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## ABSTRACT

### LATE- AND POSTGLACIAL VEGETATION CHANGE IN SOUTHWESTERN NEW YORK STATE

By

Norton George Miller

Pollen stratigraphy in sediments from four small lake basins was determined and used as evidence for vegetation change on the Allegheny Upland of southwestern New York State. The sites studied are within 35 mi of the unglaciated Salamanca reentrant and are on an important migration route for species spreading northward following the Late Wisconsin glaciations.

Forests of the hemlock-northern hardwoods type occur in southwestern New York at the present time. Point-quarter sampling of upland stands shows Acer saccharum, Fagus grandifolia and Tsuga canadensis to be the leading species in order of decreasing Importance Values. An analysis of bearing-trees recorded in the original lot survey notes for areas around three of the sites studied palynologically revealed the pre-colonial forests to be dominated by the same leading species, except Fagus was first in importance and Acer second. R values were calculated using the



pre-colonial data and a recent survey of existing timber resources in the region.

The basins studied included the Genesee Valley Peat Works in central Allegany County--on Olean drift (pre-Cary), Allenberg bog in east-central Cattaraugus County--near the Kent terminal moraine (pre-Cary) and Houghton and Protection bogs in southeastern Erie County--on Valley Heads drift (= Port Huron). The profiles obtained were divided into A, B and C zones following the Deevey classification. In addition, a T zone characterized by high nonarboreal pollen (NAP) percentages occurred at Allenberg bog. The T zone pollen assemblages compare well with the modern pollen rain at Fort Churchill, Manitoba.

The A zones differ according to the age of the drift on which the basins are situated. Most unique was the Genesee Valley site where spruce (ca. 25%) occurs with abundant NAP (40 to 45%). Spruce values decreased upward. The significance of the assemblages is obscure, but taken at face value, the presence of an open vegetation type, perhaps similar to park-tundra, is indicated. At Allenberg bog, fluctuations in Fraxinus nigra and Quercus percentages suggest correlation with climatic modifications associated with glacier advance and retreat. However, absolute pollen frequency data from this site indicate that the fluctuations occurred as a response to increasing deposition rates for pine



and spruce pollen. Wood at the bottom of zone A at Houghton bog has been dated at 11,880  $\pm$  730 years B.P. (I-3290).

Upper A zone spectra, except for the presence of pollen from temperate deciduous trees, are similar to surface spectra occurring today in the boreal woodland of central Quebec.

The spruce woodland disappeared around the Valley Heads sites about 10,500 years ago and was replaced by B zone forests dominated by Pinus strobus. At several sites lower pine-birch and upper pine-oak subzones can be distinguished. At Protection bog where the pine peak has been dated at 9030  $\pm$  150 years B.P. (I-3551), a P. strobus cone was recovered from sediments deposited about 10,500 years ago.

Zone C-1 records the development of hemlock-northern hardwoods forests. With the exception of gradually increasing Fagus values, the profiles demonstrate stability in the regional vegetation during the interval between about 8000 and 4400 years B.P. An abrupt decline in hemlock percentages marks the end of the C-1 which was dated at 4390  $\pm$  100 years B.P. (I-3550) at Protection bog.

Increased relative numbers of Acer saccharum, Betula, Carya, Fagus and Quercus occur in zone C-2. Tsuga percentages remain low. Absolute pollen frequency determinations affirm the C-1/C-2 hemlock decline but show only slight increases in the numbers of broadleaf tree pollen types being



deposited. This fact and the tendency for hemlock to exhibit high drought mortality indicate that a series of severe droughts occurring over a relatively short time span may explain the relative frequency fluctuations in C zone sediments from western New York.

Zone C-3 which began 1270  $\pm$  95 years ago (I-3549) at Protection bog was divided into the following subzones: C-3a across which Tsuga regains its position of prominence in the profiles and C-3b in which abruptly increasing percentages of NAP, including Ambrosia, Plantago and Rumex, record European settlement and attendant forest clearance.

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By

Norton George Miller

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## INTRODUCTION

This thesis treats a problem that is primarily historical in nature--vegetation change through time following deglaciation. The region involved is at the west end of New York State where surfaces, according to available data, have been ice-free for at least 12,500 years or longer, southward toward the Pennsylvania border. Temperate broad-leaf deciduous or deciduous-coniferous forests now characterize western New York. The history of their development, as well as information on other vegetation types that no longer exist in the area, are major objectives in this investigation.

The principal technique I have used is pollen analysis whereby the vertical succession of pollen and spores is determined in sediments that have been accumulating in small lake basins for thousands of years. Changes in the relative and absolute frequency of various pollen types provide a basis for inferences concerning the history of past vegetation. These are supplemented, when possible, by additional data from plant macrofossils. Conclusions on both floristic and vegetational history and character can be reached through pollen analysis, although the latter are often tentative and difficult to relate to the frequency and abundance of species now encountered on the landscape. Since major vegetation



classes presumably develop in response to regional climates, pollen analysis further provides a way to determine former climates.

Pollen analysis is ecological in approach and emphasis. An understanding of the requirements of individual species and the relationships of species to associated organisms is necessary for the interpretation of pollen profiles. Indeed, an assumption basic to paleoecologic reconstructions is that fossil representatives of an extant species had the same ecological characteristics as now occur in the living representatives.

Since the unglaciated Allegheny Plateau and Appalachian Mountains doubtless served as a refuge for certain plant species during Pleistocene glaciations, southern New York is a particularly critical area to conduct such research because it is one of several important migration routes for species that participated in the revegetation of eastern North America.

## THE REGION

For purposes of this study southwestern New York State includes Cattaraugus, Chautauqua, Allegany and the southern portions of Erie and Wyoming Counties. It is difficult and misleading to discuss this geographically restricted area, however, without reference to the surrounding region, particularly to the three northern counties of western New York, Genesee, Niagara and Orleans. Thus data from eastern New York, New England, Pennsylvania and southern Ontario will frequently be used, but because the whole of western New York forms a coherent unit, historically, vegetationally and otherwise, this area will receive the most emphasis.

The political geography of the region is shown in Figure 1.

The eight-county region includes nearly 6550 square miles. It lies between  $42^{\circ} 00'$  and  $43^{\circ} 25'$  N Lat and  $77^{\circ} 45'$  and  $79^{\circ} 45'$  W Long, or, in more general terms, extends southward from Lake Ontario nearly 100 mi to the Pennsylvania border and eastward from Lake Erie and the Niagara River 100 to 65 mi, depending on the latitude, to the Genesee River. The counties along the Pennsylvania border are by far the largest in area, but they are the least populated. At the present time, the greatest concentration of population occurs

around Buffalo and extends northward into the southwestern corner of Niagara County. Smaller population centers occur at Dunkirk, Jamestown, Salamanca, Olean, Lockport and Batavia.

As political units the counties date from the early part of the 19th century. Prior to this time the region was visited by few Europeans, although in 1679, slightly more than 50 years after the formation of the Plymouth Colony in Massachusetts, an expedition under Robert Cavélier de LaSalle established a short-lived outpost at the mouth of the Niagara River (Williams, 1947). It wasn't until 1720, however, that the region had its first permanent resident and not until the late 18th century and early 19th century that more than a handful of settlers were present. In 1810, for example, there were only about 16,000 inhabitants in the eight county region, but a decade later the population totaled about 75,000 and hardly any district lacked the beginnings of settlement (Meinig, 1966).

The principal impetus to colonization was provided by the Holland Land Company, a group of Dutch businessmen who were able to purchase from Robert Morris, through their American agents, the title to nearly all the land which comprises the eight western counties of the state. The eastern portions of what are now Orleans, Genesee, Wyoming and Allegany Counties were sold by Morris to various individuals in tracts of large acreage. Joseph Ellicott, one of the

principal agents of the Holland Land Company, directed the surveying of the land owned by the Hollanders and did much to stimulate the development of the region while working from his headquarters at Batavia in Genesee County. Ellicott planned the location of roads, established villages and directed the pattern of settlement, basing his decisions principally on economic considerations which favored his foreign employers. Many of his original developments have persisted in somewhat modified form to the present day (Evans, 1924).

Before the arrival of settlers of European descent, western New York was occupied by a succession of Indian tribes. The historically important Iroquois controlled much of the state prior to the Revolutionary War. According to one current theory, they themselves did not actually inhabit New York until about 1300 when a general northward movement of Iroquoian tribes occurred, supplanting the resident Algonkian Indians who had themselves migrated to the state from the west about three centuries earlier. The five Iroquois tribes which lived in central and eastern New York joined together in 1570 to form a confederation. One of these tribes, the "Keepers of the Western Door," as the Senecas were called, originally occupied the region between Cayuga Lake and the Genesee River, but later in the 1650's, they extended their influence to Lake Erie and the Niagara

River by conquering the Erie and Neutral tribes which previously controlled these areas.

The Iroquois generally lived in stockaded villages containing about 250 people. Their homes were often surrounded by small, partially cleared fields where corn, beans and squash were cultivated. The Indians frequently chose rich agricultural lands on alluvial soils for their villages and these sites were also highly favored by the later white settlers. It has been estimated that about 20,000 Iroquois lived throughout New York State during the 18th century (Rayback, 1966). During the Revolutionary War the Iroquois confederation which had allied itself with the British was crushed by the Americans. The Clinton-Sullivan expedition destroyed nearly every one of their large villages and ultimately paved the way for the easy extinction of the Indian title to much of the land in central and western New York. A complete summary of the archeology of Iroquoian and pre-Iroquoian Indians in New York has recently been provided by Ritchie (1965).

Today, outside the rapidly growing urban centers of the region, farming constitutes the largest percentage of land use. The most heavily cultivated areas occur in Niagara, Orleans, Genesee and northeastern Erie Counties and in a narrow strip in Chautauqua and southern Erie Counties immediately adjacent to Lake Erie (Thompson, 1966). Vegetables and fruits are the principal crops throughout this region.



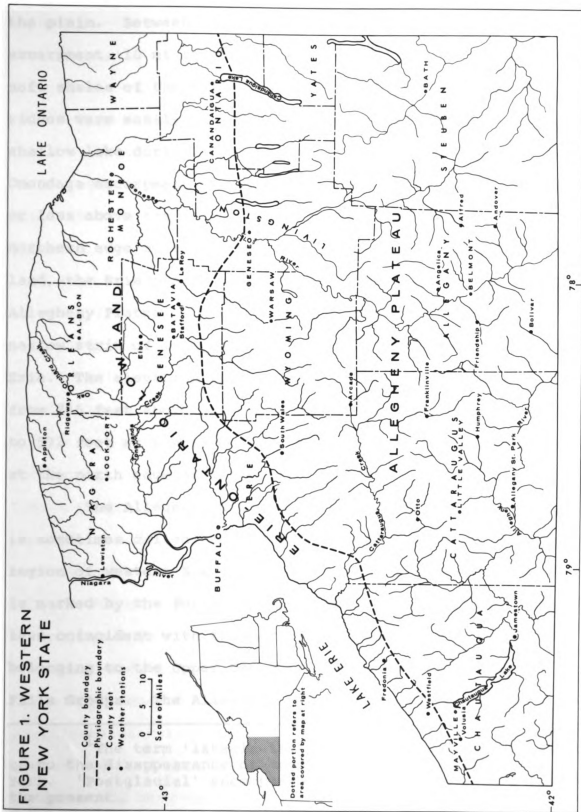
Of these counties, Niagara and Orleans contain the highest percentages of nonforest land--83% and 80% respectively (see Table 4; p. 56). Southward, but north of the Allegheny River and southeastern Allegany County, dairy farming and the supportive growing of feed crops for the cattle accounts for most of the land use. Here and in the largely non-agricultural lands of southern Cattaraugus and Allegany Counties forest covers about 60% of the area, but much of this is of secondary character.

#### PHYSIOGRAPHY

One of the principal physiographic regions of western New York State extends south from Lake Ontario to east-central Erie and southern Genesee Counties and southwestward along the south shore of Lake Erie in a strip of land about 2 miles wide at the Pennsylvania border and about 15 miles wide in central Erie County (Fig. 1). This region is generally called the Erie-Ontario Lowland (Muller, 1965) and is mostly underlain by easily-eroded shales, although two prominent east-west trending limestone escarpments occur in the area adjacent to Lake Ontario. These features subdivide the lowland into three more or less flat plains in part covered by lacustrine sediments deposited from the ancestral stages of Lakes Erie and Ontario.

The Ontario plain is located directly south of Lake Ontario and terminates about 10 mi to the south at the

FIGURE 1. WESTERN  
NEW YORK STATE



Niagara escarpment which, at places, rises 200 feet above the plain. Between the Niagara escarpment and the Onondaga escarpment, 10 mi to the south, lies the Huron plain. The soft shales of the Salina Group between the two limestone ridges were easily eroded to form a trough which held a shallow lake during late- and early postglacial time.<sup>1</sup> The Onondaga escarpment is less prominent, rising only 100 feet or less above the surrounding lowland. It is also the northern edge of the third subregion of the Erie-Ontario Lowland, the Erie plain, which ends at the northern edge of the Allegheny Plateau and includes the previously mentioned narrow strip of land bordering the southern shore of Lake Erie. The elevation of these plains increases southward from 246 feet above sea level at the surface of Lake Ontario to 572 feet at the surface of Lake Erie to about 1000 feet at the north edge of the upland plateau.

The Allegheny Plateau, or Appalachian Upland as it is sometimes called, is the second principal physiographic region of western New York. The northern edge of this unit is marked by the Portage escarpment which locally is more or less coincident with the northern erosional edge of strata belonging to the Upper Devonian Canadaway, Java and West Falls Groups. The Allegheny Plateau is characterized by

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<sup>1</sup>The term 'lateglacial' is used to include the time up to the disappearance of spruce forests in western New York. 'Postglacial' encompasses the time from this point to the present.

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flat-topped hills alternating with broad valleys. This topography is largely the result of pre-Pleistocene stream erosion, but glaciation has rounded the hills and widened many of the valleys. Elevation and relief increase southward. The highest point in western New York, 2548 feet, is found near Pikesville in southern Allegany County.

The Allegheny Plateau is sometimes subdivided into glaciated and unglaciated sections. Southeastern Chautauqua, southern Cattaraugus and southwestern Allegany Counties, an area approximately bounded by the Allegheny River, were apparently never completely invaded by ice. Muller (1963) points out that the unglaciated region is characterized by less smoothly eroded ridges, more continuous crest lines and deeply incised V-shaped valleys. He further notes that, as far as 15 miles north of the limit of glaciation, summit reduction by glacial scour was as little as 50 to 100 feet, although farther to the north greater lowering occurred. Throughout most of southern New York less than 200 feet of bedrock was removed from the plateau tops (Muller, 1964a).

The glaciated Allegheny Plateau is covered with drift of varying thickness. Deposits are generally thinnest at the approaches to the summits of hills where the bedrock is often only several feet below the surface. The drift is usually thicker in the valleys where it may reach a depth of several hundred feet. Many of the valleys are notable also because they were the sites of short-lived proglacial lakes

and now contain lacustrine sediments as evidence of their former status. Glacial Lake Zoar, for example, covered a large area in northern Cattaraugus County. Other proglacial lakes existed in the northwest-southeast trending valleys of southern Erie County, in the upper Genesee River valley and elsewhere.

The drainage of western New York is generally northward into the St. Lawrence River (see Fig. 1). Streams in only the southern portions of Chautauqua and Cattaraugus Counties and the southwestern corner of Allegany County empty into the Allegheny River which is connected to the Mississippi by way of the Ohio River. The drainage divide separating the St. Lawrence and Mississippi watersheds extends northeastward in Chautauqua County approximately following the crest of the Lake Escarpment moraine, which is several miles inland from Lake Erie. From there it may be followed eastward, across northern Cattaraugus County with a dip southward toward Little Valley and finally southeasterly across eastern Cattaraugus and western Allegany Counties. Part of eastern Allegany County is drained eastward into the Susquehanna River.

The only large inland lake in the region is Lake Chautauqua which occupies the axis of a through valley in south central Chautauqua County. It is approximately 15 miles long, but only 2 miles wide. A number of smaller lakes exist and many of these originated as pits formed where ice

blocks melted. Eastward, but outside western New York proper, lie the Finger Lakes. Several large artificial lakes occur in lowland areas and along the beds of major rivers and streams.

The Genesee River, which starts at the Pennsylvania border and follows a general northward course to Lake Ontario, is one of the major waterways of western New York. Of importance also is the Allegheny River which follows a shallow, inverted U-shaped course in southern Cattaraugus County. Cattaraugus Creek, Buffalo Creek and Tonawanda Creek and their tributaries, which flow approximately westward to Lake Erie or the Niagara River, drain a large part of central and northern western New York. Several other streams course generally northward across the Onondaga escarpment, drain a portion of the Huron plain, and empty into Lake Ontario.

#### BEDROCK GEOLOGY

Western New York State is entirely underlain by Paleozoic sedimentary rocks (Fisher et al., 1961), which are exposed at the surface in only limited areas. The beds dip gently to the south so that rocks of greater age are encountered successively northward. More or less east-west trending belts of shale, siltstone and sandstone are present throughout the region, but the most important exposures of limestone and dolomite are found in the lowland north of the

Allegheny Plateau. Complete summaries of the palenotology and bedrock geology have recently been published by Buehler and Tesmer (1963) and Tesmer (1963), for Erie and Chautauqua Counties respectively.

The red Queenston shale and siltstone of Late Ordovician age outcrops in the area immediately south of Lake Ontario and is the oldest rock exposed in the region. The predominantly calcareous rocks which comprise the Niagara escarpment were deposited during Middle Silurian time and are included in the Lockport Group, although other Middle Silurian rocks belonging to the Clinton Group are present toward the foot of the scarp. The Lockport dolomite, a member of the Lockport Group, is the erosion-resistant cap rock of present-day Niagara Falls. The Onondaga escarpment to the south is composed of limestone which accumulated during the early part of Middle Devonian time. The rocks comprising the escarpments were deposited during different periods of time when western New York was covered by warm shallow seas. The 10 miles separating the two zones of calcareous rock are mostly occupied by weak shales belonging to the Upper Silurian Salina Group.

Later in Middle Devonian time, shales of the Hamilton Group succeed the Onondaga limestone, a result of a massive influx of sediments eroded from an upland to the east. Upper Devonian rocks, mostly shales and siltstones, but occasionally sandstones, and rarely, conglomerates and thin limestones,



[illegible]

are found southward from central Erie and southern Genesee Counties. These belong, in order of decreasing age, to the following Groups: Genesee, Sonyea, Java, West Falls, Canada-way, Conneaut and Conewango. The sediments comprising these rocks gradually become coarser upward, indicating a westward movement of shoreline during the latter part of Upper Devonian time, and are part of the Catskill Delta which extends from what is now the Catskill Mountains region west to Ohio.

Near the Pennsylvania border, largely within the unglaciated area of western New York, are found shales, sandstones and conglomerates which belong to the Lower Mississippian Pocono Group and to the Lower Pennsylvanian Pottsville Group. These deposits have been greatly dissected by erosion and may be considered outliers of more continuous strata of the same age to the south. Muller (1963) suggested that the resistant conglomerates in this area may have terminated southward glacial movement.

#### GLACIAL GEOLOGY

In contrast to the age relationships of the bedrock units, surficial deposits resulting from Pleistocene glaciations are oldest in the south and youngest in the north. Drift from only the Illinoian and Wisconsin glaciations has been identified in western New York, although study of the development of the present Allegheny River suggests the

presence of pre-Illinoian glacial activity (Muller, 1963, 1965).

