major types, except that Bog D has much higher Gramineae than Bog A. The Gramineae was probably from a local stand of Zizania aquatica that was excluded from Bog A by deeper water. Bog A and Bog D ponds are the only two sites with Nymphaea, and Cindy and Martin Ponds are the only two with Brasenia. Bogs D and A have the highest value of Larix pollen and are the only sites with extensive Larix forest.

The diagrams of the two western ponds, Bad Medicine and McCrane,, show a trend toward decreasing pine and increasing deciduous-tree pollen types. This corresponds to their proximity to the Mesic Deciduous Forest. The higher NAP values at McCrane Pond reflect the prairie component of the Pinus banksiana type that occur nearby.

The deeper, older short cores, from Cindy and McCrane Ponds, have in their lower spectra relatively high deciduous-tree pollen values that decrease upward as pine increases. This hint of a succession is confirmed in the long cores. The reason for naming this assemblage for Pinus strobus will be presented in the discussion of the long cores.

Quercus-Ostrya assemblage zone. This assemblage occurs at Reichow and Terrell Ponds and corresponds to the Mesic Deciduous Forest. Reichow Pond shows a pollen succession from Quercus below 40 cm to Betula from 40 cm to 15 cm at the Ambrosia zone boundary. The values between 40 and 15 cm were chosen as representing the pre-settlement vegetation.

As in the adjacent Pine-Hardwood Forest formation, the NAP is less...
than 13%, but the deciduous-tree pollen types dominate. Their approximate values are Betula 25%, Quercus 15%, Ostrya/Carpinus 10%, Ulmus 8%, Fraxinus 2%, and Tilia 2%; Pinus is 20-25%. The slightly higher pine values at Terhell Pond compared with Reichow Pond may reflect the difference in pond size; the larger Terhell Pond received a more regional pollen rain, while a more local pollen rain is present in Reichow Pond. The increase of Betula from 40 to 15 cm in Reichow Pond may correspond with the Betula rise from 90 to 30 cm at Terhell Pond (pl. 5).

Quercus-Graminaceae-Artemisia assemblage zone. This assemblage occurs at Horse Pond and corresponds to the Oak Savanna. NAP is higher than in the forest formations; it is 25%, with Gramineae 12% and Artemisia 8%. Compared with Reichow and Terhell Ponds, pine (25%) is slightly higher, Quercus (15%) is similar, and Betula (20%), Ostrya/Carpinus (3%), Ulmus (3%), and Tilia (less than 1%) are lower. Because of the limited area of this formation and the position of Horse Pond on its western boundary, the oak value is probably a minimum for Oak Savanna.

Gramineae-Artemisia assemblage zone. This assemblage occurs at Faith and Thompson Ponds and corresponds to the Prairie. NAP is higher than in the Forest and Savanna formations; it is 30-45%, with Gramineae 15-25%, Artemisia 10%, Ambrosia 5%, and Chenopodiaceae 2%. Tuberiflorae is 3-8%.

Faith Pond is on the south edge of an area of Quercus-Populus type, but although AF is slightly higher, most values are similar to Terhell Pond. The high Cyperaceae values at Faith Pond reflect the surrounding Carex-Typha meadow vegetation. No such community occurs around Terhell and Horse Ponds to account for their high Cyperaceae values, but a possible source is Scirpus growing in shallow water, especially during low-water years.

Importance percentages of bearing trees and pollen values

Do pollen percentages represent the importance of the taxa in the vegetation? Pine, for example, is obviously over-represented in the Prairie and Mesic Deciduous Forest, where pine trees are absent; is it also over-represented in the Pine-Hardwood Forest? In Figure 9, pollen values from each site are compared with the importance percentages of the same taxon of bearing-tree. The values are the relative percentages of all trees, except the bog Laxie.

In the Pine-Hardwood Forest, pine-pollen values are lower than the bearing-tree values. However, because the bearing-tree values may be too high, the lower pollen values probably are a more reasonable measure of the importance of pine in the vegetation. There is also a parallel decrease of values from east to west. The pine pollen in the Mesic Deciduous Forest sites was wind-blown for at least three miles.

Poaceae and Abies have low, but similar, bearing-tree and pollen values.

Betula is strongly over-represented, especially in the Mesic Deciduous Forest. The bearing-tree values are probably too low, but this does not explain the disproportionate representation between the Forest formations. One possibility is that the land survey did not record the vegetation of the Mesic Deciduous Forest at a time when it had a higher proportion of Betula trees, and the area was surveyed only after a succession to Ulmus and Tilia had occurred. A second and more remote possibility is that a locally large stand of the bog shrub Betula pumila contributed the pollen.

Populus is quite under-represented. Experimental evidence suggests that the pollen is easily destroyed under conditions where pine pollen is preserved (Sanger and Dale, 1961). However, relatively low production and dispersal may be as important or more important than differential destruction in the under-representation of Populus. In older spectra of the transect, Populus pollen is over 10%.

Acer is comparatively unimportant in the vegetation, so representation is difficult to evaluate. With the exception of Acer negundo, which was recorded once as a bearing-tree, all local species are entomophiles, and under-representation would be expected from relatively low production and little wind dispersal. Acer saccharum is quite under-represented in the surface spectra of the Mesic Deciduous Forest.

Tilia is under-represented most apparently in the Mesic Deciduous Forest, where it is an important bearing-tree. The actual under-representation is greater because the bearing-tree values are too low. Again the relatively low dispersal results from entomophily. There is a parallel increase of pollen and bearing-tree values between the Forest formations.

Ulmus is under-represented, but not so much as Acer and Tilia. Values are higher in the Mesic Deciduous Forest than in the Pine-Hardwood Forest.

Quercus is somewhat over-represented in the Pine-Hardwood Forest, but more properly represented in the Mesic Deciduous Forest. The bearing-tree and pollen values have a parallel rise in the western part of the Forest.

Ostrya/Carpinus (probably nearly all Ostrya pollen because of the
rarity of *Carpinus* in this area) is strongly over-represented, but the bearing-tree values are not a good measure of the importance of *Ostrya*, as it seldom reaches bearing-tree size. However, where it occurred as a bearing-tree in the Mesic Deciduous Forest, the pollen value was highest. In the Pine-Hardwood Forest, the most probable pollen source was local, unrecorded trees of *Ostrya*.

*Frazierius* has both low pollen and bearing-tree values, with a slight parallel rise in the Mesic Deciduous Forest.

Adjustments can be made to rationalize some of the pollen and bearing-tree values. For example, if the pollen values of the Mesic Deciduous Forest were calculated without pine and *Ostrya/Carpinus*, then *Betula*, *Ulmus* and *Tilia* would approach the bearing-tree values, although *Quercus* would become over-represented and *Populus* would remain under-represented.

The source of pollen in pond sediment is from an area of indefinite size. Grains may be derived from the surface of the pond (*Nuphar*) or transported at least 600 miles (*Ephedra*). Neither obviously local aquatics nor distant exotic types are a problem in interpreting the fossil spectra of this postglacial study. *In general*, a given type pollen will occur at higher relative frequencies the closer and more abundant the source.

Pine is an interesting exception. Although pine trees are restricted to the Pine-Hardwood Forest, the relative pollen frequency of *Pinus* is lowest at Ricehow Pond in the adjacent Mesic Deciduous Forest, and slightly higher in the more distant Prairie. This probably reflects a higher absolute pollen production of Mesic Deciduous Forest than the Prairie. The same amount of pine pollen falling in the two formations would appear as a higher percentage in the Prairie.

Erdtman (1943) recommended that the relation between the pollen of surface samples and the contemporary vegetation be used as a key to the interpretation of pollen diagrams in terms of vegetation. With this in mind, the following key to the assemblage zones was constructed. The key is based on the short cores and serves to summarize them; but it also contains zones from the long-core diagrams. It not only serves to define zone boundaries but also shows the interrelationships of zonal spectra and, by inference, their corresponding vegetation formations. The key is not a stratigraphic outline.

**Key to the pollen assemblage zones, their subzones and peak zones**

A. Spectra of upper 25 cm of sediment (postsettlement time); *Ambrosia* and *Chenopodiaceae* each over twice values in remainder of upper meter ........................................ *Ambrosia*
the other zone boundaries from rates of sedimentation if several synchronous boundaries are assumed: first, the surface of the accumulating sediment represents zero years, and second, that the upper and lower boundaries of the Pinus b/r-Pteridium assemblage zone (and subzone) were synchronous at all sites.

At Bog D the lower boundary of the Pinus b/r zone at 770-790 cm was 11,000 ± 90 years B.P. (before the present) (Y-1418), and the upper boundary with the Quercus-Grassmeae-Artemisiaa zone at 705-720 cm was 8,560 ± 120 years old (Y-1419). Extrapolation of the rate of sedimentation within the Pinus b/r zone at this site indicates that sedimentation began 11,700 years ago. Similar extrapolations were made to estimate the beginning of sedimentation at the other sites.

Three other radiocarbon dates were obtained at levels of preliminary zone boundaries, but as the boundaries were subsequently adjusted these dates were only useful in calculating rates of sedimentation. At Bog D Pond these dates are 3,390 ± 100 (Y-1328) at 412-418 cm and 2,730 ± 75 at 250-260 cm (Y-1196) and at Terrell Pond 4,270 ± 100 at 545-560 cm (Y-1329). Thus all zone, subzone, and peak zone boundaries above the Pinus b/r zone and subzone boundaries are interpolations based on rates of sedimentation either between the Pinus b/r-Pteridium assemblage zone or subzone boundaries and the surface of the sediment or, where possible, between radiocarbon-dated levels.

**EARLY ASSEMBLAGES WITHOUT MODERN ANALOGS**

**Picea-Populus assemblage zone**

This zone is the deepest and earliest recorded at the long core sites. *Picea* is dominant, especially in the lowest spectrum. Other AP types with relatively high values are *Populus*, *Larix*, *Juniperus/Thuja*, *Fraxinus nigra*, *Ulmus*, and *Betula*. The entomophiles shrub *Shepherdia canadensis* is nearly confined to this zone. The NAP is less than 15% except at Martin Pond, where it reaches 60% as a result of 5-16% values each for Grassmeae and *Artemisia*. Martin Pond also has exceptionally high values for *Salix* and *Cyperaceae*.