Deposits of Illinoian drift have weak geomorphic expression. They consist mainly of terrace remnants in the Allegheny River valley 50 to 100 feet above the present river level; Wisconsin terraces are found from 10 to 20 feet above the water surface (MacClintock and Apfel, 1944). Post-Illinoian erosion and weathering have left only isolated patches of Illinoian drift in this region. Muller (1960) showed that some of the gravel terrace remnants recognized by MacClintock and Apfel bordered a lobe of an ice sheet that projected southeastward across the Allegheny valley (Fig. 2). A separate pre-Wisconsin glaciation is indicated by the occurrence beyond this border of terrace remnants produced by an additional period of ice-margin deposition. This twofold expression of Illinoian deposits has long been recognized in adjacent northwestern Pennsylvania. But it has only recently been determined that what had been called "Inner Illinoian" drift is actually referable to late mid-Wisconsin time (White and Totten, 1965). This may also be true of similar deposits in southwestern New York State. In southeastern Chautauqua County patches of attenuated drift, present beyond the Wisconsin terminal moraine, are thought to be of Illinoian age (Muller, 1963).

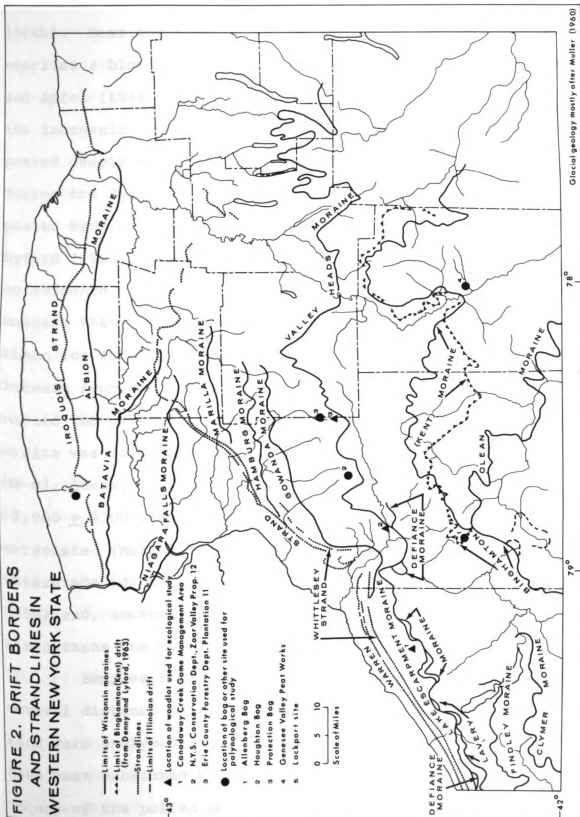
The earliest recognized deposit of Wisconsin age is the Olean drift which in western New York State is found at



the surface on the north and east sides of the unglaciated portion of the Allegheny Plateau (Fig. 2). This roughly triangular area is often referred to as the Salamanca reentrant because it is located at the junction of deposits produced by ice moving southeastward out of the Lake Erie basin and similarly derived deposits from the north and east from the Lake Ontario basin. Olean drift as mapped by MacClintock and Apfel (1944; see also Denny and Lyford, 1963) forms the terminal moraine on the north and east sides of the reentrant and follows a greatly convoluted course extending slightly south of east from about 3 miles northeast of Napoli to near Humphrey where its position extends abruptly southward toward the village of Allegheny. From this point it angles southeastward toward the corner of Cattaraugus County. It is a very subdued terminal moraine but the limit of glaciation can be accurately determined by the presence of erratic cobbles (Muller, 1965). The exact age of the Olean moraine is not known. MacClintock and Apfel (1944) considered it Iowan or Tazewell in age; other authors have concurred with this disposition. However, Denny and Lyford (1963) point out that it may be a pre-Farmdale-post-Sangamon substage. There is, at any rate, general agreement that it is pre-Cary in age.

The section exposed near the village of Otto in northwestern Cattaraugus County displays evidence of a long history of successive glaciations which are now considered

**FIGURE 2. DRIFT BORDERS  
AND STRANDLINES IN  
WESTERN NEW YORK STATE**



to have occurred entirely within the Wisconsin Stage (Muller, 1964b). Near the base of the section is a peat bed which overlies a blue-gray till and a silt deposit. MacClintock and Apfel (1944), who first described the site, considered the inorganic units to be Illinoian in age because they appeared deeply weathered, and the organic bed to have formed during the Sangamon interglacial. More recently the deposits have been assigned to the Olean substage by Denny and Lyford (1963), who have since restudied the site and found no evidence of weathering in the drift below the peat. They suggest that the peat accumulated in a bog in front of the Olean ice soon after it had deposited the underlying till. Outwash from the Olean ice which remained in the area then buried the organic material. The age of these organic deposits was initially determined to be more than 35,000 B.P. (W-87; Suess, 1954) and later to have a finite age of  $63,900 \pm 1700$  years (GRN-3213; see Muller, 1964b). They correlate (Muller, 1965) with the early Wisconsin St. Pierre interstade identified in the St. Lawrence lowland (Terasmae, 1958) and, accepting Denny and Lyford's interpretation, strengthens the case for a pre-Farndalian interpretation.

Samples from the organic deposit which is made up of several distinct peaty layers separated by silt and fine sand were analyzed for pollen by four workers whose results have been published by Muller (1964b). No distinctive change in any of the pollen percentages was found, suggesting a

nearly uniform climate during its formation. A slight warming trend may be indicated, however, by a decrease in Picea and a corresponding increase in Pinus pollen upward through one of the thicker layers. Pollen of temperate deciduous trees was practically absent. Herb pollen, mostly from members of the Cyperaceae and Gramineae, contributed about 30 percent of the total pollen throughout the layer except at the middle where tree pollen comprised about 90 percent of the total. The Compositae are well represented in the bottom half of the section. This pollen assemblage appears to indicate (ibid.), that the vegetation surrounding the site was similar to that found today in the boreal forest of Canada, roughly 50 miles north of North Bay, Ontario.

Upward in the section, rhythmites alternate with layers of till. The former represent separate developments of glacial Lake Zoar and the latter, repeated invasions of ice sheets correlative with the "classical" Wisconsin glacial advances. The youngest unit, stratified lacustrine sand, silts and clays, was deposited in the last glacial Lake Zoar which was ponded by the Defiance (?) moraine located several miles south of the margin of the Lake Escarpment moraine (Muller, 1964b).

On the west side of the Salamanca reentrant, the terminal moraine is formed by Binghamton drift. The basic distinctions between it and the Olean drift to the east have been described by MacClintock and Apfel (1944) who note that



[illegible]

the former is characterized by unmodified constructional topography and a relatively high content of carbonates which are only shallowly leached. The Olean drift is less calcareous, the carbonates are more deeply leached and there is a greater modification of its constructional topography. The Binghamton moraine, as mapped by MacClintock and Apfel (1944; see also Denny and Lyford, 1963), separates from the Salamanca reentrant at a point 3 mi northeast of Napoli where the westernmost deposits of the Olean drift are encountered (Fig. 2). From there it may be traced over a generally eastward course to near Belmont in central Allegany County from where the margin extends northward to a point near the Wyoming County line. It can be further traced southeastward across northeastern Allegany County but is lost in eastern Steuben County near Almond.

The name Binghamton was given to this drift because of its apparent equivalence to kame deposits found near the city of Binghamton in south central New York State, although this relationship has been questioned by Denny and Lyford (1963) and others. The Binghamton moraine in far southwestern New York State has been correlated with the Kent moraine of northwestern Pennsylvania and northeastern Ohio by continuous tracing (Muller, 1963). Connally (1965), who recently completed a study of the Binghamton drift sheet in the western Finger Lakes region, has traced a possible equivalent of the Kent moraine, which he calls the Almond moraine,

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eastward from the Genesee River toward Bath. The minimum age of the Kent drift is provided by a radiocarbon date of  $14,000 \pm 350$  B.P. for marl collected at the bottom of a kettle hole in Kent drift near Corry, Pennsylvania, 9 miles inside the Wisconsin drift border (W-365; Droste et al., 1959). Although this age determination indicates the Kent glaciation may be early Cary in age, more recent study has shown it to be considerably older. From sections exposed near Cleveland, Ohio, White (1968) has obtained radiocarbon dates for two wood samples embedded in lacustrine sediments interpreted as having been deposited from a proglacial lake ponded in front of the advancing Kent ice. These age determinations,  $24,000 \pm 800$  B.P. and  $23,313 \pm 391$  B.P., imply that the Kent ice overrode this area about 23,250 years ago.

A number of other moraines occur on the west side of the reentrant (Muller, 1963). Two of these, the Findley and Clymer moraines, are oriented in an east to west direction southwest of Lake Chautauqua. Comprised of stagnant ice deposits, they have been interpreted as recessional features which developed during retreat of the ice sheet that produced the Kent (Binghamton) terminal moraine. The Lavery moraine, which has been traced continuously from northwestern Pennsylvania, is located farther to the west where it is the easternmost member of the moraine complex found along the edge of the Portage escarpment. In Chautauqua County it is partly overlain by younger deposits. The Lavery glaciation



may be of Middle Cary age and is considered to mark a readvance of the ice margin following the northwestward retreat of the Kent ice. An additional weakly expressed moraine has been recognized in western Chautauqua and southwestern Cattaraugus Counties. It is of discontinuous occurrence, but has a distinctive clay till lithology. It is questionably correlated with the Defiance moraine of Late Cary age further to the west.

The well-marked Valley Heads moraine occurs across mid-central and mid-western New York State. It is a single moraine through much of this area but is represented by a group of parallel morainic deposits at the edge of the Allegheny Upland in western Chautauqua County where the complex is called the Lake Escarpment moraine.

According to Muller (1965) mapping has established the equivalence of the Lake Escarpment and Valley Heads moraines.

Recent studies of the sediments in Lake Erie support the contention that the Valley Heads-Lake Escarpment moraine marks a major readvance. A fluviially eroded drift sheet identified beneath the waters of modern Lake Erie by a seismic reflection survey and believed to be of Cary (Lake Border) age indicates that drainage was eastward over the Niagara escarpment during the Cary-Port Huron interstade (Wall, 1968). This could only have taken place if the glacier margin was north of this point. The Valley Heads-Lake

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Escarpment glaciation has not been dated precisely but wood from a depression in the Chaffee outwash plain, located at the southeast corner of Erie County and considered to be of Valley Heads age, was found to be  $12,000 \pm 300$  years old (W-507; Rubin and Alexander, 1960). Other age determinations of similar magnitude elsewhere in New York corroborate this finding and provide a minimum age for the time of glaciation. The Valley Heads-Lake Escarpment moraine is considered equivalent to the Port Huron moraine in the mid-west (Muller, 1965).

A series of recessional moraines, most which were first traced by Leverett (1902), mark the withdrawal of Valley Heads ice from western New York. These moraines, believed to record brief still-stands of the ice margin, are not prominent topographically because they were deposited in proglacial lakes where they were subject to extensive wave action. Northward they are the Gowanda, Hamburg, Marilla, Alden, Buffalo, Niagara Falls, Barre and Albion moraines. Some of these are illustrated in Figure 2. This final withdrawal of glacier ice must have been rapid, for a series of radiocarbon dates associated with sediments of Lake Iroquois, which developed in the Lake Ontario basin north of the Albion moraine, average 12,000 B.P. (Goldthwaite et al., 1965; Karrow et al., 1961). By this time the ice margin had melted to an unknown distance north of the Niagara escarpment and may have freed much of the Ontario basin, although the



St. Lawrence lowland was still blocked. New York State was apparently not invaded by Valdres ice (MacClintock and Terasmae, 1960; Terasmae, 1959).

Beaches and strand lines marking the shorelines of the ancestral stages of Lakes Erie and Ontario are found in northwestern Chautauqua County and from central Erie and Genesee Counties northward. The highest beach deposit in western New York belongs to Lake Whittlesey (737')<sup>1</sup> which was broadly contemporaneous with the Port Huron (Valley Heads) glaciation (Hough, 1963). Drainage at this time was westward from the Lake Erie basin across central lower Michigan to the Michigan basin and then southward to the Mississippi River. Lake Whittlesey came to an end with retreat of ice from the Hamburg moraine. Lake Arkona (710-695') is considered to have extended eastward into western New York during pre-Port Huron time, but its beach deposits have not been recognized in this area. A lower outlet to the west initiated the Lake Warren stages. The highest of these, Early Lake Warren (680'), is marked by a single beach ridge at about 840 feet northwest of East Aurora.<sup>2</sup> Other beach deposits ranging from 810 to 840 feet can be related to

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<sup>1</sup>This and other figures which follow named lake stages are the elevation of the lake surface in feet above sea level.

<sup>2</sup>See summary by Calkin (1966) and references cited therein.

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middle (670') and lowest (665') Lake Warren stages. Glacial Lakes Wayne (660'), Grassmere (640') and Lundy (620') are evidenced by weakly developed strand lines between 810 and 770 feet above tide (A.T.) near East Aurora. The drainage of these lake stages was westward (Hough, 1963).

Glacial Lake Iroquois was initiated as the ice margin retreated to the north and uncovered the Rome outlet which allowed discharge eastward along the Mohawk Valley to the Hudson River causing a lowering of the water level. During this time the level of Lake Lundy fell to the early Lake Algonquin stage (605'). These lakes covered the Lake Erie basin and the western end of the Lake Ontario basin, but as the water level dropped below the Niagara escarpment, two separate bodies of water were formed, Lake Iroquois in the Ontario basin and Early Lake Erie in the Erie basin. For a time Lake Iroquois is believed to have stood at 330 feet A.T. (Hough, 1958) but then drained before 10,500 B.P., as further ice retreat allowed discharge through the St. Lawrence Valley (Karrow et al., 1961). A well-developed beach ridge, on which US Route 104 is located, marks the southern shore of Lake Iroquois in western New York. Today, the surface of Lake Ontario lies at 246 feet A.T. while the modern Lake Erie surface stands at 572 feet.

Another consequence of the lowering of lake waters during post-Port Huron time was the formation of glacial Lake Tonawanda in the lowland between the Niagara and Onondaga



escarpments. Lake Tonawanda drained through five outlets across the Niagara escarpment but because of isostatic rebound the two westernmost spillways, the Lewiston and the Lockport, drained for the longest period of time (Kindle and Taylor, 1913). Deltas formed north of the spillways. The date of the extinction of Lake Tonawanda as an open body of water is unknown, but today the extensive Oak Orchard swamp is one of its last vestiges.

### SOILS

The soils of western New York, with the possible exception of those found in the Salamanca reentrant, are relatively young since they have been formed from surface material in a region that was ice covered during the Wisconsin glaciation. These soils are distributionally related to and mostly derived from the east-west trending bedrock units of the area. However, due to the direction of ice movement and the intensity of glacial scour, there has been a general distribution of parent material southward. As a result, the limestone and dolomites of the Ontario lowland are found in the drift that mantles the Erie plain and the northern edge of the Allegheny Upland. The amount of calcareous material transported away from the lowland gradually decreases toward the Pennsylvania border permitting a distinction to be made between the predominantly limy soils of northern western New York and the acid ones of the southern upland.

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Bedrock lithology also influences the texture of the soil derived from it. The sandstones, shales and conglomerates of the southern Allegheny Plateau provide both coarse and fine particles and give rise to medium- to coarse-textured soils. The shales at the northern edge of the upland supply clay and some silt-size particles which form fine textured soils, while the limestone and shale region to the north provides weathering products that result in soils of medium textures.

New York State is in a transition zone between cool humid climates which generally produce podzols and climates characterized by warmer temperatures which favor the formation of gray-brown podzolic soils (Cline, 1955). Although at the west end of the state soils of the latter type predominate, podzols occur in southwestern Allegany, southern Cattaraugus and southwestern Chautauqua Counties. The region directly south of Lake Ontario, encompassing Niagara, Orleans and the northern part of Genesee Counties is broadly categorized as an area of intra-zonal soils. Gray-brown podzolic soils are located in the intervening region (Soil Survey Division, 1938).

The podzol region is dominated by soils which belong to the DeKalb-Leetonia and the Lackawana-Culvers associations. The former are shallow, stony soils which occur on slopes and steep hillsides. They are non-calcareous and are derived from weathered bedrock. Muller (1963, p. 36),

[illegible]



writing about the occurrence of DeKalb-Leetonia soils in the driftless area at the southeastern corner of Chautauqua County, notes that their occurrence "in positions which, north of the drift border, might develop Lordstown-Volusia soils suggests more advanced soil development in the unglaciated area," but "contrasts between the DeKalb and the Lordstown soil series are not such as to demonstrate great difference in age." Soils of the Lackawana-Culvers association are weakly developed podzols found on the glaciated parts of the Allegheny Plateau. They are not heavily cropped and much of the soil has remained under forest cover.

Gray-brown podzolic soils belonging to the Lordstown-Volusia and Ontario-Honeoye-Pittsfield associations cover by far the largest area of western New York. Lordstown and Volusia soils, derived from glacial till comprised mostly of local shales and sandstones, are the most common. They occur across the central and northern parts of the Allegheny Upland and are found on plateau tops, hill slopes and valleys not filled with pro-glacial lake sediments. Located immediately to the north and east, Ontario-Honeoye-Pittsfield soils originated from calcareous till and outwash. They are mostly rich loams over limy substrata. Soils of the intrazonal Toledo-Vergennes association have developed from lacustrine silts and clays. Much of the land covered by these soils is poorly drained and unsuitable for agriculture,

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although some exceptionally rich, well-drained cropland is also present.

Of the 75 more rigidly defined soil associations recognized in New York by Cline (1955), 27 are found at the western end of the state. These are more circumscribed in character than the associations already discussed and enable one to describe the soils of western New York more precisely. Niagara and northern Erie and Orleans Counties are dominated by medium- to fine-textured soils which belong to the Collamer, Fulton-Lucas, Fulton-Toledo, Odessa-Schoharie and Williamson associations. Well-drained to somewhat poorly- and poorly-drained phases are present. There is an important inclusion of Alton, Colonie, Elmwood-Swanton and Hilton soils in northern Niagara County that developed from gravel, sand or lime-rich glacial till. A large area of muck lies along the border of Genesee and Orleans Counties, reflecting the swamp environment which followed the drainage of glacial Lake Tonawanda.

Southward, in central and north-central western New York, the soils are medium- or moderately fine-textured, of low to high lime content and are derived mostly from glacial till. The deep, well- to moderately well-drained, lime-rich Honeoye-Lima and Ontario-Hilton associations are found in eastern Genesee County but give way southwestward to the somewhat poorly- and poorly-drained soils of the Darien-Danley, Darien-Romulus and Mahoning-Trumbull associations. Farther

south in a broad northeast-southwest band from central Chautauqua to Wyoming County, medium-textured acid soils with neutral to slightly acid fragipans on glacial till are the most common. These largely belong to the Erie-Langford association. Important inclusions of coarser-textured soils, members of the Bath-Chenango association, occur throughout this area on well- or moderately well-drained sites generally accompanying morainic topography.

Most of northern Allegany County is characterized by somewhat poorly-drained, deep soils of the Volusia-Mardin association. Southern Cattaraugus and Allegany Counties are dominated by medium- to moderately coarse-textured acid soils with strongly acid fragipans weathered from glacial till or from the shale, sandstone or conglomerate bedrock of this area. The Cattaraugus-Culvers-Morris, Lordstown, Lordstown-Mardin-Volusia and Oquaga associations which include both deep and shallow soils are represented.

Azonal soils derived from recent alluvium are found along the Allegheny and upper Genesee Rivers and elsewhere. Outwash and valley train deposits throughout the region, but especially associated with the Lake Escarpment-Valley Heads moraine, have produced substantial areas of medium- to coarse-textured soils from sands and gravels.