Fossil wood was found at the till-sediment interface in three of the long cores, *Populus* at Terrell Pond and *Picea* at Bog D and Martin Ponds. Other macrofossils at Martin Pond were *Picea* and *Larix* needles, *Betula papyrifera* fruits, and an *Elaegnaceae* hair. The upper 5 cm of till at Martin and Bog D Ponds was mixed with black humus.

Before a discussion of the vegetation represented by the fossils, some comments on the origin of the basin are useful. All four basins originated from the melting of ice blocks buried in the glacial drift. The glacial chronology indicates that the active ice disappeared 12,000-13,500 years ago from northwestern Minnesota. However, according to the rate of sedimentation, the melting of the ice blocks and formation of the basins did not occur until 11,500 to 12,300 years ago (pl. 1). The persistence of till-covered ice blocks is also indicated by the occurrence of the horizon of fossil wood and soil, which implies that a forest community grew on the drift overlying the ice blocks.

A reconstruction of the local physiographic and soil conditions suggests significantly different habitats compared with modern local conditions. The melting of the ice blocks released large amounts of water, which increased or renewed the instability of drainageway and outwash surfaces. Soils were relatively shallow and not so weathered or so deeply leached as they are today, but the sandy soil parent-material was weathered enough to form shallow podzolic soils (Farnham et al., 1964). Much of the surface was poorly drained; there were more lakes than at present because of the poorly coordinated drainage systems. Peat soils were shallow and more local than at present.

Most of the fossil taxa of this zone are represented in the Pine-Hardwood Forest of the transect, but the pollen percentages are much different. Because of the differing soil conditions of the two periods it is difficult to infer modern community types. However, according to general habitat preferences of different species, it is possible to suggest hypothetical communities.

The humus and wood at the surface of the till indicates that a soil had formed and supported forest trees. When the ice block melted, the soil and forest collapsed into the newly-formed basin and were preserved by subsequent sedimentation. The extremely high *Picea* values just above the till may not be a true indication of its regional importance, for the pollen may have come from this extremely local source. *Picea* may have been localized at sites of buried ice, for the ice blocks could have been in slight depressions created by previous partial melting of the buried ice. Such depressions may have provided sheltered microhabitats for forest communities.

The succeeding spectra with more moderate *Picea* values probably reflect the regional vegetation. The vegetation on moderately well-drained sites was probably a mixture of *Picea*, *Populus*, and *Betula papyrifera*. Both *Picea mariana* and *P. glauca* were probably present (W. Watts, oral communication), with *P. glauca* on the better-drained sites. *Larix laricina* was probably associated with *P. mariana* on the more poorly-drained sites,
but not necessarily on organic soils (Roe, 1957). *Ulmus* and *Prairieus nigra* also grew on moister soils—perhaps those with seasonal flooding.

The high *Populus* values cannot be matched by modern analogs even in areas where *Populus* trees are predominant. These high values can most easily be explained either by assuming that *Populus* trees were overwhelmingly predominant or that there were special conditions for preservation of the delicate pollen.

The appreciable amounts of *Artemisia* and shrub pollen suggest openings in the general forest cover, probably on extremely well-drained south-facing slopes and hill tops. *Artemisia frigida* is most tolerant of such habitats. It may also have occurred on the unstable soils of active drainageways. The relatively high *Juniperus/Thuya* values indicate that one or both areas were present and perhaps abundant. Watts and Winter (1965) found a *Juniperus communis* needle in sediments having a similar pollen assemblage. This heliophilous shrub species could have been an associate of *Artemisia* on open sites as it is in heavily grazed pastures in western Wisconsin and eastern Minnesota today. *Thuja occidentalis* could have occurred on poorly-drained sites. The relatively low values of *Pinus* and *Quercus* indicate a source outside the transect, perhaps many miles distant, although there may have been a very few nearby. The moderately low values of *Ostrya/Carpinus*, *Ulmus*, and *Acer* suggest that these were of relatively little importance.

Although this zone has few analyses, the unity of the assemblage at all four sites indicates a regionally uniform vegetation not strongly influenced by regional topography or soil parent-material. The many dominants present suggest a diversity of microhabitats conditioned by local or unstable topographic and soil-moisture conditions.

**Pinus banksiana/resinosa-Pteridium assemblage zone**

This pine-dominated zone succeeds the *Picea-Populus* zone at Martin and Bog D Ponds. In the Bog D core, at least 50 pine grains per sample were separated into *Pinus b/r* or *P. strobos* types. The grains were predominantly of the *Pinus b/r* type; the insignificant number of *P. strobos* type is attributed to long-distance transport. *Pteridium* spores are characteristic of this zone. Also present in significant percentages are *Picea*, *Larix*, *Betula*, *Ulmus*, and *Abies*. Martin Pond differs from Bog D Pond in having relatively poorly preserved pollen in mossy sediment and in having higher values of *Picea*.

Although this zone does not have a modern analog in the transect, in many ways it is similar to the *Pinus strobus* assemblage. The low NAP together with high pine indicate a pine-dominated forest. The two assemblages are also similar in having significant amounts of *Picea*, *Larix*, *Betula*, and *Abies*. However, they differ in that the *Pinus b/r* zone has higher values of *Pteridium* and *Ulmus*, and the younger *P. strobus* zone has a richer assemblage that includes *P. strobus*, *Ulmus*, and *Acer rubrum*.

Judged by modern distributions and community types, *Pinus banksiana* rather than *P. resinosa* was the chief dominant. *Pinus resinosa* is unlikely because it has the same general geographic range as *P. strobus*, *Ulmus*, and *Acer rubrum*. On the other hand *Pinus banksiana* ranges well north of this Pine-Hardwood Forest group throughout much of the Boreal Forest. The curves for *Pteridium* and *Pinus b/r* are nearly congruent, suggesting that these species were part of the same community type. *Pteridium* today commonly forms a dense ground cover beneath thin forest canopies on sandy soils, notably in the *Pinus banksiana* community type. However, *Pinus resinosa* is commonly present in the same communities and thus cannot be completely excluded from the flora of the *P. b/r-Pteridium* zone.

The interpretation of this zone is that *Pinus banksiana* migrated into the transect, largely replaced *Picea* on the upland, and formed open stands with an understory of *Pteridium*. *Abies* also entered the flora, but its low pollen values indicate sparse, local occurrence on the more mesic soils. *Betula populifera* and *Pinus* are still important components of the upland forest while *Picea* and *Larix* perhaps became restricted to boggy sites. The high *Picea* values and poorly preserved pollen at Martin Pond may reflect low water in the basin and exposure of organic soils that both degraded the pollen and provided a local habitat for *Picea mariana*. *Ulmus* remained an important tree on finer-textured and wetter soils.

Superficially, the succession from shade-tolerant *Picea* to shade-intolerant *Pinus banksiana* seems highly improbable. However, natural openings in the *Picea* canopy were probably being formed by fire and windthrow, and under these conditions, if pine had a competitive advantage over *Picea*, succession to pine would occur. For example, if *Picea* set viable seed infrequently, pine with abundant seed would replace it after a fire allowed full light to reach the ground. It is concluded that *Picea* was succeeded by pine because it failed to complete its life cycle as efficiently as pine and that this loss of vigor was probably caused by a climatic change.

The pine-dominated vegetation did not extend far west as Terrell Pond and probably had its western limit at the eastern margin of the Des Moines Lobe silty till, as *P. banksiana* does today. Pine-forest dominance...
lasted for approximately 2,500 years, from 11,000 to 8,500 B. P., before it was succeeded by Oak Savanna. Prairie succeeded the vegetation of the *Picea-Populus* zone on the Des Moines Lobe silty till.

Wright (1964) reviewed the evidence for early forest successions in Minnesota and adjacent states. Pollen and macrofossil studies indicate that prior to 10,500 years ago (late-glacial) *Picea*-dominated vegetation similar to that proposed for the Itasca transect not only prevailed in Minnesota but westward into North and South Dakota. In southeastern Minnesota, the macrofossil evidence indicates the presence of *Betula papyrifera*, but sites in northeastern Minnesota indicate *B. glandulosa* as well as other tundra species. There is no evidence for tundra in northwestern Minnesota.

The source of the late-glacial flora after deglaciation remains largely speculative, but the most likely source of pine is from the east. On the basis of low pine pollen values in southern Minnesota and South Dakota, Wright (1964) rejects migration from a southern refugium. If the pine is *P. engelmannii*, which seems most probable, he postulates a source from refugia either in the unglaciated Yukon or Appalachian Mountains. He rejects a northwestern Yukon source because he considers Lake Agassiz formed a barrier for migration. However, such a large lake may not be a barrier but may indeed present a highway for seed dispersal when it is frozen and strong winds prevail. On the other hand a northwestern migration route through southern Manitoba can be discarded because of low pine pollen values there at this time (Ritchie, 1964). In southeastern Minnesota pine pollen values exceed 35% between 10,000 and 11,000 years. This contemporaneity of pines in northwestern and southeastern Minnesota points to an Appalachian refugium for pine.

**Later assemblages with modern analogs**

*Gramineae-Artemisia* assemblage zone

This zone succeeds the *Picea-Populus* zone at Terhell and Thompson Ponds, and at Thompson Pond it continues until settlement time. This Prairie assemblage has NAP over 25% and *Quercus* less than 10%. Two named subzones are delimited by variation in tree pollen frequencies.

In general *Gramineae* (15-30%) is dominant. The pollen probably reflects primarily upland prairie grasses, although some aquatic grasses may be represented. *Artemisia* (10-20%) had pollen types of several species, and the source was probably *A. ludoviciana*, *A. frigida*, and *A. glauca*. The pollen percentage probably overrepresents the abundance of these upland prairie species.

*Ambrosia* (over 5%) is also characteristic of this zone, but its source is not certain. For *Iva axillaris* and *Prunus* there have similar pollen. *Iva axillaris* does not occur east of central North Dakota, however. *Prunus* is a sand-dune plant, but sand dunes do not occur in the transect. So neither of these two alternative genera is a probable source for *Ambrosia*-type pollen. Three species of *Ambrosia* occur in the transect, the annuals *A. trifida* and *A. artemisiaefolia* on disturbed soils and the perennial *A. palustre* on grazed prairie. Although not reported from prairie communities in the transect, *Ambrosia artemisiaefolia* is common on all but very wet prairie communities in Wisconsin (Curtis, 1959).