Little work has been done in western New York relating soils and vegetation. It has been pointed out that there is an approximate equivalence between the Hemlock-white



pine-northern hardwoods region and the area characterized by podzols, and that a similar relationship holds for the Eastern deciduous Forest region and the region of gray-brown podzolics (Braun, 1950; Gordon, 1940). However, this correspondence is not apparent in western New York. In this area the boundary separating these two major vegetation units is coincident with the Portage escarpment: deciduous forests occupy the lowland adjacent to Lakes Erie and Ontario, while coniferous-deciduous forests are situated on the uplands (Braun, 1950). The podzol/gray-brown podzolic boundary, in contrast, is far south of the escarpment so that no simple relationship between soils and vegetation is visible in this case.

Gordon (1940) in less general terms has briefly described the forest communities found on certain soil series in Cattaraugus County. The deepest podzols found on the higher parts of the plateau just north of Pennsylvania are covered by forests of hemlock, white pine, red maple, chestnut, sweet birch and cucumber tree. Podzols of the DeKalb series support forests dominated by hemlock and beech. Mixed mesophytic forests of red oak, beech, chestnut, red maple, sweet birch, white ash and black cherry, or other species often associated with them, characterize the thinner, drier soils of this series. Oak-chestnut forests are found on the driest upland soils. Hemlock, beech, sugar maple, yellow birch, basswood and white pine forests grow on Volusia soils,

while sugar maple, basswood, white ash, hop hornbeam and black cherry are more abundant on the better-drained Langford and Lordstown soils. Imperfectly drained soils, developed from lacustrine deposits, support swamp forests in which American elm, swamp white oak, beech and occasionally white pine, hemlock, yellow birch, black ash, red maple and balsam fir occur. Similar data from elsewhere in western New York have not been published.

### CLIMATE

Warm-to-hot summers, cold winters and adequate precipitation, typical of humid continental climates in general, characterize New York State. In the western counties the terrain and nearby Lakes Erie and Ontario exert a powerful influence on the overall climate of the area. The Allegheny Plateau, between 3 and 10 times the elevation of the Erie-Ontario Lowland, is colder and wetter than the plains to the north and west.

Lakes Erie and Ontario act as accepters or releasers of energy depending on the time of year. During the fall they slowly liberate the heat accumulated during the summer months and thereby lengthen the frost-free period. In the spring, having become cold during the preceding winter, they keep the surrounding area cool and delay plant growth until the danger of frost is past. This latter phenomenon is responsible for the successful vineyards of western Chautauqua County and

the orchards of the Ontario plain. At higher elevations the tempering effect of the lakes is less apparent.

Specific differences in climate between upland and lowland sections of western New York are illustrated by the data presented in Tables 1 and 2. Mean annual temperatures (Table 1) at weather stations in the Erie-Ontario Lowland are nearly uniformly 2-3°F higher than those of the upland. This is true also of mean July temperatures, although the monthly averages for January are nearly equal. It is, however, the plateau stations which have recorded the lowest winter temperatures, in many cases several tens of degrees lower than those measured on the plains. Both regions have experienced nearly the same maximum temperatures, but maps on which isolines of mean maximum July temperatures are plotted show central western New York to have slightly lower maximums than the regions to the north and south, whereas the southern upland receives the lowest mean minimum temperatures during the same month (Johnson, 1960). The higher elevation and the comparatively dry atmosphere over the plateau combine to give high day and low night temperatures resulting in an almost typical continental type of climate (Mordoff, 1949).

The land adjacent to Lakes Erie and Ontario is favored with a longer growing season than areas further inland (Frederick et al., 1959). Northwestern Erie County has a 180 day frost-free period, the longest in upstate New York



except for limited areas south and southeast of Lake Ontario beyond western New York. A growing season of between 180 and 160 days characterizes the western half of Chautauqua and Erie Counties and the northeastern half of Genesee County. Nearly all lowland areas have more than 140 days with no frost. Southward the length of the growing season decreases until 100 days or less is reached at the region of highest elevation in southeastern Cattaraugus and southwestern Allegany Counties. The mean date of the last spring 32°F minimum in the lowland generally occurs in the first week of May (see Table 2). In the upland it is two to three weeks later. At the end of summer the first 32°F minimum at highland stations takes place during the second or third week of September and, although there is greater variability in the first occurrence of fall frost in the lowland, the dates are nearly always two weeks after the first freezing temperatures at higher elevations.

The basic difference between energy reception in the upland as opposed to the lowland is well illustrated by figures for potential evapotranspiration and growing degree months. The former, a theoretical measurement of the amount of energy gained by the ground through solar radiation, is presented as an estimate of the quantity of water required to expend this energy by means of evaporation and transpiration. A growing degree month is a temperature efficiency index which consists of the sum of all average monthly

TABLE 1  
SELECTED CLIMATIC DATA FROM WEATHER STATIONS IN WESTERN NEW YORK STATE  
BY PHYSIOGRAPHIC REGION<sup>1</sup>

Location	County	Mean Annual Temp.	Mean January Temp.	Mean July Temp.	Mean Growing Season <sup>2</sup> Temp.	Highest Temp.	Lowest Temp.
<b>Erie-Ontario Lowland</b>							
Appleton (300') <sup>3</sup>	Niagara	47.1	25.7	70.1	63.8	106	-13
Buffalo (693')	Erie	47.0	25.2	70.0	64.0	97	-20
Elba (750')	Genesee	45.7	23.4	69.7	63.4	100	-21
Fredonia (750')	Chautauqua	48.6	27.6	71.3	65.4	98	-26
Le Roy (900')	Genesee	46.1	23.2	68.9	64.0	99	-14
Lockport (520')	Niagara	47.1	24.9	70.3	64.3	103	-24
Ridgeway (420')	Orleans	47.4	24.8	71.3	64.9	96	-9
Stafford (925')	Genesee	47.6	25.4	71.7	65.8	103	-33
<b>Intermediate</b>							
South Wales (1073')	Erie	46.0	24.5	69.5	63.7	103	-31
Westfield (1050')	Chautauqua	47.7	25.1	70.2	64.6	98	-19
<b>Allegheny Upland</b>							
Alfred (1760')	Allegany	44.8	22.9	67.2	61.8	101	-35
Allegheny State Park (1500')	Cattaraugus	45.6	25.2	66.6	61.7	101	-35
Andover (1670')	Allegany	45.4	24.1	67.4	62.3	100	-34
Angelica (1420')	Allegany	45.3	23.7	67.8	62.3	104	-40
Arcade (1707')	Wyoming	44.0	20.6	67.4	61.6	95	-38
Bolivar (1800')	Allegany	45.1	22.9	66.7	61.5	101	-37
Franklinville (1590')	Cattaraugus	45.0	23.0	67.3	61.9	99	-45
Humphrey (1951')	Cattaraugus	45.4	22.7	68.3	62.8	93	-17
Jamestown (1390')	Chautauqua	47.6	25.3	70.0	64.7	100	-31
Otto (1260')	Cattaraugus	46.8	23.3	69.7	64.3	99	-24
Volusia (1560')	Chautauqua	45.6	23.4	68.4	62.9	98	-18

<sup>1</sup>Data from Mordoff (1949); temperatures in degrees Fahrenheit.

<sup>2</sup>May 1 to September 30.

<sup>3</sup>Elevation in feet above sea level.



TABLE 2  
SELECTED CLIMATIC DATA FROM WEATHER STATIONS IN WESTERN NEW YORK STATE  
BY PHYSIOGRAPHIC REGION<sup>1</sup>

Location	County	Ave. Date of Last Spring Frost	Ave. Date of First Fall Frost	Mean Annual Precip.	Mean Growing Season <sup>2</sup> Precip.	Mean Annual Snowfall	Mean Annual Days with Precip.
<b>Erie-Ontario Lowland</b>							
Appleton (300') <sup>3</sup>	Niagara	May 4	Oct. 16	27.33	12.01	44.1	114
Buffalo (693')	Erie	Apr. 26	Oct. 22	35.16	14.57	75.7	165
Elba (750')	Genesee	May 8	Oct. 6	36.72	15.21	95.2	111
Fredonia (750')	Chautauqua	May 1	Oct. 21	36.72	16.89	57.1	156
Le Roy (900')	Genesee	May 8	Oct. 6	36.45	15.86	102.1	161
Lockport (520')	Niagara	May 5	Sept. 19	30.91	14.39	50.7	114
Ridgeway (420')	Orleans	May 4	Oct. 3	32.98	16.79	67.2	142
Stafford (925')	Genesee	May 12	Oct. 4	31.63	14.39	65.6	147
<b>Intermediate</b>							
South Wales (1073')	Erie	May 13	Oct. 1	38.99	16.25	74.1	143
Westfield (1050')	Chautauqua	May 2	Oct. 21	38.53	18.91	58.1	125
<b>Allegheny Upland</b>							
Alfred (1760')	Allegheny	May 18	Sept. 28	35.83	17.84	71.4	150
Allegheny State Park (1500')	Cattaraugus	May 28	Sept. 18	42.82	19.95	82.5	165
Andover (1670')	Allegheny	May 21	Sept. 25	33.64	17.25	47.0	124
Angelica (1420')	Allegheny	May 25	Sept. 24	35.26	17.61	62.6	142
Arcade (1707')	Wyoming	May 22	Sept. 28	41.96	21.08	86.7	156
Bolivar (1800')	Allegheny	June 1	Sept. 17	39.83	19.87	65.5	118
Franklinville (1590')	Cattaraugus	May 21	Sept. 22	38.76	18.09	85.9	149
Humphrey (1951')	Cattaraugus	May 14	Sept. 25	44.45	22.30	103.6	156
Jamestown (1390')	Chautauqua	May 12	Oct. 5	43.83	19.26	97.9	157
Otto (1260')	Cattaraugus	May 13	Oct. 16	33.09	16.79	---	122
Volusia (1560')	Chautauqua	May 10	Sept. 22	38.53	17.26	92.0	134

<sup>1</sup>Data from Mordoff (1949); precipitation and snowfall in inches.

<sup>2</sup>May 1 to September 30.

<sup>3</sup>Elevation in feet above sea level.

temperatures over 40°F, the minimum threshold of plant growth and seed germination under normal conditions. Both higher temperatures and longer growing seasons enlarge this index. Calculations for only a few stations in western New York are available (see Table 3), but they clearly show larger values at lowland localities. Plant distribution in this region correlates well with these indices. Such southern species as Asimina triloba, Celtis occidentalis, Juniperus virginiana and others are found only in the lowlands where the more favorable climate probably ensures their survival, although in certain cases other factors may also have some control.

Moisture is brought to New York State from the Gulf of Mexico and the Atlantic Ocean through the activity of cyclonic storms. Lakes Erie and Ontario are local sources of moisture, particularly in the winter, when water picked up over the lakes is deposited on the adjoining land during snowsqualls. As previously pointed out, the upland receives more moisture than the lowland (see Table 2), often up to as much as 10 inches more. A map on which isohyets of mean annual precipitation measured between 1931 and 1955 were plotted (Johnson, 1960) reveals that precipitation increases irregularly southward in western New York until the 48 inch maximum for the region is reached in northwestern Cattaraugus County. It is interesting and perhaps significant that one of the largest areas of upland sphagnum bog occurs within this zone of maximum precipitation. The northern half of

TABLE 3  
POTENTIAL EVAPOTRANSPIRATION AND GROWING DEGREE MONTHS AT  
SELECTED WEATHER STATIONS IN WESTERN NEW YORK STATE<sup>1</sup>

Location	County	Potential Evapotranspiration	Growing Degree Months
Erie-Ontario Lowland			
Buffalo	Erie	24.1	134.1
Lewiston	Niagara	24.7	143.9
Allegheny Upland			
Allegany State Park	Cattaraugus	22.0	119.2
Arcade	Wyoming	22.1	117.2
Friendship	Allegany	22.1	124.0
Humphrey	Cattaraugus	23.7	125.7

<sup>1</sup>Data from Carter (1966).

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Niagara County and nearly all of Wyoming County, in contrast, are among the driest parts of the whole state.

Precipitation is fairly evenly distributed throughout the year, but summer months characteristically receive more than the others. During the period from May 1 to September 30, the limits of the growing season (see Table 2), less rain falls in lowland areas than on the upland. Although summer is the season of greatest precipitation, it is also the time of greatest moisture need, so small moisture deficits occasionally occur. These are most critical in the heavily cultivated lowland region and may sometimes lead to crop failure. Few major droughts, however, have affected the region. A serious one occurred in 1899 when the total precipitation for the three summer months was less than 3 inches at many localities bordering Lake Ontario (Mordoff, 1949). There has been at least one noteworthy period of drought every 20 years.

The prevailing winds are westerly across the region but often shift to the north in winter and toward the south during the summer. At Buffalo the winter months are characterized by west-southwest winds, while during the rest of the year, except the fall months when the wind is from the south, wind direction is from the southwest. Winter is the time of maximum cloud cover. At Buffalo only 1 to 3 days during the months of December, January and March are listed as clear days with less than 0.2 percent cloud cover. During



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most of the spring, summer and fall nearly 10 days of every month are clear. The whole of New York State lies within the eastern cloudy belt which ranks well below central and western states in the amount of sunshine received (ibid.).

#### FLORA

Floristic research in western New York State began in earnest during the mid-1800's. Before this time, however, Niagara Falls had attracted naturalists and plant collectors to the region, many of whom published botanical observations made at the Falls (see Dow, 1921) or while travelling across the Erie-Ontario Lowland. Unfortunately, most of this information seems to have been gathered casually or, in some cases, by untrained people, making it of questionable scientific value. Three of the more notable visitors were Peter Kalm, who viewed the cataract in 1750 (Kalm, 1751), François André Michaux, who travelled throughout the eastern Great Lakes area in 1806 or 1807 (Zenkert, 1934), and Thomas Nuttall, who undertook a pedestrian trip from Philadelphia to Canandaigua and west to Niagara Falls in 1809 (Graustein, 1967).

Zenkert (1934) has traced the history of botanical exploration in western New York from early times through the 1930's. Members of the Buffalo Society of Natural Sciences were particularly active collectors during the last half of the 19th and the early part of the 20th centuries. In recent

years field work has been largely carried out under the auspices of the New York State Museum at Albany. Much of this more recent study remains to be published.

A total of 1587 species are listed by Zerkert (1934) as growing in the Niagara Frontier region which encompasses the area within a 50 mile radius of Buffalo. Of these, 1187 are native species; the remaining 400 are introduced. The total number of species probably has been enlarged somewhat since 1934. In comparison, House (1924) enumerates nearly 2950 native and introduced species in his flora of New York State, and for the area covered by Gray's Manual (Fernald, 1950), 4425 native and 1098 introduced species are listed.

Three more or less distinct floristic regions occur at the west end of the state. The most northern is bounded on the south by the Wisconsin terminal moraine which approximately separates the glaciated and nonglaciated parts of western New York (see Fig. 2). This boundary marks the southern limit of a number of boreal species. In large part these are bog plants which presumably are not found south of the drift limit because of the absence of kettle holes and other suitable habitats generally associated with glaciated terrain.

Zenkert (1934) has noted 55 species which exhibit this distribution pattern in western New York, although a few occur at disjunct stations southward beyond the New York-Pennsylvania border. Some of the species he lists are:



Andromeda glaucophylla,<sup>1</sup> Brasenia schreberi, Eriophorum  
spissum, Galium labradoricum, Habenaria dilatata, Kalmia  
polifolia, Larix laricina, Ledum groenlandicum, Myrica gale,  
Picea mariana, Pinguicula vulgaris, Populus balsamifera,  
Primula mistassinica, Rhynchospora alba, Saxifraga aizoides,  
Vaccinium oxycoccus and Viola renifolia.

An interesting plant community containing relict boreal species occurs within the unglaciated Salamanca re-entrant in the Red House valley at the west side of Allegany State Park (House and Alexander, 1927). When this site was visited during the summer of 1966, only a quarter acre patch of what was once an extensive Pinus strobus stand was still in existence. The principal trees present at this time were Abies balsamea, Acer rubrum, Betula alleghaniensis, Fraxinus nigra, Pinus strobus, Tsuga canadensis and Ulmus americana. Gaultheria hispidula, a boreal species once found there, could not be located, although Vaccinium myrtilloides, another northern plant, was still present. Borings made with a Davis sampler revealed that beneath 10 to 13 cm of humified peat lay a bed of heavy blue clay, the thickness of which was not determined. This inorganic sediment was apparently deposited at some time during the Pleistocene from a lake ponded in the valley of Red House Brook, a small tributary

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<sup>1</sup>Nomenclature follows Fernald (1950) with the exception of the binomials used for yellow birch and leatherleaf which are Betula alleghaniensis Britton and Cassandra calyculata (L.) D. Don, respectively.

of the Allegheny River. The community seems to be a remnant of a swamp forest developed on soil of large water holding capacity (Taylor, 1928).

Superimposed on the glaciated-nonglaciated distribution pattern is another type which shows no relationship to the presence or absence of glaciation. The floristic regions delimited by the new pattern correspond to the Erie-Ontario Lowland and the Allegheny Upland and are best illustrated by species which occur in the former area but not in the latter. The boundary between the two regions is usually depicted as part of the well-known tension zone that crosses Minnesota, Wisconsin, Michigan, southern Ontario and western and central New York to the eastern end of Lake Ontario. In New York State it is coincident with the Portage escarpment (Fig. 1). Typical upland species occur on both sides of the glacial boundary.

In central and western New York this tension zone has not been extensively studied. Plant distribution maps similar to those which support its existence in Wisconsin and elsewhere have not been published for New York State. However, in western New York it is clear that the upland is characterized by species which are absent or are of greatly restricted occurrence in the lowlands bordering Lakes Erie and Ontario. Conversely, Asimina triloba, Celtis occidentalis and Sassafras albidum grow in the lowland or on the flank of

the upland, and either do not occur in the upland or are rare there.

Soper (1962) has discussed a large number of species which are found in southern Ontario below a line extending from Grand Bend on Lake Huron southeastward past London, then northeastward in the vicinity of Aylmer to Toronto. These species occur nowhere else in Canada and because of their obvious southern affinities they are considered as part of the Carolinian flora of Canada, using the terminology of Merriam (1898). The ranges of only a few of them extend into the coniferous-deciduous forest region of northern Ontario. Of the plants listed by Soper, those which occur in western New York State are restricted to stations in the lowland, with the exception of a few found along the Allegheny River or in the region intermediate between the lowland and the higher parts of the upland.

Zenkert (1934) recognized the distinction between the lowland and upland flora and enumerated 96 species which he considered to represent an austral element best developed in the region adjacent to Lakes Erie and Ontario. This distribution pattern is the basis for Bray's recognition (1915) of two zones in western New York separated approximately by the Portage escarpment and characterized by different tree species. His Zone B, in which chestnut, oaks, hickories and tulip-poplar are typical, occurs in the Erie-Ontario Lowland, while his Zone C, characterized by sugar

maple, yellow birch, hemlock and white pine, corresponds in area to the Allegheny Upland.

It is noteworthy that the northern elements of the flora are best developed on the Allegheny Plateau in southern western New York, while the southern elements are best developed to the north in the Erie-Ontario Lowland, a situation which is directly opposite that found in Michigan and Wisconsin. Climate may be the major factor controlling this distribution, although soil and other edaphic factors may also have a role. The more rigorous climate of the upland would tend to eliminate species adapted to higher mean winter temperatures and a longer growing season.

The flora of western New York can be divided into a number of phytogeographic elements, each of which is made up of species that share a similar type of geographical range today. These species are typical of a certain natural area, that is, the entire region of distribution of a taxonomic unit attained through natural dispersal mechanisms, whether they now grow within that area or not (Cain, 1944). They often have the same center of dispersal, but may or may not share a common center of origin. The identification of elements in a regional flora is based upon their being typical of certain well-defined phytogeographical areas elsewhere.

Elements may be categorized as either extraneous or intraneous. The former contains species at or near the limits of their range which may, therefore, exhibit



disjunctions of various types, while the latter includes widespread species whose occurrence in a particular region is well within the plants' total range (Braun, 1937; Cain, 1944). Intraneous species, which may comprise as much as 60 percent of a flora (Parker, 1936; Thompson, 1939), tell us little about the geographical affinities of that flora, but extraneous ones are considerably more helpful in this regard. Most of Curtis' discussion (1959) of the extraneous elements in the flora of Wisconsin can be applied to New York State, so much of the following account is drawn from this source.

The Alleghenian element contains a group of species of Arcto-Tertiary origin which center in the southern Appalachians and extend northward into southern Canada. Such well-known and important forest trees as Acer saccharum, Betula alleghaniensis, Fraxinus americana, Ostrya virginiana, Pinus strobus, Quercus alba, Tilia americana and Tsuga canadensis are members of this element. Also of Tertiary origin is the Ozarkian element which contains more drought tolerant species developed in isolation from the southern Appalachians on the Ozark upland of Missouri and Arkansas. Acer saccharum var. nigrum, Carya spp., Quercus macrocarpa, Q. muehlenbergii and Q. velutina are components of this element. Steyermark (1939) has compiled a list of plants common to both the Appalachians and the Ozarks which presumably acted together as a single center of origin and dispersal



for certain species. Magnolia acuminata is one he mentions that is found in western New York.

Members of the Boreal element are not rare in western New York but in most cases they occupy positions in bog communities generally associated with senescent kettle hole lakes. Abies balsamea, Larix laricina and Picea mariana occur here as members of this element. These trees are characteristic of the boreal forest which ranges across central Canada from eastern Alaska to the Atlantic seaboard, south to the upper Great Lakes with a discontinuous extension down the Appalachian mountains at higher elevations. Also occurring in western New York are such typical boreal shrubs and herbs as Andromeda glaucophylla, Cassandra calyculata, Ledum groenlandicum, Linnaea borealis var. americana and Menyanthes trifoliata among others.

Another group of species characteristic of the region farther to the north but often found southward at mountain stations of high elevation belongs to the Arctic-alpine element. As expected it is very poorly represented in western New York but has better expression in the high peak areas of the Adirondack and Catskill Mountains to the east. Pinguicula vulgaris and Saxifraga aizoides which grow together on a wet vertical gorge wall near a falls of the Genesee River in southeastern Wyoming County, their only station at the west end of the state (Zenkert, 1934), are members of this element.

Species typical of western North America but which are also found eastward are members of what can be broadly called a Western element. Actually this category includes several types of distinct distribution patterns, two of which particularly pertain to western New York. The Prairie element is made up of species whose ranges center on the existing prairies. Certain members of this element such as Andropogon gerardi, A. scoparius and Sorghastrum nutans have a wide distribution through the Erie-Ontario Lowland in New York State where they apparently grew mostly in oak openings before and for a while after the settlement of the region. They are now generally found in abandoned fields, in hedgerows and in thin second growth oak stands and are often associated with prairie forbs. Shanks (1966) felt that the oak openings in this area were essentially edaphic prairies, remnants of more extensive grasslands which occurred in this region when the Prairie Peninsula extended farther east. The shallow dry soils and the occasional water deficits characteristic of the Erie-Ontario Lowland would seem to favor the persistence of prairie species and exclude more mesophytic competitors.

The Cordilleran or Western Mountain element, another type of Western element, was early recognized in eastern North America by Fernald (1925). More recently Iltis (1965, 1966) has redirected attention to it, pointing out that " . . . the ranges of many of our commonest as well as rarest

species in the northeastern United States . . . fall into the standard pattern of eastern North America -- western North America vicarious species pairs with the post-glacially produced modern ranges overlapping in glaciated northeastern North America" (1965, p. 149). As examples, Iltis (*ibid.*) cites a substantial list of paired species including the following in which both members are found in western New York: Actaea rubra (western-w) -- A. pachypoda (eastern-e), Cinna latifolia (w) -- C. arundinacea (e), Cypripedium parviflorum (w) -- C. pubescens (e), Gentiana procera (w) -- G. crinita (e), Juniperus horizontalis (w) -- J. virginiana (e), Populus tremuloides (w) -- P. grandidentata (e), Salix serrissima (w) -- S. lucida (e) and Viola adunca (w) -- V. conspersa (e). Certain additional species claimed by Iltis (*ibid.*) and others to be members of this western element are found at the west end of New York as well. These include Carex flava, Oryzopsis asperifolia, Potentilla arguta, P. fruticosa, Pterospora andromeda, Salix candida and Valeriana uliginosa.

Another group of species belonging to the Atlantic Coastal Plain element has a limited distribution along the beaches of Lakes Erie and Ontario and westward around the upper Great Lakes (Peattie, 1922). These species apparently attained their current range sometime during late- or post-glacial time, perhaps by migrating along the St. Lawrence or Mohawk River valleys and thence along the shores of the ancestral Great Lakes. Cakile edentula, Euphorbia



polygonifolia, Lathyrus maritimus and Xyris caroliniana are a few of the coastal plain species which occur in western New York.

The Exotic element containing non-native species which have entered the region through the activities of man remains to be discussed. Of particular interest palynologically are certain species of Plantago, especially P. lanceolata and P. major, two European species widely naturalized in North America. The appearance of Plantago pollen in postglacial sediments which can be mostly attributed to these species clearly marks the arrival and spread of Europeans in America. However, there are many other examples of the Exotic element in the flora and, as has been pointed out earlier in this section, 25 percent of the total flora of the Niagara Frontier region is comprised of introduced species.

## VEGETATION

### General Statement

Authors of the earliest histories which have been published about western New York are uniform in stating that the region was completely covered by forest except for discontinuous openings in the oak forests of the Erie-Ontario Lowland and other small partially cleared areas associated with Indian villages. A general account of the whole region published a few years after settlement began contains an

interesting discussion of the kinds of timber present and the agricultural potential of the land on which grew certain forest types (Munro, 1804).

. . . in the better or most even parts of the country . . . the most common sorts of timber . . . [are] . . . sugar maple, beech, lyn (here called basswood), oak, ash, and elm; and the hilly parts are mostly timbered with oak. Where the sugar maple and basswood are most common, the land is generally esteemed best for grass, and probably grain, and is experienced to be durable; the lands which produce mostly beech timber, are considered as generally clayey, wet, and cold. A considerable portion of the better part of the country is timbered with oak, and lands on which it is of a large growth are by many esteemed the most durable, although at first not productive of as good crops as maple lands, and harder in tillage.

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The sorts of trees and shrubs which are most scarce are hemlock fir, cucumber tree, white poplar, white and black birch, turmeric tree, spruce pine, locust tree, prickly ash, spice wood, hazel nut, willow, and alder (p. 1173-1174).

The observations of Rev. Mr. E. J. Hill, an accomplished botanist, although made four to six decades later, provide a more complete description of the forest cover of western New York. Rev. Hill was born at Le Roy in Genesee County in 1833 and spent much of the early part of his life in this region at a time during which undisturbed tracts of forest were still fairly abundant. Hill (1895) reports that:

The most abundant trees of the upland woods are the Beech and Hard Maple. On light soils, and where there is a considerable mixture of sand or gravel with the clay loam, the Oaks predominate, interspersed with Hickory, and sometimes with the Chestnut. In colder and higher tracts or along the banks of streams, the Hemlock, is frequent or even abundant. The Basswood is common in the richer uplands, among



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Beeches and Maples. Here also the White Ash is most often seen. . . .

Where the Beech and Maple abound the White Oak is occasionally mixed with them, but is mostly confined to the low land, where it is much more common than the Swamp White Oak. The Red Oak is much more commonly seen with the Beech and Maple. In flinty and gravelly soils the most common Oaks are the White, Red and Black Oaks. Here also occurs the Chestnut Oak; it is usually less abundant than the other kinds and may also be found in the wet lands (p. 382).

Turning briefly to historical records which pertain to either of the two physiographic regions, an informative account of the original timber covering of Orleans County indicates in a general way the nature of the forests throughout the Erie-Ontario Lowland during the period of European settlement (Arad, 1871).

In its natural state Orleans County was thickly covered with trees. On the dry, hard land, the prevailing varieties of timber were beech, maple, white, red and black oak, white wood or tulip tree, basswood, elm, hickory, and hemlock. Swamps and low wet lands were covered with black ash, tamarack, white and yellow cedar, and soft maple; large sycamore or cotton ball trees were common on low lands and some pine grew along Oak Orchard Creek, and in the swamps in Barre; and a few chestnut trees grew along the Ridge<sup>1</sup> in Ridgeway, and in other places north of the Ridge (p. 29).

In comparison, C. G. Locke's description of the forests of Cattaraugus County, which pertains to much of the western Allegheny Upland in New York State, emphasizes the prevalence of hemlock and pine in this region at the time of settlement (in Adams, 1893).

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<sup>1</sup>Lake Iroquois strandline.

This table-land was originally covered with a heavy growth of deciduous trees intermixed with hemlock and some pine, and this same description of the original forest would apply to the entire northern portion of the county, excepting that pine was generally found along the low-lands. The southern part of the county was covered with forest of the choicest pine and hemlock, with a mixture of deciduous trees. Here we find the home of the white and red oak and chestnut, which apparently did not cross the dividing ridge, as very little of this timber is found in the northern part of the county (p. 50).

These passages clearly indicate that the forests of the lowland and upland were of a different type with beech maple, oaks and other deciduous species predominating in the former, while a mixed forest of conifer and deciduous trees occurred in the latter. Most botanists who studied the vegetation of this region in more recent years have also made this distinction. For example, Kùchler (1964) has recognized three main types of forest in western New York in his treatment of the potential natural vegetation of the contiguous United States (see Fig. 3B): (1) Beech-maple forest dominated by Acer saccharum and Fagus grandifolia, (2) Northern hardwoods forest dominated by Acer saccharum, Betula alleghanensis, Fagus grandifolia and Tsuga canadensis and (3) Appalachian oak forest in which Quercus alba and Q. rubra are dominant but generally occur with many other subdominant species. The boundary between (1) and (2) roughly corresponds to the Portage escarpment with the Northern hardwoods forest area in the upland and the Beech-maple forest area in the lowland, although inclusions of one type are mapped in the

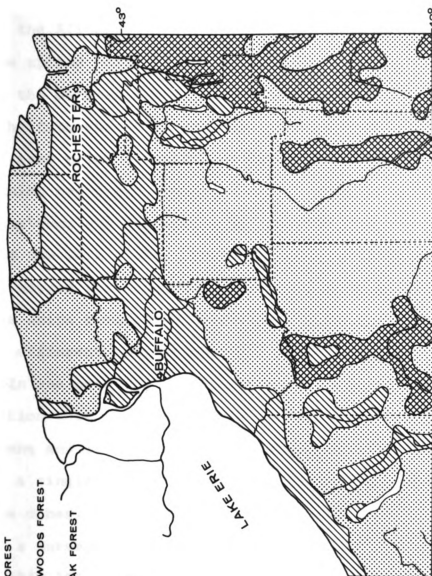
# FIGURE 3. VEGETATION MAPS

MAP A. POTENTIAL NATURAL VEGETATION OF WESTERN NEW YORK STATE

BEECH-MAPLE FOREST

NORTHERN HARDWOODS FOREST

APPALACHIAN OAK FOREST



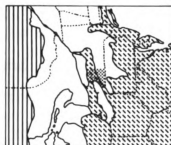
A. After Küchler (1964)

79°

B. Boundaries from Braun (1964)

78°

MAP B. FOREST REGIONS OF EASTERN NORTH AMERICA



Boreal Forest

Conifer-hardwood Forest

Deciduous Forest

Region covered by MAP A

other and vice versa. The Appalachian oak forest is restricted to the Allegheny River valley and to several small areas in the upland north of the Salamanca reentrant and adjacent to the Genesee River. It occurs more widely in the region of the Susquehanna River drainage immediately to the east of the area being treated in this study.

Küchler has drawn heavily on the map of major forest types in Armstrong and Bjorkbom's study (1956) of the timber resources of New York State. Although the boundaries of the units being mapped are essentially the same in both publications, the units themselves differ somewhat. This is a result of two different approaches used in the preparation of the maps. In one case the potential natural vegetation, or "the vegetation that would exist today if man were removed from the scene and if the resulting succession were telescoped into a single moment" (Küchler, 1964, p. 2), is mapped, while in the other, the actual or "real" vegetation determined by a survey of existing forests carried out during the period 1949-1952 is represented. Armstrong and Bjorkbom's work does tell us what the general pattern and composition of existing forest vegetation is and for this reason a brief discussion of their units and those of Küchler follows. The area of currently existing forests in western New York is given in Table 4.

The Northern hardwoods forest mentioned earlier is distributionally equivalent to the Maple-beech-birch forest

TABLE 4

TOTAL AREA, NON-FOREST LAND AREA AND FOREST LAND AREA OF  
WESTERN NEW YORK STATE BY COUNTIES<sup>1</sup>

COUNTIES	TOTAL LAND AREA <sup>2</sup>	NON-FOREST LAND AREA		FOREST LAND AREA		
		ACRES <sup>3</sup>	PERCENT	NON-COMMERCIAL <sup>4</sup>		COMMERCIAL
				ACRES <sup>3</sup>	PERCENT	ACRES <sup>3</sup> PERCENT
Chautauqua	691.2	343.0	49.6	1.8	0.3	346.4 50.1
Cattaraugus	854.4	326.1	38.2	61.3	7.2	467.0 54.7
Allegany	670.7	259.4	38.7	2.5	0.4	408.8 60.9
Erie	674.7	468.4	69.4	2.5	0.4	203.7 30.2
Wyoming	382.7	259.8	67.9	6.6	1.7	116.3 30.4
Niagara	341.1	283.0	83.0	0.1	0.0	58.0 17.0
Genesee	320.6	227.1	70.8	1.3	0.4	92.2 28.8
Orleans	253.4	202.5	79.9	1.2	0.5	49.7 19.6

<sup>1</sup>Data from, "Preliminary forest survey statistics by counties and units, New York--1967," Northeastern Forest Experiment Station, U.S. Forest Service, Upper Darby, Pennsylvania.

<sup>2</sup>In thousands of acres.

<sup>3</sup>Times 1000.

<sup>4</sup>Includes non-productive and productive but reserved forest land.

type of Armstrong and Bjorkbom. Maple-beech-birch forest is mapped as occurring widely across the upland but as having a more restricted distribution in the lowland. It is made up of stands in which 50 percent or more of the trees are Acer saccharum, Betula alleghaniensis and Fagus grandifolia either singly or in combination. In addition Pinus strobus, Tilia americana, Tsuga canadensis and Ulmus sp. often occur in such stands. Similarly, the Beech-maple forest region of Kùchler is nearly the same as Armstrong and Bjorkbom's region of Elm-ash-maple forest which is comprised of stands in which 50 percent or more of the trees are Acer rubrum, Fraxinus sp. and Ulmus sp. by themselves or together. The widespread occurrence of this forest type throughout the lowland today indicates the prevalence of swamp forests in this region. The Appalachian oak forest of Kùchler is areally equivalent to the Oak-hickory forest of Armstrong and Bjorkbom. In the latter type of forest 50 percent or more of a stand is in oak species.

Armstrong and Bjorkbom also recognize areas of limited occurrence of other forest types in western New York not noted by Kùchler. Small tracts of the White-red pine type have been mapped southwest of Lake Chautauqua and along Cattaraugus Creek in southern Erie and northern Cattaraugus Counties, but since red pine is native to western New York only along the Genesee River in southwestern Wyoming County (Zenkert, 1934), white pine is the dominant species in stands of this type.

Common associates of white pine include Tsuga canadensis, Populus spp., Betula spp. and Acer spp. Small areas typed as Aspen-birch forest occur in the Cattaraugus Creek Valley just west of the white-red pine area, in south-central Erie County and in north-central Allegany County. These forest areas are presumably just aspen stands however, because, of the two birch codominants listed with aspen, only Betula papyrifera is native to western New York and it is a rare species that does not occur in either area of Aspen-birch forest (*ibid.*). The other birch, Betula populifolia, is found eastward from central New York State to New England. The percentages of total commercial forest land by forest types recognized by the Forest Service in the eight counties of western New York are given in Table 5.

The distinction between the deciduous forest of the lowland and the coniferous-deciduous forest of the upland is discussed more fully by E. Lucy Braun (1951) in her monograph on the forests of eastern North America. As depicted by Miss Braun, the boundary separating these two forest types also coincides with the Portage escarpment (*see* Fig. 3A). The Beech-maple forest region, which in this work is mapped as extending from central Indiana, southern Michigan and western Ohio around Lake Erie and across southern Ontario and north-eastern Ohio to northwestern New York State, is located north of the escarpment, and a portion of the Hemlock-white pine-northern hardwoods forest region occurs south of it. This



TABLE 5

PERCENT OF TOTAL COMMERCIAL FOREST LAND BY FOREST TYPE IN  
EIGHT WESTERN COUNTIES OF NEW YORK STATE, 1967<sup>1</sup>

COUNTY	WHITE-RED PINE	OTHER SOFT-WOOD <sup>2</sup>	OAK <sup>3</sup>	ELM-ASH- RED MAPLE	MAPLE-BEECH- BIRCH	ASPEN- BIRCH
Chautauqua	4.2	6.5	8.9	16.7	56.1	7.5
Cattaraugus	4.5	6.3	8.1	16.2	56.8	8.0
Allegany	4.1	5.7	9.0	17.2	56.8	7.2
Erie	2.4	5.2	5.3	40.1	41.4	5.7
Wyoming	2.3	5.8	5.7	39.6	41.4	5.2
Niagara	1.9	4.8	4.7	43.4	41.2	4.0
Genesee	1.7	4.9	3.5	40.9	42.5	6.5
Orleans	1.6	5.6	4.4	41.2	41.6	5.4

<sup>1</sup>Data from, "Preliminary forest survey statistics by counties and units, New York--1967," Northeastern Forest Experiment Station, U.S. Forest Service, Upper Darby, Pennsylvania.

<sup>2</sup>Includes spruce-fir type.

<sup>3</sup>Includes oak-pine and oak-hickory types.

latter forest region extends westward from maritime Canada and northern New England across southern Ontario and Quebec to western Minnesota and includes seven subdivisions, each of which is characterized by forests of somewhat different composition which occur in distinct parts of the total region.

The Mixed mesophytic and the Oak-chestnut forest regions, as they are mapped by Miss Braun, closely approach western New York. The former extends from the Allegheny and Cumberland plateaus northward along the Allegheny River to southern Cattaraugus County, while the latter occurs across the east flank of the Appalachians to central Pennsylvania and northward to southern New England, with an extension up the Hudson River Valley.

#### Forests of the Erie-Ontario Lowland

The forests of the Beech-maple region in northwestern New York are imperfectly known. Although as its name implies, Fagus grandifolia and Acer saccharum are the predominant forest trees throughout the whole forest region, many other species are present, and in the Erie-Ontario Lowland, oaks and hickories are particularly abundant. This suggests that the beech-maple area in western New York may not be solely an eastward extension of the deciduous forest of the midwest but that it may also have an affinity to the Oak-chestnut region of the eastern United States. This

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relationship has been emphasized by Bray (1915). It is also clearly depicted by Shantz and Zon (1924) who, in their treatment of the natural vegetation of the United States, map what they call Chestnut-chestnut oak-yellow poplar forest throughout the lowland areas adjacent to Lakes Erie and Ontario, in a wide band on either side of the Hudson River up to about Glens Falls and in most of the larger river valleys in the southern part of the Allegheny Upland. They represent these areas as northern extensions of oak forests of the same type which occur in broad areas on both sides of the Appalachians.