The source of Chenopodiaceae (Chenopodiaceae and Amaranthaceae) pollen is uncertain, for species of these families are not common members of the prairie communities of the transect. *Chenopodium leptophyllum* is common in the upland prairie of North Dakota (Hanson and Whitman, 1938). Most probably sites disturbed by bison, particularly around ponds, supported *Amaranthus* spp. as well as *Chenopodium hybridum* and *C. rubrum*. Macrofossils of these two Chenopodium species have been found with the related *Quercus* Gramineae-Artemisia assemblage at Martin Pond. *Chenopodium rubrum* occurs in prairie marshes in southwestern Minnesota (Moyer, 1936).

Relatively high values of entomophilous prairie species are also characteristic of this zone. Tubuliflorine pollen (5%) was probably derived from such prairie genera as *Aster*, *Helianthus*, *Helianthus*, *Ratibida*, and *Solidago*. Although occurring only as occasional grains, *Amorpha*, *Patagonium*, and *Symphoricarpos occidentalis* are more frequent than in other assemblages. Altogether these entomophilous taxa are underrepresented when compared with anemophilous taxa.

The source of the prairie flora was probably south of the ice border, and although some elements, e.g. *Artemisia* and grasses, may have been present during the time of the *Picea-Populus* zone, the bulk of the prairie flora probably arrived when the *Picea*-dominated vegetation disappeared 11,000 years ago.

**Pinus b/r-Peridium subzone**

This subzone occurs at both Terhell and Thompson Ponds and is characterized by moderate values of *Pinus* and *Peridium* relative to the corresponding assemblage at Bog D and Martin Ponds. All the *Pinus* pollen is thought to have been wind-transported from pines growing on the sandy soils of the Itasca Moraine. *Pinus* is well represented because of the relatively low absolute pollen production of the prairie type. The higher
Pine values at Terrell Pond relative to Thompson Pond reflect its closer proximity to the pine forest. Pteridium spores may likewise have been blown from the east.

The AP types prominent in the preceding Picea-Populus assemblage are present in moderate percentages in this subzone. This suggests that the prairie had groves of trees that were relics of the preceding vegetation. Picea and perhaps Larix had become restricted to poorly-drained soils. Populus groves with a small component of Betula and Ulmus occupied mesic sites on north-facing slopes and fire-protected sites. These groves were most abundant on the topographically diverse Big Stone Moraine and sparse on the topographically less diverse area to the west. The paucity of groves west of the Big Stone Moraine is probably also related to a less suitable climate caused by its lower altitude.

The Terrell Pond diagram indicates that Quercus became a dominant on the crest of the Big Stone Moraine, about 8,500 years ago, but the high NAP values indicate that the prairie elements remained. At Thompson Pond there is no corresponding Quercus rise, so Quercus did not expand westward to the lower altitudes.

**Ambrosia peak zone**

Between 7000 and 8000 years ago large amounts of Ambrosia pollen were deposited at Thompson Pond (60%) and at Terrell Pond (35%). Associated with the peak are high values of *Iva ciliata* and, at Thompson Pond, Cretaceous types including *Conocephalites*, *Aquilapollenites*, *Buuveyesiculites*, and *Striatolites*.

At Thompson Pond the source of the pollen and spores is thought to be from the soil surface and the till parent-material. Here the zone is found in a stratum of silt with little organic matter relative to the gyttja above and below. The Cretaceous spores and pollen must have been eroded from unweathered till and deposited with the silt, and such rapid erosion implies a sparsely vegetated, unstable surface. Ambrosia would find a suitable habitat on such unstable soils. Although Ambrosia is wind-pollinated, the extremely high percentages suggest that it was locally abundant and that the pollen was washed into the pond from the surrounding soil. The Ambrosia pollen was well-preserved, although the other pollen grains were degraded to the extent that most of them could not be identified. The unidentified pollen were probably degraded on the soil surface before deposition, but because Ambrosia grew on the soil it was a constant source of fresh pollen. If the pollen degradation occurred after deposition through the drying out of the pond, the Ambrosia pollen would have been degraded also.

At Terrell Pond there is no lithologic change; relatively few Cretaceous types occur, and poorly-preserved pollen is rare. Thus here the Ambrosia source may not have been the plants of the pond margin but rather from a greater distance. Ambrosia artemisiifolia fruits have been found in sediments containing high values of Ambrosia pollen in a prairie lake in South Dakota (W. Watts, oral communication).

The identification of up to 10% *Iva ciliata* pollen is of interest because this species does not grow in Minnesota today. It is known to occur at only one station north of Iowa and Nebraska, namely in eastern North Dakota, where it grows in a saline marsh (Stevens, 1950). The high values of this essentially southern species indicate it was present in the region, perhaps associated with saline soils, although southward it is not restricted to these soils.

**Ostrya-Ulmus subzone**

Above about 450 cm at Thompson Pond there is a slight but significant rise in the pollen of a number of deciduous trees, notably Ostrya, Ulmus, and Betula, along with the first occurrence of *Tilia*. This is attributable to long-distance transport of pollen from the morainic areas to the east, where Mesic Deciduous Forest was developing. However, some of the pollen could have come from gallery forest along rivers.

**Quercus-Grassinae-Artemisia assemblage zone**

This zone occurs at Martin and Bog D Ponds, where it succeeds the *Pinus b/r-Pteridium* zone, and at Terrell Pond, where it succeeds the Grassinae-Artemisia zone. The zone is named for the three taxa that dominate it. Characteristic of the zone are relatively high values of Ambrosia, Chenopodiaceae, and Tubuliflorae as well as occasional grains of *Amorpha*, *Petalostemon candidum*-type and *P. purpureum*. Aquatic types are abundant, especially *Myriophyllum*, *Cyperaceae*, and *Salix*. Tree types other than Quercus are relatively low; *Pinus* fluctuates between 10% and 20%. Ambrosia and Chenopodiaceae are most abundant in the lower part of this zone.

This assemblage is believed to reflect a vegetation equivalent to the Oak Savanna that occurred on the west flank of the Big Stone Moraine just prior to settlement. The spectra from Horse Pond are a reasonably good match, except that there Quercus is lower (15%) than the 30-40% in the long cores. The lower Quercus percentages at Horse Pond probably
reflect the narrowness of the Oak Savanna at this point and the location of the pond on the margin of the formation.

The vegetation represented by this assemblage probably consisted of prairie, oak savanna, and oak groves concentrated around lakes and ponds. *Quercus macrocarpa* was probably the most abundant oak, but *Q. ellipsoidalis* may have been common on outwash soils. *Populus* scrub groves may have been present, but there is little fossil evidence, in fact less than in the preceding zones. The other AP, particularly *Pinus*, probably came from northeastern Minnesota, where a pine forest was present at this time (Fries, 1962).

Although oak savanna was probably the most striking feature of the vegetation, the structural variations found at the Sedvy Lake stand are possible, *i.e.* xeric oak forest, isolated oak trees in prairie, and oak groves in prairie. The fossil evidence gives no indication of the presence of these variations.

*Quercus-Ostrya assemblage zone*

This zone occurs at Martin, Bog D, and Terhell Ponds, where it succeeds the assemblage representing Oak Savanna. At Martin Pond and Bog D Pond it is succeeded by the *Pinus strobus* assemblage, but at Terhell Pond it persisted until settlement. The NAP under 25% indicates a closed forest; the dominant pollen types are deciduous-tree types, especially *Quercus* and *Betula*. Characteristic of this zone are relatively high values of *Ostrya/Carpinus*, *Ulmus*, *Tilia*, *Fraxinus*, and *Acer saccharum*. In addition, conifer types such as *Abies*, *Picea*, *Larix*, and (upward) *Pinus* show significant increases.

This assemblage represents Mesic Deciduous Forest, which replaced Oak Savanna on the glaciated upland at about 4,000 years B.P. The deciduous trees invaded the prairie and oak-savanna types and shaded out the prairie species, although oak savanna probably persisted on xeric sites such as south-facing slopes and dry upland outwash soils.

The macrofossils at Martin Pond indicate *Betula papyrifera* was present, and this species, together with *Quercus*, and perhaps *Populus*, were the chief upland dominants. According to modern analogs, both *Quercus macrocarpa* and *Q. rubra* were present; the former persisted from the previous Oak Savanna and the latter was a new migrant. Three species of *Populus* were probably present, with *P. tremuloides* and *P. balsamifera* as holdovers from the Oak Savanna and perhaps *P. grandidentata* as a new migrant. Other migrants included *Ostrya*, which was widespread, and *Tilia*. Mesic sites were occupied by *Ulmus*, *Tilia*, and *Acer saccharum*. Other new arrivals were *Larix*, *Picea*, and *Abies*; these probably occurred only on the peat soils that had begun to form.

The Mesic Deciduous Forest reached its maximum western extent along the crest of the Big Stone Moraine. The successions on the two till soil parent materials were not the same. On the Wadena Lobe sandy till of the Itasca Moraine the succession began with *Betula* and then proceeded to *Ostrya*, then *Tilia*, and then *Acer saccharum*. This is an approximate order of increasing light tolerance and soil requirements; it indicates a regional tendency toward increasing mesophytism. This succession is not indicated on the silty soils of the Big Stone Moraine. Apparently the soil requirements of these species were met there without regional soil development.

The Deciduous Forest persisted on the crest of the Big Stone Moraine until about 60 years ago, when it was partially logged and cleared for cultivation. Selective logging removed much of the *Quercus* and *Tilia* component. The Deciduous Forest was succeeded on the Itasca Moraine by a mixture of pine and hardwoods, as shown by the *Pinus strobus* assemblage.

*Pinus strobus assemblage zone*

This zone, found in the long cores at Martin and Bog D Ponds, is dominated by *Pinus* and to a lesser extent by *Betula*. Characteristically present are *Larix*, *Picea*, and *Abies*. The lower spectra of this zone at Bog D (and presumably also at Martin Road) are dominated by the *Pinus strobus* type, but the *P. b/r* type increases gradually to half the pine grains near the top of the zone. The *Pinus banksiana/raimosa* subzone of the *Pinus strobus* zone was distinguished where the values of the *P. b/r* type rose above 25% of the determined pine grains. *Pinus strobus* needles are found in the lower part of the zone at Martin Pond, and needles of all three species are found in the upper part.