#### Deciduous Forest Region of Southern Ontario

As the deciduous forests of southern Ontario and northwestern New York are placed in the same forest region, the communities which comprise both display many similarities. For this reason, Rowe's description (1959) of the deciduous forest region in Canada, which he designates the Niagara Section, generally applies to northwestern New York State and provides a capsule summary of the forests in these areas:

The forest communities are dominated by broad-leaved trees. The characteristic association . . . consists primarily of beech (Fagus grandifolia) and sugar maple (Acer saccharum), together with basswood (Tilia americana), red maple (Acer rubrum), red oak (Quercus rubra), white oak (Q. alba) and bur oak (Q. macrocarpa). Also within this area is found the main distribution in Canada of black walnut (Juglans nigra), sycamore (Platanus occidentalis), swamp white oak (Quercus bicolor) and shagbark hickory (Carya ovata) with the more widely distributed

butternut (Juglans cinerea), bitternut hickory (Carya cordiformis), rock elm (Ulmus thomasi), silver maple (Acer saccharinum) and blue beech (Carpinus caroliniana var. virginiana). Other species with a sporadic occurrence as scattered individuals or groups, either on specialized sites or within the characteristic forest types of the Section, are the following: tulip tree (Liriodendron tulipifera), black cherry (Prunus serotina), mockernut and pignut hickories (Carya tomentosa, C. glabra), chinquapin oak (Quercus muehlenbergii), chestnut oak (Q. prinus), pin oak (Q. palustris), scarlet and black oaks (Q. coccinea, Q. velutina), black gum (Nyssa sylvatica), blue ash (Fraxinus quadrangulata), cucumber tree (Magnolia acuminata) [and] papaw (Asimina triloba). . . . There is . . . a poor representation of needle-leaved species, though eastern hemlock (Tsuga canadensis) is sometimes scattered through upland forests, [and] white pine (Pinus strobus) occurs locally in small stands on coarse-textured soils . . . (p. 43-44).

Maycock (1963) has made a detailed study of the deciduous forests of the Niagara Section of Ontario. By sampling a large number of woodlots and relating his findings to the water-retaining capacity of the soils upon which a particular stand was located, he has demonstrated a gradual shift in the importance of the tree species which comprise the forests of this area along the moisture gradient. He asserts that, rather than being found in distinct natural groupings or associations, the species behave individualistically and display independent relationships to the moisture gradient.

For nearly all of the tree species encountered in his study, Maycock has calculated an "index of regional importance" which serves well to summarize the overall importance of a particular species in this region. An index

is computed by adding together the average importance values for a species in each of the five sections of the moisture gradient and then dividing this figure by the grand sum of the importance values for all species in all of the five parts of the gradient. The sum of the indices will thus total 100. Of the 56 species treated by Maycock, the following have the greatest influence in the deciduous forests of Ontario: Acer saccharum (13.4), Ulmus americana (11.3), Fagus grandifolia (10.1), Fraxinus americana (6.0), Acer rubrum (5.7), Quercus alba (5.0), Q. rubra (4.4), Q. velutina (4.4), Acer saccharinum (3.2) and Tilia americana (2.8). Together these comprise 66.3 percent of the total regional influence.

#### Deciduous Forests of Northwestern New York

The only available detailed study of the vegetation of the deciduous forest region in western New York deals specifically with Monroe County (Shanks, 1966; see Fig. 1). However, its findings in general apply to other parts of the Erie-Ontario Lowland. Although recently published, it was written before 1943, summarizing field work carried out from 1938-1940, and thus it reflects outlooks and methods differing from those of Maycock's study. Analysis of notes made by the first land surveyors, in conjunction with study of existing woodlots and forest remnants, permitted Shanks to prepare a map of the original vegetation of Monroe County.

Measurements by planimetry of the areas covered by the recognized vegetation types showed that the Beech-sugar maple type accounted for 61 percent of the original vegetation cover. In order of decreasing areas the remaining types were Hemlock-hardwoods (12 percent), Upland oaks and Oak-hickory (11 percent), swamp forest (6 percent), Oak-chestnut-pine (4 percent), Mixed mesophytic (2 percent) and bog forest (2 percent). The remaining 2 percent was occupied by either marsh land or oak openings. Today in contrast only 16 percent of the total area is forested (Northeastern Forest Experiment Station, 1967).

In Monroe County, the Oak-chestnut-pine type occurred on the driest sites underlain mostly by sandy deltaic sediments deposited in glacial lakes. An exact equivalent probably did not occur westward through Genesee, Orleans and Niagara Counties, for, although the three dominant oaks, Quercus alba, Q. rubra and Q. velutina, have a wide distribution in this area, as does one of the dominant pines, Pinus strobus, P. rigida is at the present time native no farther west than the vicinity of Rochester. There are no historical records of its occurrence west of this area. Castanea dentata, originally a member of this forest type has been removed as a forest canopy dominant by the chestnut blight.

Several other types of oak forest grew at slightly more mesophytic sites. The Upland oak type, in which Quercus

alba, Q. rubra and Q. velutina were the usual dominants, occurred on the tops and sides of drumlins and kames and on dry, flat-lying, gravelly soils of high porosity. Deficient soil moisture during the growing season probably characterized such sites. Carya ovata was frequently a codominant in such stands and at certain locations additional species of Carya attained dominant rank along with the oaks, resulting in the Oak-hickory type. Transitional Oak-sugar maple associations occurred at favorable locations between lowland Beech-sugar maple and Upland oak types. Other transitional types called Mixed mesophytic forests occupied positions between Oak-chestnut-pine and Beech-sugar maple types, between Oak-chestnut-pine and Hemlock-northern hardwoods types and in some cases in conjunction with Upland oak forests. Such transitional forests which are generally characterized by a large number of tree species occurring in about equal abundance rather than just a few dominant species were of limited occurrence in Monroe County.

Originally Beech-sugar maple forest occupied more than half of Monroe County where it occurred on a wide variety of soil types. At the better sites in the region such forest tends to maintain itself and some data are available which suggest that it succeeds adjacent less mesophytic forest types. Typical beech-sugar maple stands exhibit abundant regeneration of the dominant species. Sugar maple seedlings often form a continuous undergrowth and beech is



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abundantly represented by rootsprouts. Tilia americana is often codominant in Beech-sugar maple forests and other common associates include Ulmus americana, Fraxinus americana, Ostrya virginiana, Acer rubrum, A. nigrum, Quercus rubra, Carya ovata, Prunus serotina and Liriodendron tulipifera.

Areas of Hemlock-northern hardwoods forest were originally found in the northeastern and northwestern corners of the county, mostly on the Lake Iroquois plain, and in sheltered ravines in the vicinity of the Genesee River. Stands of this forest were dominated by Tsuga canadensis, Fagus grandifolia and Acer saccharum which in many places occurred with Betula alleghaniensis, Tilia americana, Acer rubrum, Fraxinus americana, Quercus rubra, Ostrya virginiana, Prunus serotina and Ulmus americana. Hemlock-northern hardwoods forests have a dense canopy and light intensity on the forest floor is typically very low. Shrubs and herbs often listed as characteristic of the Hemlock-white pine-northern hardwood Forest region were present in some remnant stands but were absent from others. Those with the greatest frequency include: Acer pensylvanicum, Aster acuminatus, Dryopteris spinulosa var. intermedia, Lonicera canadensis, Lycopodium lucidulum, Maianthemum canadense, Sambucus pubens and Taxus canadensis.

Large swamp forests were widely distributed in Monroe County and probably occupied about 6 percent of the total area. Deficient soil aeration is the most important factor

preventing invasion of the swamp habitats by more mesophytic species. In order of decreasing abundance the following species occur in various combinations as dominants in different phases of the swamp forest: Ulmus americana, Acer rubrum, A. saccharinum, Tilia americana, Fraxinus americana, Quercus bicolor, Fraxinus pennsylvanica and Fraxinus nigra.

The Dutch elm disease has made serious inroads on Ulmus populations. The former role of U. americana as a dominant or subdominant has ceased to exist over wide areas.

#### Forests of the Allegheny Upland

Considering now the forest vegetation of the upland south of the Portage escarpment, Braun (1950), as already noted, has mapped this area as part of the Hemlock-white pine-northern hardwoods Forest region. More specifically, she assigns nearly all of southern New York and northern Pennsylvania to the Allegheny Section of the Northern Appalachian Division. This and the Great Lakes-St. Lawrence Division are the two major parts of the forest region as it is treated by Miss Braun. The Northern Appalachian Division, including two other sections in addition to the one already mentioned, occupies much of the northeastern United States and extends into maritime Canada south of the Gulf of St. Lawrence. It differs from the Great Lakes-St. Lawrence Division, which stretches westward from the St. Lawrence River valley to western Minnesota, in the presence of Picea rubens

at higher elevations throughout the northeastern mountain region, in the absence of Pinus banksiana and the rarity of P. resinosa, in the admixture of Liriodendron tulipifera and Magnolia acuminata and other species characteristic of the central deciduous forest and in the presence of Aster acuminatus, Tiarella cordifolia and Viburnum alnifolium and some shrubs and herbs which are rare or absent in the western division.

The Hemlock-white pine-northern hardwoods region includes the Birch-beech-maple-hemlock (northeastern hardwoods) forest of Shantz and Zon (1924); the Beech-birch-maple forest type as it is recognized in Pennsylvania (Illick and Frontz, 1928); the Lake forest of Weaver and Clements (1938); the Maple-beech-birch forest type of Armstrong and Bjorkbom (1956) as it is applied by them to New York State; the Great Lakes-St. Lawrence forest region of Canada (Rowe, 1959); the Northern hardwoods region as identified in south-central New York State and north-central Pennsylvania (Goodlett and Lyford, 1963); the Northern hardwoods, the Northern hardwoods-fir, the Great Lakes pine, the Great Lakes and Northeastern spruce-fir and the Conifer bog forests of Kùchler (1964); and the Beech-birch-maple and White pine-hemlock-hardwood forest regions as applied throughout the northeastern United States by Lull (1968). For further equivalents and a review of the literature pertaining to the recognition

of the Hemlock-white-pine northern hardwoods Forest region, the reader is referred to Nichols (1934).

The original forest cover of upland southwestern New York has been greatly modified by lumbering and by clearing for agricultural purposes. The upland counties have at the present time the largest areas of commercial and noncommercial forest land of any at the west end of the state because of the poorer agricultural potential of this area (see Table 4). Here, as elsewhere in western New York, an important stimulus for forest clearance during the early period of settlement was the demand for the ashes which remained after burning the cut trees. Crude field ashes were worth 4 to 9 cents a bushel and, if the settler wished to refine these somewhat, 600 bushels could be leached and boiled down into a ton of pot or pearl ash (also called black salts) worth 125 to 150 dollars (Munro, 1804; Young, 1875). Lye manufactured in this manner was used to make soap.

The nature and composition of the original forest is indicated by several virgin tracts which have been preserved in northwestern Pennsylvania. These include Cook Forest (Morey, 1936), the East Tionesta Creek Natural Area (Hough, 1936a) and Hearts Content (Lutz, 1930b) which are all within the Allegheny National Forest. These and additional studies in northwestern Pennsylvania have been summarized by Hough and Forbes (1943).

Judging from early land survey records for a 175,000 acre tract in northwestern Pennsylvania (Lutz, 1930a), the forest existing today along the East Tionesta Creek is fairly typical of that which originally covered dissected areas of the Allegheny Plateau, particularly N-facing slopes. Tsuga canadensis and Fagus grandifolia in both abundance and frequency values are the dominant canopy trees on the plateau tops and on the middle and lower slopes (Hough, 1936a). Betula alleghaniensis is third in order on middle and lower slopes, but on the plateau top Acer saccharum holds this rank. In order of decreasing totals of abundance and frequency values associated species are: Betula alleghaniensis, Acer rubrum, Prunus serotina, Fraxinus americana, Liriodendron tulipifera, Magnolia acuminata and Tilia americana. Viburnum alnifolium is the most abundant shrub in this forest and common herbaceous plants include Dryopteris spinulosa, Lycopodium lucidulum, Maianthemum canadense, Mitchella repens, Oxalis acetosella and Tiarella cordifolia.

Within forests of this type there is a tendency toward segregation of hemlock-beech, beech-hemlock-sugar maple and beech-sugar maple communities which differ from one another in the relative abundance of the dominants. Hough (1936a) and Morey (1936) have suggested that there is an alternation in the occupation of a given spot by hardwoods and hemlock-hardwoods. Uprooting or death of the hemlocks permits the hardwoods in the understory to become established as the

canopy trees, while removal of the hardwoods, either catastrophically or by aging, releases the hemlocks in the undergrowth so that they eventually grow to occupy the canopy again. In Cattaraugus County forest of the Beech-sugar maple type originally occupied the better drained soils near ridge tops and was apparently more extensive in the glaciated portion of the plateau (Gordon, 1940). However, most of it in this region today is of secondary origin, having developed after the removal of hemlock and white pine for lumber. Fagus grandifolia and Acer saccharum comprise 97 percent of the canopy in an undisturbed beech-sugar maple stand on a northeast slope in the Big Basin at Allegany State Park (Braun, 1950, Table 82).

White pine has an interesting position in the virgin forests of northwestern Pennsylvania. It is absent from the East Tionesta tract, but at Hearts Content, 30 miles to the west, it is abundant both in the hemlock and in the hemlock-beech communities. An age analysis showed that the pine started there as an even-aged stand at about 1680 (Lutz, 1930b). Similar data gathered at other localities on the Allegheny Plateau suggest that the presence of white pine stands can nearly always be correlated with fire, windfall or some other event that opens a portion of the forest for seeding (Hough and Forbes, 1943). If no openings are made, the white pine apparently matures, dies and is replaced by hemlocks or hardwoods but not by other white pines.

Forest communities essentially the same as those in the Allegheny National Forest have been preserved at a few places in southwestern New York State, both outside and inside the glacial boundary. Gordon's map (1940) of the vegetation of Cattaraugus County at the time of settlement, which was prepared by analyzing the original lot survey data in conjunction with an examination of existing stands, shows that the prevailing forest type in this area belonged to the Hemlock-white pine-northern hardwoods forest. Hemlock-northern hardwoods communities with little or no white pine comprised the typical stand. Quantitative data are unfortunately sparse but the virgin tract of forest in Stoddard Hollow in the Big Basin at Allegany State Park has "a composition almost exactly similar to the Hemlock-Beech association at Heart's Content" (Gordon, 1937, p. 39). The principal trees on lower slopes in the Big Basin in order of decreasing abundance are Fagus grandifolia, Tsuga canadensis, Acer saccharum and A. rubrum (Braun, 1950, Table 82). Together they total 87 percent of the canopy. The leading dominants in the Hemlock-beech association at Hearts Content are Tsuga canadensis, Fagus grandifolia, Acer rubrum, Pinus strobus and Castanea dentata in order of decreasing totals of the relative frequency and density for each of the species, recalculated in part from the data provided by Lutz (1930b).

A number of other forest types are also recognized in Cattaraugus County (Gordon, 1940). As in Monroe County



the drier sites, which in the upland occur on ridges and exposed south and southwest slopes, were occupied by forest of the Oak-chestnut type. Quercus alba, Q. rubra, Q. prinus and Q. velutina are now typically the dominant trees at these sites, but prior to about 1934, before being eliminated by the chestnut blight, Castanea dentata was codominant with them. Associated species which sometimes reach dominant status include Pinus strobus, Acer rubrum, Carya glabra, Betula alleghaniensis, Populus tremuloides and occasionally others. Similar communities also occur on dry S-facing slopes throughout northwestern Pennsylvania (Hough, 1936a). In Cattaraugus County secondary forests rich in oak species commonly result after fires and excessive logging. To the east just beyond Allegany County in the region straddling the New York-Pennsylvania border, Goodlett and Lyford (1963) have mapped the current extent of oak forest using Quercus alba as an indicator species. Species with frequencies greater than 50 percent in oak forests studied by these workers include Quercus rubra, Q. alba, Acer rubrum, Pinus strobus, Quercus velutina and Q. prinus. Such forests occupy a greater area in this region than they do in western New York and Pennsylvania.

Communities transitional between the Oak-chestnut type of dry slopes and ridges and the Beech-sugar maple and Hemlock-beech types of the lower, more mesophytic sites are considered to be somewhat attenuated examples of the Mixed

mesophytic forests which occurs across much of the southern part of the unglaciated Allegheny Plateau. Similar communities have been recognized at places in the Erie-Ontario Lowland associated with Upland oak forest (Shanks, 1966). Mixed mesophytic forests in Cattaraugus County occupy moist well-drained and well-aerated sites which are favorable to the growth of a wide variety of tree species. Such forests are dominated by Quercus rubra, Fagus grandifolia, Acer rubrum, Betula alleghaniensis, Fraxinus americana, Prunus serotina, and, formerly, Castanea dentata. Magnolia acuminata, Quercus alba, Liriodendron tulipifera, Pinus strobus, Tilia americana, Carya cordiformis, Acer saccharum, Ostrya virginiana and Acer pensylvanicum also occur but less frequently.

Similar communities occur today in other areas of the upland. For example, in a stand near Lily Dale in Chautauqua County (Braun, 1950, Table 85), the following trees comprised the canopy (in percent): Tsuga canadensis (20.9), Fagus grandifolia (16.9), Prunus serotina (12.4), Acer rubrum (11.3), Acer saccharum (8.5), Pinus strobus (8.5), Magnolia acuminata (5.7), Quercus rubra (5.6) Fraxinus americana (4.5), Betula alleghaniensis (2.8), Tilia americana (1.7) and Carya ovata (1.1). Acer saccharum accounted for 37 percent of the second layer trees suggesting greater dominance by this species at the site in the future.

Two additional forest types restricted to bottomlands have been recognized in Cattaraugus County (Gordon, 1940). The White pine-American elm forest occupied flood plains of the major rivers and streams in the county, especially those which were filled with impervious lacustrine sediments. The great value of Pinus strobus as a timber tree led to the early destruction of these forests, but their former distribution has been well-documented (ibid.). The largest area of this forest, occupying many hundreds of acres, occurred along the axis of the preglacial Allegheny River whose course ran toward Lake Erie from the northwest side of the Salamanca reentrant along what is today Connewango Creek (see Muller, 1963 for further details). These forests also contained Fraxinus nigra, Quercus bicolor, Acer rubrum, Betula alleghaniensis, Tsuga canadensis and occasionally Abies balsamea and Larix laricina.

Of less widespread occurrence are the Bottomland hardwood forests which are found on recently deposited alluvium, especially along the Allegheny River and Cattaraugus Creek and their tributaries. In composition these forests are variable, but they are by no means as rich in numbers of species as are the bottomland forests of Ohio and southern Michigan. Populus deltoides, Salix nigra, Acer negundo and A. rubrum are frequent along disturbed stream courses, while Platanus occidentalis and Juglans cinerea are typically found on the more stabilized flood plains.

### Stands Sampled by the Quarter Method

A good understanding is needed of the distribution and composition of existing forests in the upland around the sites where cores for palynological analysis were collected. During the summers of 1966 and 1967 I studied about 35 woodlots scattered across southwestern New York State from western Chautauqua County to central Steuben County. Notes were taken on nearly all of the stands, but three of them were studied more carefully by the point quarter method (Cottam and Curtis, 1956). Briefly, this technique involves taking measurements at a number of sampling points spread throughout a woodlot. I used a grid of 48 points (eight points by six points) in which the points along a traverse line were 20 m apart. The initial point was chosen randomly.