About 2,700 years ago *Pinus strobus* migrated onto the Itasca Moraine and by 2,000 years ago dominated the forest. It probably invaded areas where deciduous trees had been destroyed by windthrow and fire and probably developed an understorey of mesic hardwoods such as *Acer saccharum*, *Tilia*, *Quercus rubra*, *Ulmus*, and *Ostrya*. Such communities were common in the western part of the Pine-Hardwood Forest portion of the Itasca transect at the time of the land survey.

About 1,000 years ago *Pinus banksiana* and *P. resinosa* migrated into the transect area and occupied the most xeric and least fertile sandy soils. On outwash plains *Pinus banksiana* probably replaced oak savanna.
On more mesic soils they also played a pioneer role after fire. Their lesser importance in the western part of the transect may reflect either later migration or an environmental difference between the two parts.

**Concluding remarks**

The regional postglacial succession of vegetation in northwestern Minnesota is regarded largely as a function of climatic change as it acts upon seed dispersal, seedling establishment, and general success of the life cycles of the dominants. Other factors important in the successions were the availability of species to partake in the successions, changes in fire frequency, animal populations, and soil conditions, but these in turn were strongly influenced by climatic change. In the Itasca transect the plant formations of settlement time, namely the Prairie, Oak Savanna, Mesic Deciduous Forest, and Pine-Hardwood Forest, serve as analogs in the reconstruction of the vegetation of the previous 11,000 years. Because the formations have a distribution that corresponds to different climatic values, these values can be applied to areas having analogous formations in the past. Several communities of the past have no analog in the transect, but analogs outside the transect can be suggested.

About 12,000 years ago a Boreal Forest type of vegetation was present with *Picea* and *Populus*. Except for the absence of *Pinus* at that time, a possible modern analog is the southern Boreal Forest adjacent to the Aspen Parkland in southern Manitoba and Ontario. Wright (1964) attributed the absence of *Pinus* in this early vegetation to a lag in migration rather than an unfavorable climate. The analog has a lower mean annual temperature (32°F) and mean annual precipitation (20 in.) (Thomas, 1953) than the forested area of northwestern Minnesota (38.5°F and 25 in.). The climate of the lower part of the *Picea-Populus* zone became rapidly warmer, as indicated by the melting of buried ice blocks.

The warming trend continued, and about 11,000 years ago it resulted in a succession to prairie in the west and to a pine-dominated forest in the east. The vegetation of the transect from 11,000 to 8,500 years ago was analogous to the vegetation just before settlement, except that no Oak Savanna or Mesic Deciduous Forest occurred between that Pine Forest and the Prairie, although *Populus* scrub may have formed the transition. Another difference is the absence of *Pinus strobus*, which may not have been part of the available flora. The climate may have been similar to that of today in the area (Table 1). Compared to the previous time, this would indicate an increase for the Agassiz lowland of 8.5°F annual temperature and 2 in. annual precipitation and for the glaciated upland 6.5°F and 5 in. The postulated increase in precipitation probably did not result in increased soil moisture, because the higher temperatures increased the evapotranspiration, particularly in the Agassiz lowland.

The trend toward a warmer and drier climate resulted in a replacement of Pine Forest by Oak Savanna about 8,500 years ago. The Oak Savanna also occupied the prairie area along the crest of the Big Stone Moraine. The replacement of prairie by oak savanna could have been the result of the late immigration of the xeric *Quercus macrocarpa* into the region to occupy an ecological niche that had been available to it for the previous 2,500 years.

The *Ambrosia* peak zone between 8,000 and 7,000 years ago marked the maximum of temperature and aridity. The erosion of the pond margin at Thompson Pond probably occurred when drought and fluctuating water levels reduced the pond-margin vegetation to annuals, which included *Ambrosia* and the southerly *Iva elata*. The occurrence of the annual *Chenopodium rubrum* at Martin Pond, characteristic of saline soils, indicates high evaporation and low water levels. Widespread aridity during this millennium is indicated by the increase in herb pollen in northeastern Minnesota (Fries, 1962) and by low lake levels in east-central Minnesota (Cushing, 1960).

The climate that resulted in Oak Savanna on the glaciated upland was probably similar to the present climate of the Agassiz lowland; the oaks persisted because the rugged topography and many lakes provided many fire breaks. Thus the glaciated upland would have had an annual temperature of about 40°F and annual precipitation of about 22 inches, and the Agassiz lowland would probably have a slightly warmer and drier climate. The suggested means may be misleading, however, because the warmth and aridity may have taken the form of a large number of drought years, closely spaced.

About 4,000 years ago Mesic Deciduous Forest succeeded the Oak Savanna on the Itasca Moraine and on the crest of the Big Stone Moraine. It was similar to the Mesic Deciduous Forest that occupied the Big Stone Moraine at settlement time. Most of the dominants (*Quercus*, *Betula*, *Ostrya*, *Ulmus*, and *Acer saccharum*) may have been present in the transect during the Oak Savanna time that preceded, perhaps in very mesic, fire-protected sites along lakes and streams. *Tilia*, on the other hand, did not migrate into the transect until about 4,000 years ago, although it was present within 150 miles according to pollen diagrams of Cushing (1963) and Wright *et al.* (1964). The succession indicates a trend toward greater
soil moisture, probably as a result of an increase in precipitation, especially summer precipitation, and perhaps a decrease in mean annual temperature.

Beginning about 2,700 years ago pine trees began appearing on the Itasca Moraine, and by 2,000 years ago they had formed the Pine-Hardwood Forest. The migration of pine at this time did not result from a lack of a nearby seed source, for pine was present 80 miles southeast of the transect for the previous several thousand years (McAndrews, 1959). *Pinus strobus*, the first pine to migrate into the transect, was present in Minnesota 7,200 years ago (Cushing, 1963). The invasion and subsequent dominance of pine on the Itasca Moraine is attributed to decreased summer temperatures, a shortening of the growing season, and an increase in winter snowfall.

It is reasonable to assume that while forest succession resulting from climatic change was progressing on the high-altitude end moraines, the climate of the prairie area was also changing toward cooler, less arid conditions; it did not change enough to allow forest development, however, although the Aspen Parkland may have expanded at the expense of the Prairie.

**Summary**

The west to east distribution of Prairie, Oak Savanna, Mesic Deciduous Forest, and Pine-Hardwood Forest formations correspond with gradients or boundaries of climate, soil texture, and fire frequency. Drier and warmer summers occur to the west. The climatic gradient is steep because of the altitudinal increase of 500-1,000 ft. from the Lake Agassiz lowland in the west to the glaciated uplands eastward.

The study area is a west-east transect of 11 townships that include portions of each formation. The natural vegetation prior to settlement was mapped from the General Land Office Survey notes of 1871-1879. The Pine-Hardwood Forest occurred chiefly on coarse-textured till soils and was dominated by trees of *Pinus strobus*, *P. resinosa*, *P. banksiana*, *Populus* spp., and *Betula papyrifera*, with small amounts of *Acer* spp., *Quercus* spp., and *Tilia americana*. The Mesic Deciduous Forest occurred on fine-textured soils and was dominated by trees of *Quercus* spp., *Populus* spp., *Ulmus* spp., *Tilia americana*, *Acer saccharum*, *Betula papyrifera*, and *Ostrya virginiana*. A relatively small area of Oak Savanna was identified between the Mesic Deciduous Forest and Prairie at an intermediate altitude. It was dominated by widely-spaced trees of *Quercus macrocarpa*, with prairie herbs beneath and between the trees. The Prairie was a grassland essentially without trees except along rivers.

The mapped vegetation was compared with contemporaneous fossil pollen spectra in the sediment of 11 ponds. The pollen rain of each formation was distinctive, with most of the dominants well represented.

The postglacial history of the vegetation formations is reconstructed with the aid of pollen diagrams for four pond sites. The diagrams encompassing the past 12,000 years are zoned and interpreted with respect to the regional vegetation. Absolute dating of the chronosequence of vegetation is aided by five radiocarbon dates.

From 12,000 to 11,000 years ago the vegetation throughout the transect was a boreal-type forest dominated by *Picea* and *Populus* trees. About 11,000 years ago trees essentially disappeared from the low-altitude western part of the transect and were replaced by Prairie, which persisted until the time of settlement. At the same time, the vegetation on the coarser-textured soils of the higher-altitude eastern part of the transect became a forest dominated by *Pinus*, probably *P. banksiana*, but not *P. strobus*.

About 8,500 years ago the high-altitude part of the transect was succeeded by Oak Savanna, which lasted until 4,000 years ago, when Oak Savanna was succeeded by Mesic Deciduous Forest except in the area of intermediate altitude. The Mesic Deciduous Forest occupied the western part of the high-altitude area until the time of settlement.

*Pinus strobus* migrated into the eastern part of the transect and came to dominate the forest about 2,000 years ago. About 1,000 years ago it was joined by *Pinus resinosa* and *P. banksiana*, and together with hardwoods the three pine species formed the Pine-Hardwood Forest, which persisted until the time of settlement.

The vegetation succession is thought to have been basically caused by climatic change acting on the available flora. The period 8,500-4,000 years ago was a time of higher temperature and greater aridity compared with the preceding and succeeding periods.

Species absent from Minnesota, e.g. *Ephedra* and *Sarcobatus*, have pollen frequencies less than a fraction of 1%, but *Iva ciliata*, whose main range now is south of Minnesota, occurred in the sediment deposited in the most arid period, 8,000-7,000 years ago, at frequencies up to 10%; it must have been present in the local areas as a plant at this time.

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Plate 1. Itasca transect: physiography (above), vegetation (middle), and chronosequence (below) of assemblage zones.

Plate 2. Pollen diagrams of the upper 45-100 cm of sediment in the seven short-core sites of the Itasca transect, along with an average spectrum for each of the four long-core sites from levels just below the settlement horizon. Order of stations is from east at the top to west at the bottom (Plate 1). Fruiting species were not differentiated at some sites and levels.

Plate 3. Pollen diagram of Martin Pond. Vertical lines indicate stratigraphical ranges of macrofossils.


Plate 5. Pollen diagram of Terbell Pond.

Plate 6. Pollen diagram of Thompson Pond.