Within a meter-square quadrat centered over each of the 48 points, the presence of seedlings<sup>1</sup> over and under 30 cm in height and the presence of herbs were noted and tallied by species. The area around a point was then divided into four quarters using the transect line as a bisect and another line which passed through the point at right angles to the bisect. Bamboo wands were used to temporarily mark these lines. For each of the quarters the distance between

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<sup>1</sup>The size classes used follow Curtis (1959): trees--greater than 4 inches (ca. 10 cm) diameter at breast height (d.b.h.), saplings--between 1 inch (2.5 cm) and 4 inches d.b.h. and seedlings--less than 1 inch d.b.h.

the point and the nearest tree, its species and diameter at breast height were determined and recorded. Each of the four trees generally occurred well beyond the original 1 m quadrat. The number and species of saplings which occurred within an area 1 m on each side of a line between the points were also recorded.

The three stands selected for sampling were chosen because they met the following criteria: (1) greater than 15 acres in size permitting the influence of surrounding fields and secondary forests to be reduced, (2) absence of disturbance in the form of fire, grazing or excessive cutting (none or very little during the past 40 years) and (3) occurrence on upland soil types. After the information was collected, it was divided into four equal parts and a Chi-square test of homogeneity was applied to determine if the number of major tree species within any segment deviated significantly from the number expected on the basis of uniform distribution (Curtis and McIntosh, 1951). In no case did the Chi-square values exceed the expected values at the 5 percent level indicating that the stands were homogeneous according to this test.

The location of the stands in relation to the sites selected for palynological study is indicated in Figure 2. Other pertinent data concerning the sites are summarized in Table 5. Relative frequency (percent frequency), density (percent occurrence) and dominance (percent basal area), and

the sum of these three figures, the Importance Value, in addition to the absolute density (no. trees/acre) and dominance (basal area/acre) were calculated for each of the tree and sapling species tallied during the sampling (Curtis, 1956). The relative frequency of seedling and herb species was also computed. These figures are given in Tables 6 through 11.

The stands sampled, although too few in number to permit a complete assessment of the variability in the existing forests of southwestern New York, nevertheless do provide quantitative data on the composition of several upland communities. Acer saccharum, Fagus grandifolia and Tsuga canadensis in order of decreasing importance values are the leading dominants in all three stands. The similarly high importance values for sugar maple, beech and hemlock saplings suggest continued dominance by these species at the sites, although hemlock seedlings were infrequent within the sampled areas. Quantitative data for comparison are unfortunately not available, but the three stands clearly seem to belong to the Hemlock-white pine-northern hardwoods forest (Nichols, 1935). This unit is recognized by Gordon (1937, 1940) to be the climatic climax of the entire upland in southwestern New York State where it is expressed by associations in which Tsuga canadensis occurs by itself or mixed with Fagus grandifolia, Acer saccharum and Betula alleghaniensis. Although present in all three of the stands

TABLE 6

## FOREST STAND DATA: GENERAL INFORMATION

Stand Name	Date Sampled	Soil Type	Drainage Class	Topography
Canadaway Creek	September 1966	Volusia silt loam or Bath (Wooster) silt loam (Morrison <u>et al.</u> , 1919) <sup>1</sup>	well, or some- what poorly	gently rolling, nearly flat-lying; lacustrine sedi- ments (Muller, 1963)
Erie County Plantation #11	June 1966	Bath (Wooster) gravelly loam (Taylor <u>et al.</u> , 1929)	well	rolling, weak morainic topography
NYS Zoar Valley Property #12	August 1966	Bath (Wooster) silt loam (Taylor <u>et al.</u> , 1929)	well	gentle NW-facing slope

<sup>1</sup>The topographic base on which this soil map was printed is apparently misdrawn in the vicinity of the stand as more recent maps show somewhat different relief and stream arrangement in the area. For this reason it is impossible to determine which of the two soil types lay beneath the stand. The recent soil association map for Chautauqua County shows the area covered by soils of the Langford-Erie Association which contains soils very similar to those belonging to the Bath-Mardin-Volusia Association (Feuer, 1955).

TABLE 7

FOREST STAND DATA: TREES AND SAPLINGS CANADAWAY CREEK GAME MANAGEMENT AREA,<sup>1</sup>

CHAUTAUQUA COUNTY, NEW YORK

SPECIES AND SIZE CLASS	RELATIVE FREQUENCY	RELATIVE DENSITY	RELATIVE DOMINANCE	IMPORTANCE VALUE	ABSOLUTE DENSITY/ACRE	ABSOLUTE DOMINANCE/ACRE
<u>Acer saccharum</u> Trees	58.5%	76.6%	80.1%	215.2	76.4	19,596.6
Saplings	60.0%	79.8%	70.6%	210.4	315.0	768.6
<u>Fagus grandifolia</u> Trees	22.0%	12.5%	16.4%	50.9	12.5	3,982.9
Saplings	18.6%	11.2%	11.9%	41.7	44.1	129.2
<u>Tsuga canadensis</u> Trees	17.1%	9.9%	3.4%	30.4	9.9	844.5
Saplings	8.6%	3.7%	8.0%	20.3	14.7	87.2
<u>Prunus serotina</u> Trees	1.2%	0.5%	0.1%	1.8	0.5	11.9
<u>Magnolia acuminata</u> Trees	1.2%	0.5%	0.1%	1.8	0.5	14.2
<u>Fraxinus americana</u> Saplings	5.7%	2.7%	5.4%	13.8	10.5	58.9
<u>Betula alleghaniensis</u> Saplings	4.3%	1.6%	3.0%	8.9	6.3	32.3
<u>Ostrya virginiana</u> Saplings	1.4%	0.5%	0.6%	2.5	2.1	6.6
<u>Cornus alternifolia</u> Saplings	1.4%	0.5%	0.6%	2.5	2.1	6.6

<sup>1</sup>New York State Conservation Department.



TABLE 8

FOREST STAND DATA: HERBS AND SEEDLINGS CANADAWAY CREEK

GAME MANAGEMENT AREA,<sup>1</sup> CHAUTAUQUA COUNTY, NEW YORK

SPECIES AND SIZE CLASS	RELATIVE FREQUENCY
<u>Acer saccharum</u>	
under 12 inches	24.2%
over 12 inches	9.2%
<u>Arisaema triphyllum</u>	18.3%
<u>Viola incognita</u>	9.2%
<u>Fraxinus americana</u>	
under 12 inches	6.5%
<u>Dryopteris spinulosa</u> var. <u>intermedia</u>	5.9%
<u>Euonymus obovatus</u>	5.9%
<u>Dennstaedtia punctiloba</u>	3.3%
<u>Epifagus virginiana</u>	2.6%
<u>Phytolacca americana</u>	2.6%
<u>Aster divaricatus</u>	1.9%
<u>Viola canadensis</u>	1.9%
<u>Allium tricoccum</u>	0.7%
<u>Asarum canadensis</u>	0.7%
<u>Caulophyllum thalictroides</u>	0.7%
<u>Disporum lanuginosum</u>	0.7%
<u>Fagus grandifolia</u>	
under 12 inches	0.7%
over 12 inches	1.9%
<u>Galium</u> sp.	0.7%
<u>Hepatica acutiloba</u>	0.7%
<u>Monotropa uniflora</u>	0.7%
<u>Rhus radicans</u>	0.7%
<u>Viola rotundifolia</u>	0.7%

<sup>1</sup>New York State Conservation Department.

TABLE 9  
FOREST STAND DATA: TREES AND SAPLINGS FORESTRY DEPARTMENT<sup>1</sup> PLANTATION #11,  
ERIE COUNTY, NEW YORK

SPECIES AND SIZE CLASS	RELATIVE FREQUENCY	RELATIVE DENSITY	RELATIVE DOMINANCE	IMPORTANCE VALUE	ABSOLUTE DENSITY/ACRE	ABSOLUTE DOMINANCE/ACRE
<u>Acer saccharum</u> Trees Saplings	24.8% 41.3%	24.0% 49.2%	34.0% 51.7%	82.8 142.2	66.9 63.0	11,694.1 264.6
<u>Fagus grandifolia</u> Trees Saplings	23.3% 33.3%	26.0% 26.2%	26.6% 26.9%	75.9 86.4	72.5 33.6	9,113.3 137.8
<u>Tsuga canadensis</u> Trees Saplings	21.7% 20.0%	24.5% 21.3%	13.6% 15.6%	59.8 56.9	68.3 27.3	4,671.7 79.2
<u>Prunus serotina</u> Trees	16.3%	16.1%	19.7%	52.1	44.9	6,735.6
<u>Tilia americana</u> Trees Saplings	6.2% 2.7%	4.2% 1.6%	2.3% 2.9%	12.7 7.2	11.7 2.1	812.0 14.9
<u>Ostrya virginiana</u> Trees	2.3%	1.6%	0.9%	4.8	4.5	332.6
<u>Fraxinus americana</u> Trees	1.6%	1.0%	0.5%	3.1	2.8	149.5
<u>Betula alleghaniensis</u> Trees Saplings	1.6% 2.7%	1.0% 1.6%	0.3% 2.9%	2.9 7.2	1.4 2.1	46.3 14.9
<u>Juglans cinerea</u> Trees	0.8%	0.5%	1.1%	2.4	1.4	376.3
<u>Ulmus americana</u> Trees	0.8%	0.5%	0.6%	1.9	1.4	215.5
<u>Acer rubrum</u> Trees	0.8%	0.5%	0.4%	1.7	1.4	121.3

<sup>1</sup>County of Erie.

TABLE 10

FOREST STAND DATA: HERBS AND SEEDLINGS FORESTRY DEPARTMENT<sup>1</sup> PLANTATION #11,

ERIE COUNTY, NEW YORK

SPECIES AND SIZE CLASS	RELATIVE FREQUENCY	SPECIES AND SIZE CLASS	RELATIVE FREQUENCY	SPECIES AND SIZE CLASS	RELATIVE FREQUENCY
<u>Acer saccharum</u> under 12 inches over 12 inches	15.7% 8.9%	<u>Trillium grandiflorum</u> <u>Ostrya virginiana</u> under 12 inches	2.0%	<u>Athyrium felix-femina</u> <u>A. thelypteroides</u>	0.4%
<u>Prunus serotina</u> under 12 inches	11.7%	<u>Botrychium virginianum</u>	1.2%	<u>Botrychium</u> sp.	0.4%
<u>Acer rubrum</u> under 12 inches over 12 inches	10.1% 0.4%	<u>Polygonatum pubescens</u> <u>Actaea pachypoda</u>	1.2%	<u>Carex plantaginea</u> <u>Carya cordiformis</u> under 12 inches	0.4%
<u>Fraxinus americana</u> under 12 inches	6.5%	<u>Carex</u> sp.	0.8%	<u>Dicentra</u> sp.	0.4%
<u>Viola</u> sp.	4.0%	<u>Caulophyllum thalictroides</u>	0.8%	<u>Epipactis helleborine</u>	0.4%
<u>V. incoqnita</u>	3.2%	<u>Circaea quadrifida</u>	0.8%	<u>Hepatica acutiloba</u>	0.4%
<u>Arisaema triphyllum</u>	2.4%	<u>Cornus alternifolia</u>	0.8%	<u>Hieracium</u> sp.	0.4%
<u>Geranium robertianum</u>	2.4%	<u>Epifagus virginiana</u>	0.8%	<u>Maianthemum canadense</u>	0.4%
<u>Ulmus americana</u> under 12 inches	2.4%	<u>Impatiens</u> sp.	0.8%	<u>Mitella diphylla</u>	0.4%
<u>Dentaria diphylla</u>	2.0%	<u>Lycopodium complanatum</u> var. <u>flabelliforme</u>	0.8%	<u>Osmorhiza claytoni</u>	0.4%
<u>Dryopteris spinulosa</u> var. <u>intermedia</u>	2.0%	<u>Mitchella repens</u>	0.8%	<u>Oxalis acetosella</u>	0.4%
<u>Fagus grandifolia</u> under 12 inches over 12 inches	2.0% 0.4%	<u>Ribes</u> sp.	0.8%	<u>Phlox divaricata</u>	0.4%
<u>Tilia americana</u> under 12 inches	2.0%	<u>Tiarella cordifolia</u> <u>Viola canadensis</u> <u>V. rotundifolia</u>	0.8%	<u>Podophyllum peltatum</u>	0.4%
				<u>Polystichum acrostichoides</u>	0.4%
				<u>Tsuga canadensis</u> over 12 inches	0.4%
				<u>Veronica officinalis</u>	0.4%

<sup>1</sup> County of Erie.

TABLE 11  
FOREST STAND DATA: TREES AND SAPLINGS ZOAR VALLEY PROPERTY #12,<sup>1</sup>  
ERIE COUNTY, NEW YORK

SPECIES AND SIZE CLASS	RELATIVE FREQUENCY	RELATIVE DENSITY	RELATIVE DOMINANCE	IMPORTANCE VALUE	ABSOLUTE DENSITY/ACRE	ABSOLUTE DOMINANCE/ACRE
<u>Acer saccharum</u> Trees Saplings	48.0% 20.5%	68.2% 22.2%	52.9% 27.4%	169.1 70.1	78.9 33.6	13,789.4 131.7
<u>Fagus grandifolia</u> Trees Saplings	26.0% 43.2%	16.2% 51.4%	35.7% 31.1%	77.9 125.7	18.7 77.7	9,313.7 149.2
<u>Tsuga canadensis</u> Trees Saplings	16.0% 29.5%	10.4% 22.2%	2.7% 35.9%	29.1 87.6	12.0 33.6	692.3 172.3
<u>Tilia americana</u> Trees	4.0%	2.1%	3.2%	9.3	2.4	838.5
<u>Fraxinus americana</u> Trees	3.0%	1.6%	2.6%	7.2	1.9	699.5
<u>Betula alleghaniensis</u> Trees	1.0%	0.5%	0.1%	1.6	0.6	38.2
<u>Ostrya virginiana</u> Saplings	4.5%	2.8%	5.3%	12.6	4.2	25.3
<u>Carpinus caroliniana</u> Saplings	2.3%	1.4%	0.3%	4.0	2.1	1.6

<sup>1</sup>State of New York, Conservation Dept., Division of Lands and Forests, Multiple Use Land, Acquisition # Catt. 8.3.9.

TABLE 12

FOREST STAND DATA: HERBS AND SEEDLINGS ZOAR VALLEY PROPERTY #12,<sup>1</sup>

ERIE COUNTY, NEW YORK

SPECIES AND SIZE CLASS	RELATIVE FREQUENCY	SPECIES AND SIZE CLASS	RELATIVE FREQUENCY	SPECIES AND SIZE CLASS	RELATIVE FREQUENCY
<u>Acer saccharum</u> under 12 inches over 12 inches	13.4% 12.4%	<u>Carva cordiformis</u> under 12 inches over 12 inches	0.7% 0.4%	<u>Adiantum pedatum</u>	0.4%
<u>Arisaema triphyllum</u>	10.2%	<u>Dennstaedtia punctiloba</u>	1.1%	<u>Aster divaricatus</u>	0.4%
<u>Fraxinus americana</u> under 12 inches over 12 inches	9.2% 2.1%	<u>Galium</u> sp.	1.1%	<u>A. lateriflorus</u>	0.4%
<u>Fagus grandifolia</u> under 12 inches over 12 inches	2.5% 6.0%	<u>Geranium robertianum</u>	1.1%	<u>Athyrium felix-femina</u>	0.4%
<u>Viola incoqnita</u>	4.9%	<u>Prunus serotina</u> under 12 inches over 12 inches	0.4% 0.7%	<u>Carex plantaginea</u>	0.4%
<u>Dryopteris spinulosa</u> var. <u>intermedia</u>	3.9%	<u>Botrychium virginianum</u>	0.7%	<u>C. sp.</u>	0.4%
<u>Caulophyllum thalictroides</u>	2.8%	<u>Cornus alternifolia</u>	0.7%	<u>Circaea alpina</u>	0.4%
<u>Hepatica acutiloba</u>	2.8%	<u>Epipactis helleborine</u>	0.7%	<u>Eupatorium rugosum</u>	0.4%
<u>Viola rotundifolia</u>	2.5%	<u>Monotropa uniflora</u>	0.7%	<u>Impatiens</u> sp.	0.4%
<u>V. pensylvanica</u>	2.5%	<u>Osmorhiza claytoni</u>	0.7%	<u>Lycopodium lucidulum</u>	0.4%
<u>V. canadensis</u>	2.1%	<u>Tilia americana</u> under 12 inches	0.7%	<u>Potentilla</u> sp.	0.4%
<u>Circaea quadrisulcata</u>	1.4%	<u>Ulmus americana</u> under 12 inches	0.7%	<u>Ribes</u> sp.	0.4%
<u>Maianthemum canadense</u>	1.4%	<u>Viola</u> sp.	0.7%	<u>Sambucus canadensis</u>	0.4%
<u>Actaea pachypoda</u>	1.1%	<u>Acer rubrum</u> under 12 inches	0.4%	<u>Tiarella cordifolia</u>	0.4%
<u>Athyrium thelypteroides</u>	1.1%	<u>Actaea</u> sp.	0.4%	<u>Trillium erectum</u>	0.4%
				<u>T. sp.</u>	0.4%
				<u>Urtica procera</u>	0.4%

<sup>1</sup> State of New York, Conservation Dept., Division of Lands and Forests, Multiple Use Land, Acquisition # Catt. 8.3.9.

I sampled, Betula alleghaniensis has uniformly low importance values. Since this species reproduces best at moist sites (Hough and Forbes, 1943), the three stands may not be edaphically suited to greater domination by yellow birch.

In the Erie County Forestry Department Plantation #11 Prunus serotina had a relatively high importance value in the tree class, but the sample included no saplings. However, seedlings, mostly plants with cotyledons still attached, ranked second in frequency in the meter-square quadrats. These data accord well with the behavior of black cherry as it is known in the forests of northwestern Pennsylvania (ibid.). Although black cherry seedling mortality is high in this region, a few always survive growing slowly in moderate shade, and if logging, fires or windthrow exposes them to full sunlight, they are able to outgrow all important competitors. Several well-rotted stumps in Plantation #11 are evidence that selective cutting, perhaps as long ago as the turn of the century, may have been the factor which opened the stand enough to allow the establishment of Prunus serotina in the canopy.

Tilia americana occurs as the fourth and fifth most important tree in two of the stands, but it was not encountered while sampling the third. Judging by early land survey notes (Lutz, 1930a) and data published by Braun (1951), Gordon (1940) and Hough (1936a), Tilia americana is a fairly consistent member of forests in various successional

stages across the northern Allegheny Plateau. It is also a member of the mature forests along the East Tionesta Creek. Fraxinus americana occurs in all three sampled stands, but as a tree it has slightly lower importance values than Tilia. In the undisturbed virgin forests of northwestern Pennsylvania Fraxinus americana reproduction and saplings are fairly abundant and, as a species, it persists in these forests as successfully as Betula alleghaniensis but more successfully than Prunus serotina (Hough and Forbes, 1943).

Of the 16 herbaceous taxa listed by Nichols (1935) as characteristic of the Hemlock-white pine-northern hardwoods Forest region, only four appeared within quadrats in all three sampled stands: Dryopteris spinulosa var. intermedia, Viola canadensis, V. incoqnita and V. rotundifolia. Other species such as Actaea pachypoda, Lycopodium lucidulum, Maianthemum canadense, Mitchella repens, Oxalis acetosella, Trillium erectum and T. grandiflorum which he also considered characteristic were present in only one or two of the stands, but eight additional species mentioned were not encountered at all in my quadrats. A total of 49 species were recorded in all the samples, although many other species were noted outside the quadrats. It is interesting that in all three stands at the time of sampling Arisaema triphyllum and Viola incoqnita had the highest relative frequency values of the herbaceous plants identified to species.

### R values

One of the basic assumptions in the use of pollen analysis to investigate vegetation change is that a relationship exists between the number of pollen grains of a given type recovered from a sediment sample and the abundance of the species producing this pollen in the vegetation surrounding the site at the time of deposition. Studies which have related current pollen rain to contemporary vegetation within a given region, however, have demonstrated that the relationship is often not proportional (Curtis, 1959; Davis and Goodlett, 1960; Janssen, 1967; McAndrews, 1966). Although some pollen types in surface samples apparently are represented in relation to the abundance of the parent plants, others are either over-represented or under-represented. The causes of disproportionate representation are many, but the most important seem to include the great variability in pollen production by different species, the type of pollination and ease with which pollen dispersal takes place in wind pollinated species and the differential susceptibility of pollen to degradation by chemical and biological agents, once deposition has taken place.

When interpreting fossil pollen assemblages, one way to compensate for problems of disproportional representation is to apply numerical correction factors based on the relationship between the percentage of pollen grains of a certain type in a sample and a quantitative abundance measure



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of the one or more species producing that type in the vegetation. Pollen percentages are of course available throughout a sediment column, but there is no known method of determining forest composition in any other than two levels: (1) the surface, where the composition of the vegetation contributing to the surface pollen rain can be directly sampled or derived from published studies, and (2) the spectrum immediately below the pre- to post-settlement boundary where the original lot survey records, which include quantitative data amenable to ecological analysis, can be used to estimate composition. The ratio between the pollen percentages of a given species and its vegetational percentage provides the correction factor, or R value (Davis, 1963), which when divided into the number of pollen grains of that species, as they are tallied by spectra along the sediment column, adjusts the counts to conform more closely to the presumed abundance of the species in the vegetation. Pollen types with R values  $< 1$  are under-represented in sediments, those with values  $> 1$  are over-represented and those with values about 1 are proportionately represented.

I have calculated R values for nearly all of the tree pollen types which occurred in the sediments I studied from southwestern New York State. At the present time, the pollen of different species of Betula, Carya, Quercus and Ulmus apparently cannot be identified except, in some cases, by time consuming size-frequency measurements. Therefore,

only generic level R values can be obtained for these taxa. However, because other pollen types can be identified to the species level, R values for these apply to units which are of greater usefulness in ecological interpretation. The other portion of the ratio, the abundance of given components of the vegetation, has been estimated in three ways, but all of these involve certain limitations including the absence of data corresponding to a number of pollen types recognized in the spectra and the accuracy of the sampling technique used to provide the information on vegetation composition.

#### U.S. Forest Service Survey Statistics

The Northeastern Forest Experiment Station (1967) has published the most recent source of quantitative data on the present vegetation of southwestern New York State. This information was collected during a resurvey of the forest resources of the state that was undertaken to obtain an estimate of the total timber volume, total periodic tree growth and other statistics of use principally to foresters and economic planners and to update the initial survey of the state completed in 1952 (Armstrong and Bjorkbom, 1956). The sampling design used in both surveys is fully described by Bickford et al. (1953). The initial survey involved the use of aerial photographs on which a large number of points were randomly selected for photo-interpretation. Each point was assigned to a class based on the volume of timber occurring

on a one acre plot surrounding it, and subsequently a certain number of the plots from each of the classes was measured on the ground. The resurvey used the same sampling technique, but in addition some plots from the initial survey were re-measured and new ground plots were established.

The most meaningful figures in the resurvey data for use in calculation of R values are those of total volume by species on commercial forest land. To facilitate this computation, raw data listing commercial timber species five inches in diameter and upwards in millions of cubic feet have been recalculated in percentages. The percent total volume figures for species recognized in the survey are listed by county in Table 13. The figure which pertains to a given species within the county where the bog was located was used in the R value calculation.

The surface samples analyzed were collected at the exact sites where the sediment sampling was done. In each case the sample taken was from a fairly dense but actively growing sphagnum polster and comprised the upper 1 to 2 cm from an area of about 10 sq cm. Two subsamples from each were macerated in the laboratory and their residues were ultimately combined and counted together. Inasmuch as about 50 percent of the total pollen in the surface spectra was contributed by herbaceous plants, reflecting the large area of nonforest land in southwestern New York State (see Table 4), the counts were recalculated using the sum of the arboreal

TABLE 13  
PERCENT TOTAL VOLUME OF TREES<sup>1</sup> ON COMMERCIAL FOREST LAND  
IN EIGHT WESTERN COUNTIES IN NEW YORK STATE<sup>2</sup>

COUNTY TREE SPECIES	CHAUTAUQUA	CATTARAUGUS	ALLEGANY	ERIE	WYOMING	NIAGARA	GENESEE	ORLEANS
<u>Acer saccharum</u>	23.7	21.8	24.9	18.6	19.3	18.6	17.6	18.1
<u>Fagus grandifolia</u>	8.6	9.0	8.5	4.6	4.7	4.4	4.3	4.5
<u>Tsuga canadensis</u>	8.6	8.4	8.9	5.1	4.7	5.0	5.1	4.9
<u>Betula alleghaniensis</u>	1.0	1.2	1.0	1.8	1.7	1.7	1.8	1.4
<u>B. lenta</u>	1.1	1.3	1.0	0.5	0.4	0.6	0.4	0.3
<u>Fraxinus americana</u>	6.5	6.0	5.7	8.9	9.0	9.2	9.4	9.4
<u>Tilia americana</u>	3.8	4.0	3.6	8.0	8.3	8.6	7.8	7.6
<u>Prunus serotina</u>	3.4	3.6	3.3	3.9	3.8	3.9	3.9	4.2
<u>Ulmus sp. or spp.</u>	2.7	3.0	2.8	9.4	8.5	8.6	10.8	9.0
<u>Acer rubrum</u>	13.2	12.9	13.5	14.7	14.3	14.2	14.9	13.9
<u>Quercus spp.</u>	15.0	15.0	14.6	5.9	5.6	6.4	5.5	6.6
<u>Carya spp.</u>	2.1	2.4	2.0	5.6	5.7	5.6	5.3	5.9
<u>Pinus strobus</u>	2.0	2.1	1.9	4.0	4.4	4.2	3.5	4.9
<u>P. resinosa</u>	3.7	3.6	3.5	2.1	3.2	2.5	1.8	2.8
<u>Populus sp. or spp.</u>	3.1	3.9	3.3	2.7	2.3	2.8	3.3	3.1
Misc. <sup>3</sup>	1.6	1.8	1.5	4.4	4.0	3.9	4.7	3.5

<sup>1</sup>Commercial tree species 5 inches in diameter or greater.

<sup>2</sup>Data from, Table 11 in "Preliminary forest survey statistics by counties and units, New York--1967," Northeastern Forest Experiment Station, U.S. Forest Service, Upper Darby, Pennsylvania.

<sup>3</sup>Includes other hardwoods and softwoods.

pollen as the percentage base. This is necessary because the forest composition percentages are based on total forest land, not on land of all classes. R values calculated from these two sets of data are listed in Table 16.

#### Original Lot Survey Data

The original land survey of western New York was privately sponsored, but was similar in organization to the rectangular pattern used in the General Land Office Survey of public lands west of the Appalachian Mountains. This system of surveying was authorized by Congress in 1785, but prior to this time metes and bounds, the establishment of property boundaries according to natural features, was the rule (Bourdo, 1956). In the rectangular survey of western New York a grid of north-south range and east-west township lines bounding townships generally six miles square was surveyed west of a line extending north from central Allegany County through eastern Wyoming, Genesee and Orleans Counties, the area encompassed by the Holland Purchase (Evans, 1924; Turner, 1850). The number of townships per range varied from sixteen in the eastern ranges to three in far western Chautauqua County between Lake Erie and the Pennsylvania border. These townships have only partly retained their identity as political units in contrast to those in the region surveyed by the rectangular method to the west.

The laying out of township and range lines began under the direction of Joseph Ellicott in the spring of 1798, shortly after the Holland Land Company acquired clear title to western New York, and continued until 1800. The internal survey of townships into lots was largely completed by 1810 but a few of the townships in southern Cattaraugus County were not divided until 1819. The first 24 townships surveyed were subdivided into sixteen sections 120 chains (1.5 mi) square, and each section was then partitioned into twelve 60 chain (0.75 mi) by 20 chain (0.25 mi) lots containing 120 acres each. The remaining townships were divided into lots of 360 acres, 60 chains square. These in turn were often subdivided into three parts of 120 acres each depending on the requirements of the prospective buyer.

It was the custom in the Ellicott survey to mark each lot corner with a post. Records were kept of the direction, diameter and species of from one to four bearing-trees located in different quarters surrounding the post. Since land sale was of paramount concern to Ellicott, he directed his surveyors to take careful notes on the topography, soils, timber, windfalls, springs and other natural features along the survey lines. When running a lot line the surveyors made a list of the predominant timber encountered and, if the forest composition varied along a lot line, several lists were recorded. It is perhaps logical to assume that the species listed were arranged in order of decreasing abundance,

as they were in the General Land Office Surveys, but no evidence exists that this was the case.

The richness of the data included in the Ellicott survey is illustrated by the notes<sup>1</sup> pertaining to lot 60, T.9 R.5 (southeastern Erie County). The boundary line of this lot begins at a beech post marking the northeast corner and passes westward across an upland of the first quality timbered with beech (Fagus grandifolia), hemlock (Tsuga canadensis), bass (Tilia americana) and elm (Ulmus sp.), to an upland of the second quality, then across a deep gully and abruptly back again to an upland of the first quality with hemlock, beech and sugar maple (Acer saccharum) timber, and finally to a beech post at the northwest lot corner. Southward from this point the line passes through land considered excellent for meadow and timbered with sugar maple, cherry (Prunus serotina), bass and elm, to a sugar maple post at the southwest corner of the lot. A short distance to the east of the post the line crosses an interval of the first quality timbered with buttonwood (Platanus occidentalis), elm, white ash (Fraxinus americana) and bass, crosses a stream and rises onto an upland of the first quality. It then crosses two adjacent streams separated by land with

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<sup>1</sup>The following information was extracted from field books kept at the Erie County Clerk's Office, County Hall, Eagle and Franklin Streets, Buffalo, New York. Certain phrases closely follow the original wording of the surveyor.



hemlock and beech timber, from where it crosses through a sugar maple stand on an upland of the second quality with yellow loam soil to a beech post at the southeast corner of the lot. Northward, returning to the point of origin, the line crosses land broken with deep gullies and covered by hemlock, beech and sugar maple timber. The surveyor listed seven bearing-trees, two at each of three posts and one at the fourth. One of these was a hemlock 8 inches in diameter, while the remaining six were beeches, 6, 7, 8, 12, 24 and 30 inches in diameter.

I have examined the lot survey notes for the region around those palynologically studied sites where the pollen diagrams evidenced the pre- to post-settlement boundary, permitting the pre-settlement pollen rain to be determined. The notes for Houghton and Protection bog areas in Erie County<sup>1</sup> are contained in small leather-covered notebooks which are authenticated copies of the originals, while the notes pertaining to the Allenberg bog area in Cattaraugus County<sup>2</sup> were copied many years ago into folio-sized record books. For this county plat maps are also available on which the bearing-trees are noted at the lot corners.

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<sup>1</sup>Kept by the Erie County Clerk, Buffalo, New York; both of these areas were surveyed by Cotton Fletcher in 1807-1808.

<sup>2</sup>Kept by the Cattaraugus County Clerk, County Buildings, 303 Court Street, Little Valley, New York; surveyor or surveyors unknown.

Gordon (1940) utilized these data during the preparation of his map of the original vegetation of Cattaraugus County.

Estimates vary as to the area which contributes to the pollen rain accumulating at a given point. Faegri and Iversen (1964) consider that in forested regions pollen is not transported in significant quantities for more than 50 km (ca. 30 mi) which, assuming that pollen is contributed for equal distances in all directions, results in a source area of about 8000 sq km (2800 sq mi). An investigation of the survey notes for an area as large as this in western New York was not attempted, but a map of the lots surrounding each of the three bogs was drawn on graph paper and bearing trees and other information pertaining to the vegetation were noted at the appropriate places along the lot lines.

An area seven lots by seven lots (ca. 30 sq mi) was studied around Allenberg and Houghton bogs, but because the notes for western Wyoming County could not be located, the area of study around Protection bog had to be restricted to a tract of 16 sq mi, seven lots (north to south) by four lots (east to west). Although these areas are considerably smaller than the source area recognized by Faegri and Iversen, examination of additional data beyond the included lots suggests that the basic data would not be altered greatly by enlarging the areas investigated, except that more species of infrequent mention would appear.

The data collected were analyzed in two ways. Since the bearing-trees recorded by the surveyors represent a low density sample of the forest within each of the three areas, the relative frequency, relative density and relative dominance of each of the species noted can be calculated following the methods used in treating the forest stands discussed earlier. The sum of these three measures or the Importance Value for all the species within one area totals 300, but for purposes of R value computations, the percent total for each of the species, or an importance percentage (McAndrews, 1966), was calculated. The trees mentioned along the lot lines were treated in a different manner. For each area the total number of times a given species was mentioned was tallied and this sum was rendered as a percentage of the total trees of all kinds mentioned throughout the area.

Pollen percentages used as the numerators in the R value ratio were provided by the first spectrum immediately below the pre-settlement to post-settlement boundary which is clearly marked by a sharp increase in the pollen of Ambrosia, Plantago and other species associated with forest clearance. The percentage base used in this calculation included both arboreal and nonarboreal pollen types because the latter were only sparsely represented and did not measureably reduce percentages of tree pollen types.

In all three areas Fagus grandifolia accounts for 50-75 percent of the sum of bearing-tree importance values (see Table 14). Acer saccharum is consistently second in importance and, while Tsuga canadensis and Betula alleghaniensis rank third and fourth in the Houghton and Protection bog areas, they rank sixth and fifth respectively around Allenberg bog. About the same arrangement of species occurs in Table 15 where the frequency of mention values are listed in decreasing order. Fagus grandifolia is the most frequently mentioned tree, followed by Acer saccharum. Tsuga canadensis shares the third position with Tilia americana around Allenberg bog; it ranks fourth around Houghton bog, preceded by Tilia americana, and third around Protection bog where Tilia americana directly follows it in importance. With a few exceptions, the three species with the highest bearing-tree importance and frequency of mention values in the survey data are also the three leading species in the data derived from the stands studied by the point quarter method except that in the latter Acer saccharum and Fagus grandifolia have exchanged rank.

Both of the estimates of pre-settlement forest composition may be somewhat biased samples. Fagus grandifolia was by far the commonest bearing-tree, but whether beech was indeed the dominant tree in the forest around the bogs might be questioned. Presumably, the surveyors selected trees which were closest to the lot corner irrespective of species,

TABLE 14

PRE-SETTLEMENT SURVEY DATA: RELATIVE FREQUENCY, RELATIVE DENSITY, RELATIVE DOMINANCE, IMPORTANCE VALUES AND IMPORTANCE PERCENTAGES OF BEARING-TREES

USED IN THE ORIGINAL LOT SURVEY OF THE AREAS AROUND ALLENBERG,

HOUGHTON AND PROTECTION BOGS

TREE SPECIES AND BOG AREA	RELATIVE FREQUENCY	RELATIVE DENSITY	RELATIVE DOMINANCE	IMPORTANCE VALUE	IMPORTANCE PERCENTAGE
<u>Fagus grandifolia</u>					
Alленberg Bog area	70.1%	86.5%	84.1%	240.7	80.2
Houghton Bog area	65.2%	74.7%	71.4%	211.3	70.4
Protection Bog area	53.8%	62.3%	47.9%	164.0	54.7
<u>Acer saccharum</u>					
Alленberg Bog area	17.2%	8.7%	8.1%	34.0	11.3
Houghton Bog area	16.7%	12.1%	11.8%	40.6	13.5
Protection Bog area	26.2%	21.7%	22.2%	70.1	23.4
<u>Tsuga canadensis</u>					
Alленberg Bog area	1.2%	0.4%	1.4%	3.0	1.0
Houghton Bog area	7.6%	5.1%	9.8%	22.5	7.5
Protection Bog area	7.7%	6.6%	14.9%	29.2	9.7
<u>Betula alleghaniensis</u>					
Alленberg Bog area	2.3%	0.9%	2.3%	5.5	1.8
Houghton Bog area	3.0%	2.0%	2.1%	7.1	2.4
Protection Bog area	4.6%	2.8%	5.2%	12.6	4.2
<u>Prunus serotina</u>					
Alленberg Bog area	2.3%	0.9%	3.2%	6.4	2.1
Houghton Bog area	3.0%	3.0%	1.1%	7.1	2.4
Protection Bog area	----	----	----	---	---
<u>Acer rubrum</u>					
Alленberg Bog area	----	----	----	---	---
Houghton Bog area	----	----	----	---	---
Protection Bog area	3.1%	2.8%	5.8%	11.7	3.9
<u>Ulmus sp.</u>					
Alленberg Bog area	----	----	----	---	---
Houghton Bog area	3.0%	2.0%	2.1%	7.1	2.4
Protection Bog area	1.5%	0.9%	1.0%	3.4	1.1
<u>Carpinus/Ostrya</u>					
Alленberg Bog area	4.6%	1.7%	0.4%	6.7	2.2
Houghton Bog area	----	----	----	---	---
Protection Bog area	1.5%	0.9%	0.2%	2.6	0.9
<u>Fraxinus americana</u>					
Alленberg Bog area	1.2%	0.4%	0.4%	2.0	0.7
Houghton Bog area	----	----	----	---	---
Protection Bog area	1.5%	1.9%	2.9%	6.3	2.1
<u>Pinus strobus</u>					
Alленberg Bog area	----	----	----	---	---
Houghton Bog area	1.5%	1.0%	1.7%	4.2	1.4
Protection Bog area	----	----	----	---	---
<u>Juglans cinerea</u>					
Alленberg Bog area	1.2%	0.4%	0.1%	1.7	0.3
Houghton Bog area	----	----	----	---	---
Protection Bog area	----	----	----	---	---

TABLE 15

PRE-SETTLEMENT SURVEY DATA: FREQUENCY OF MENTION  
 OF TREE SPECIES ALONG LOT SURVEY LINES FOR  
 AREAS AROUND ALLENBERG,<sup>1</sup> HOUGHTON,<sup>2</sup>  
 AND PROTECTION<sup>3</sup> BOGS

TREE SPECIES	ALLENBERG BOG AREA	HOUGHTON BOG AREA	PROTECTION BOG AREA
<u>Fagus grandifolia</u>	30.6%	30.0%	28.2%
<u>Acer saccharum</u>	22.1%	24.3%	17.3%
<u>Tsuga canadensis</u>	14.6%	11.1%	19.7%
<u>Tilia americana</u>	14.6%	13.0%	14.6%
<u>Ulmus</u> sp.	5.1%	6.2%	3.2%
<u>Betula</u> sp.	1.6%	3.2%	5.1%
<u>Fraxinus americana</u>	1.4%	5.4%	2.9%
<u>F. nigra</u>	1.0%	2.5%	3.9%
<u>Acer rubrum</u>	0.4%	0.5%	3.2%
<u>Magnolia acuminata</u>	1.8%	0.2%	0.7%
<u>Prunus serotina</u>	0.2%	2.1%	0.2%
<u>Alnus</u> sp.	1.4%	0.8%	0.2%
<u>Castanea dentata</u>	2.4%	----	----
<u>Quercus rubra</u> and/or <u>velutina</u>	1.0%	----	----
<u>Juglans cinerea</u>	----	0.3%	0.5%
<u>Pinus strobus</u>	0.2%	0.3%	0.2%
<u>Picea mariana</u>	0.4%	0.2%	----
<u>Abies balsamea</u>	0.4%	----	----
<u>Larix laricina</u>	0.4%	----	----
<u>Quercus alba</u>	0.2%	----	----

<sup>1</sup>Area equal to 17,640 acres.

<sup>2</sup>Area equal to 17,640 acres.

<sup>3</sup>Area equal to 10,080 acres.

but because beech has a light colored, easily marked bark and is of lesser value as a timber tree, they may have chosen it as a bearing-tree over other species. Gordon (1940), however, noting the preponderance of beech bearing-trees throughout Cattaraugus County, has concluded that in spite of possible bias, beech was probably the most common tree in the original forest, a conclusion which is substantiated by the high percentage of beech pollen in pre-settlement spectra.

Tilia americana was not used at all as a bearing-tree, although it had a fairly high rank in the frequency of mention data. This discrepancy perhaps can be explained because Tilia is not a long-lived, rot resistant tree and is therefore not entirely suitable for use as a bearing-tree. Its high position in the frequency of mention data may be in part a reflection of its value as an easily worked wood often employed in pioneer carpentry. It seems likely, therefore, that bias exists in both sets of data. In the frequency of mention list, those timber species of high economic value may have been stressed more than other less valuable but more common species, and, as bearing-trees, species most useful in relocating lot corners may have been disproportionately utilized.

#### Discussion

The three sets of R values from the different bog areas are compared in Table 16. Although the values for certain pollen taxa are fairly consistent, others vary widely.

TABLE 16  
R VALUES CALCULATED USING VARIOUS ESTIMATES OF VEGETATION COMPOSITION

R values Pollen taxa	Allenberg Bog			Houghton Bog			Protection Bog		
	Modern	Importance % age	Freq. of mention	Modern	Importance % age	Freq. of mention	Modern	Importance % age	Freq. of mention
<u>Pinus</u> spp.	1.04	---	56.50	1.61	7.14	33.33	5.00	---	38.00
<u>Taxus canadensis</u>	1.40	23.60	1.62	2.08	2.81	1.90	1.33	2.53	1.24
<u>Betula</u> spp.	9.92 <sup>b</sup>	8.61	9.69	10.26 <sup>b</sup>	5.67	4.25	7.43 <sup>b</sup>	2.43	2.00
<u>Fagus grandifolia</u>	0.70	0.22	0.58	1.37	0.36	0.85	1.48	0.42	0.82
<u>Quercus</u> spp.	0.97	---	12.83	1.83	---	---	1.90	---	---
<u>Acer saccharum</u>	0.55	0.46	0.24	0.67	0.52	0.28	0.42	0.34	0.49
<u>A. rubrum/</u> <u>saccharinum</u>	0.22	---	1.00	0.13	---	---	0.06	---	0.25
<u>Carya</u> spp.	0.79	---	---	0.25	---	---	0.23	---	---
<u>Ulmus</u> spp.	2.56	---	0.57	1.23	1.38	0.53	0.53	4.73	1.63
<u>Tilia americana</u>	0.03	---	0.03	0.03	---	0.02	0.01	---	0.07
<u>Fraxinus</u> <u>4-colpate</u>	0.22	0.57	0.29	0.11	---	0.15 <sup>d</sup>	0.17	1.00 <sup>d</sup>	0.48
<u>3-colpate</u>	---	---	0.70	---	---	---	---	---	0.18
<u>Populus</u> spp.	0.38	---	---	0.74	---	---	0.81	---	---
<u>Carpinus/Ostrya</u>	---	0.23	---	---	---	---	---	2.11	---
<u>Juglans cinerea</u>	---	0.67	---	---	---	1.00	---	---	---
<u>Castanea dentata</u>	---	---	0.29	---	---	---	---	---	---

<sup>a</sup> Not present in pre-settlement vegetation data; <sup>b</sup> Forest survey percentages of Betula lenta lumped with B. allenhamiensis; <sup>c</sup> lumped with Acer saccharum; <sup>d</sup> Includes Fraxinus 3-colpate; <sup>e</sup> No forest survey statistics available.



The best example of the latter group is Pinus spp. whose values range from about 1 to 5 using the modern data and from 7 to 57 using the pre-settlement data. These figures, particularly the ones derived from the pre-settlement data, emphasize pine pollen's typical over-representation. One difficulty in obtaining truly accurate R values for pine from surface sample pollen percentages, however, is that both native and exotic species now grow and contribute to the pollen rain in western New York, and thus the pollen dispersal capacity of pines of both types influences surface counts. Since only native species are represented in pre-settlement spectra, the R values obtained from such data cannot be applied indiscriminately throughout postglacial time. Another problem is that locally growing reforested pine stands may contribute more pollen to surface spectra than is typical of the region from which the vegetation composition data were derived. The R value of 5.0 at Protection bog probably reflects the influence of several nearby mature, planted Pinus resinosa and P. strobus stands. That local over-representation is indeed operative at this site is substantiated by the sharp decrease in Pinus Diploxylon and P. Haploxylon percentages in the upper 5 cm of sediments. Pollen below this depth accumulated before the plantations existed.

R values for Ulmus spp. are also variable but to a lesser degree. They range from 0.5 to about 5.0, but most

of them are over one, implying over-representation. Similarly, over-representation is indicated for Quercus spp. The R values for this pollen type calculated from the modern data suggest that the oaks are somewhat less than twice over-represented, while the only pre-settlement value implies that they are nearly thirteen times over-represented. Little emphasis should be given to this one pre-settlement value, however, because of the rather small area used to obtain the percentage of oaks in the vegetation. Since Quercus pollen seems to be transported easily for long distances, a much larger area should be sampled to gain an accurate estimation of the abundance of oak trees contributing to the pollen rain. In northern Vermont where Quercus rubra is the principal pollen producing oak, Davis and Goodlett (1960) have found oak pollen to be the most over-represented of all pollen types in their spectra.

The R values for Tsuga, with one exception, are fairly constant and imply that Tsuga pollen is somewhat over-represented. My figures compare fairly well with those calculated for hemlock in northern Vermont (ibid.) but differ from the correction factor for the species used in Wisconsin by Curtis (1959) who has multiplied numbers of hemlock pollen in fossil spectra by three to obtain proportional representation. Since R values seem to differ from one major geographic region to another (see Comanor, 1967), the use of one correction factor over a wide area may lead to incorrect results.

The R values for Betula spp., using both modern and pre-settlement data, indicate that it is greatly over-represented, a finding that is substantiated by the studies in Vermont and Wisconsin cited above. Although I cannot be certain which species of birch produced a given pollen grain, it is likely that only two species, Betula lenta and B. alleghaniensis, have contributed most of the birch pollen to the spectra because the other species reported from western New York, B. papyrifera and B. pumila, occur either at the periphery or well beyond the source area of the bogs.

According to my data only Fagus grandifolia and Juglans cinerea are about proportionately represented. To these may be added Carpinus/Ostrya if the average of the two R values in the table is taken to be meaningful. The pollen of Carpinus caroliniana and Ostrya virginiana are morphologically very similar, so no attempt was made to tally them separately. Since the autecology of the two species differs and the abundance of Carpinus in the vegetation is unknown, undue significance cannot be given to the R values for this pollen type. Davis and Goodlett (1960) found the basal area percentage of Ostrya virginiana in the forest north of Brownington Pond, northern Vermont, to be nearly equal to the percentage of its pollen in the surficial pond sediments. These authors also have found Fagus grandifolia to be + proportionately represented in this region, although the percentage of beech pollen in the surface sediment was slightly

greater than the percentage of beech in the surrounding forest.

Acer rubrum/saccharinum, A. saccharum, Carya spp., Castanea dentata, Fraxinus 4-colpate (incl. F. americana and F. pennsylvanica), F. 3-colpate (F. nigra), Populus spp. and Tilia americana are under-represented. Also in this category, although not listed in Table 16, is Prunus serotina, a species which is apparently entirely insect pollinated because its pollen was not found in any of the spectra analyzed even though black cherry did occur in the surrounding forest. The low values for Tilia and Acer species may likewise reflect the influence of insect pollen vectors.

Sangster and Dale (1964) have emphasized an additional reason for under-representation. They have demonstrated that pollen of different species vary in their resistance to degradation, implying that species of low resistance will be under-represented regardless of the amount of pollen they produce or the effectiveness of its dispersal. Working mostly with species native to eastern North America, these authors have experimentally shown Acer saccharinum and A. saccharum pollen to be less well preserved in peat than the pollen of Betula, Fraxinus, Pinus, Quercus, Ulmus species, and that Populus tremuloides pollen is the most severely degraded of all the types they investigated.

Similar results pertaining to Populus are implied in data from New York State. At the four stations in the

southwestern corner of the state where airborne pollen data have been collected (Ogden and Lewis, 1960), Populus pollen is well represented, exceeding Pinus in numbers of grains per sq cm of slide surface, and occasionally equalling such other heavy producers as Quercus and Ulmus. Similar counts do not occur in samples analyzed from bog surfaces. This may reflect both the ease and the speed with which Populus pollen is decomposed, as Sangster and Dale in an earlier study (1961) showed that 80 percent of fresh poplar pollen samples planted in the surface of a peat bog was degraded within 32 days.

The most accurate R values from the standpoint of the method used to determine vegetation composition are those calculated from the modern data. Since the three sites where the current pollen rain was measured are close enough to be considered in about the same source area as far as the regional pollen rain is concerned, the most useful way to summarize the R values is to compute the average for each of the taxa. These averages arranged in decreasing magnitude and placed in the three classes of representation are: (1) over -- Betula spp., Pinus spp., Quercus spp., Tsuga canadensis; (2) proportional -- Fagus grandifolia; and (3) under -- Populus spp., Acer saccharum, Carya spp., Fraxinus americana and/or pennsylvanica, Acer rubrum/saccharinum and Tilia americana.

Few differences occur between this list and another in which decreasing average values calculated from both modern and pre-settlement figures are arranged. Use of these averages is less justifiable, however, because different techniques were used to obtain the basic data. Nevertheless the order of the taxa remains the same as above except Betula spp. and Pinus spp. switch positions. In class 2 Carpinus/Ostrya and Juglans cinerea are added before Fagus and in class 3 Fraxinus nigra and Castanea dentata are placed between Populus spp. and Acer saccharum and between Acer rubrum/saccharinum and Tilia americana respectively.

#### Summary

New York State occupies a position intermediate between the northern coniferous boreal forest and the southern deciduous forest region. Two more or less well-defined floristic provinces occur at the west end of the state. Species confined to the warmer and drier plain south of Lake Ontario are mostly of southern affinity. Those of the cooler and wetter upland are characteristically more northern in distribution and reach their maximum abundance in the plateau but many also extend to the lowland. This difference in abundance is apparent in the plant communities which characterize the two provinces. At the best sites the typical upland community is a mixture of hemlock and northern hardwoods including beech, sugar maple and yellow birch. Although these species form similar communities in the

lowland, they are much less frequent than deciduous tree communities which contain mainly beech and sugar maple at mesic sites and oak species at drier sites. In the plateau region of southwestern New York each of three typical stands sampled on upland soil types was dominated by sugar maple, beech and hemlock in that order. No precise line can be drawn separating the deciduous forest and the coniferous-deciduous forest in western New York emphasizing the broad ecotonal nature of this region.

The pre-settlement forests, judging from studies which have used the first land survey notes, had this same basic pattern. However, due to the settlement of the region beginning about 1800, the forests have been greatly modified. The three counties along the shore of Lake Ontario are today the least forested of any area in the Northeast (Lull, 1968), and in general less than 50 percent of the land in the eight western counties is forested. Since about 1880, however, an ever increasing amount of the area originally cleared for farms has reverted to forest. Armstrong and Bjorkbom (1956) and Lull (1968) show the current forest vegetation to be composed of beech-birch-maple and white pine-hemlock-hardwoods types in the upland throughout the Allegheny Plateau but at places also extending northward to Lake Ontario. These authors also recognize oak-yellow poplar and elm-ash-maple types in the lowland adjacent to Lakes Erie and Ontario.

Superimposed on this general pattern are other forest communities whose presence reflects local favorable edaphic situations. Bog and swamp forests, mostly occupying small areas, and riverine communities occur throughout the region, but of more restricted occurrence are the oak rich forest types that occupy well-drained sites associated with sandy deposits or areas of moderate relief in the lowland and dry south and southeast hill slopes in the upland. Other deciduous tree communities called Mixed mesophytic Forests have been recognized at sites between dry hilltops and more moist lower slopes.



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## THE POLLEN DIAGRAMS

### METHODS

Most of the techniques which I have used to prepare the pollen diagrams are detailed in Faegri and Iversen (1964), but a brief review of them is presented here.

#### Field Techniques

The four basins chosen for palynological study (see Fig. 2), all appear to be ice block depressions. Protection and Houghton bogs are associated with the Valley Heads moraine and were chosen because their proximity permitted a check for parallel trends in the pollen profiles. Such trends, if found duplicated at many sites throughout a region, have greater significance in reconstructing the pattern of vegetation change than smaller, short-term changes present at only one site. The other two deposits are located south of the Valley Heads moraine on drift deposited at an earlier time. Allenberg bog is near the terminal position of the Kent moraine, while the Genesee Valley Peat Works is on a still older surface, apparently of Olean age. Thus, two of the deposits began to accumulate at approximately the same time, while the other two began at earlier times.

At each site a series of compass-oriented transects was run, along which depths and sediment lithology were determined using a Davis sampler. As three of the four sites investigated lack a central bog lake, traverses were easily made across the semi-firm bog surface. At the fourth site, however, a small lake 50 m in diameter is present, so a series of soundings was made around the mat at the edge of the open water. The goal in all cases was to find the deepest spot in the basin at which samples for pollen analysis could be collected. At two of the sites the upper sediments were too watery to be sampled with the instruments used, and a supplementary sample series was collected in the firmer sediments to one side of the main sampling point.

A set of three standard samplers was available and these were employed depending on the nature of the sediments encountered. At most sites a Hiller sampler (Borros, Solna, Sweden) with a 50 cm long chamber was used. This instrument worked best in coarse, fibrous peat of variable compactness, in finer peat deposited from water and in the stiffer lake muds or gyttjas. Lake sediment cores were also collected with a Livingstone sampler of the style described by Cushing and Wright (1965). An adapter which allowed the sturdy Livingstone rods to be coupled to a Davis head (Eberbach, Ann Arbor, Michigan) was found to be particularly effective in penetrating heavier clayey sediments, mainly because the

piston of the Davis sampler I used had a stronger catch than the piston of the Livingstone sampler.

Two of the samples for radiocarbon analysis collected at Protection bog were obtained with the Livingstone sampler, equipped with a 2-inch barrel, from a location 50 cm to one side of the point where samples were taken for pollen analysis. Subsamples 10 cm in length were removed from the cores and submitted for age determination. To check the location of these age-date samples, in reference to the pollen diagram, the sediments immediately above and below were also collected and their pollen content determined. These spectra matched well those expected on the basis of depth alone (cf Diagram 1 and Appendix A).

The uppermost date at this site was based on peat collected with a specially made piston sampler four inches in diameter built after the principle of the Livingstone sampler. The bottom 10 cm of wet peat from the core was submitted for age determination.

The Houghton bog date was obtained from wood which lodged in the Davis instrument during an exploratory probe of the area adjacent to the site where samples for pollen analysis were taken. An insufficient amount of wood was collected to permit both C-14 analysis and microscopic study, so the species was not identified.

Extreme care was taken not to contaminate the samples collected for pollen analysis. When using the Hiller sampler,

successively deeper samples 50 cm long were collected alternately from two holes 50 cm apart. The outer several mm of sediment uncovered by turning the outer sleeve to open the sediment chamber were cut away and discarded. The sediments thus exposed were removed with a micro-spatula from points midway between lines five cm apart stamped on the sampler head.

Individual samples were placed in pint polyethylene bags labelled with the appropriate data. The cores collected with the Livingstone sampler were extruded in the field, wrapped in aluminum foil, labelled and placed in plywood core boxes. Cores taken with the Davis sampler were also wrapped in foil and labelled in the field. Subdivision of the cores was done in the laboratory. All samplers were washed with clean water after each use. The sediment samples were refrigerated until macerated in the laboratory.

#### Laboratory Techniques

The standard methods for separating and concentrating pollen from sediments by removing inorganic and unwanted organic material were used in the preparation of the samples. A 1 cc subsample, measured with a graduated cylinder cut down to hold  $1 \pm 0.05$  ml of water, was macerated in each case. The schedule employed during the maceration procedure depended on the type of sediment being analyzed.

Two main types of organic sediments were encountered. The pollen in peat was concentrated by following the successive steps detailed below:

- (1) place sample in 40 ml tapered centrifuge tube, cover with 10 percent KOH and heat for 5 min in boiling water bath;
- (2) wash sample through #60 mesh seive (250  $\mu$ ) with enough distilled water to stop the KOH reaction; use seive residue for identification of plants making up the peat;
- (3) centrifuge and decant;
- (4) glacial HAc wash, acetolysis solution (Erdtman, 1960) in boiling water bath for 3 min and glacial HAc wash.

Since gyttja, the other principal organic sediment found, generally does not deflocculate in KOH, a partial breakdown of this sediment was accomplished using cold 10 percent HCl. The sediment was gently teased apart with a glass rod. After centrifuging and then pouring off the HCl, the sample was acetolyzed and, if deflocculation had not completely taken place, the sample was heated for 5 min in 10 percent KOH in a boiling water bath. The KOH was removed from the residue by centrifugation and distilled water washes.

Inorganic sediments containing calcium carbonate were treated first with 10 percent HCl, then acetolyzed and, if necessary, finally treated with 10 percent KOH. If the samples contained silts and clays, these were generally treated with cold, 72 percent HF for 24 hours culminated by an additional 30 min in a boiling water bath. After centrifuging and decanting the HF, 10 percent HCl was added to the residue and the mixture heated in a boiling water bath for

3 min to remove colloidal silicon dioxide and silico-fluorides. The acids were then thoroughly washed from the residue with distilled water. Acetolysis, and in some cases a 10 percent KOH treatment, completed the maceration. If heavy minerals such as pyrite were present in the sample, heavy liquid separation using zinc chloride (sp. gr. 1.93) immediately followed the HF treatment.

After maceration, all residues were treated in the same manner. They were thoroughly washed in distilled water, put through successive washes in 96 and 100 percent ethyl alcohol, stained with 2-4 drops of safranin-O in 100 percent ethyl alcohol, given a final 100 percent ethyl alcohol wash and then pipetted into labelled 3 dr vials. The staining was best if the residues were soaked for 24 hours in distilled water previous to alcohol dehydration. Residues were stored in vials at room temperature until mounted for counting.

The technique used in mounting residues for microscopic study was devised to enable the calculation of the number of pollen grains per unit volume of sediment and is an adaptation of the method described by Davis (1965a, 1966). The residue was washed into a 12 ml graduated centrifuge tube with tertiary butyl alcohol (TBA) and brought to a known volume. After thoroughly mixing the residue and the TBA by vigorous pumping with a large bulb pipette, a certain volume of the mixture was removed from the tube with the

pipette and from 3 to 15 drops were released onto a small amount of silicone oil (2000 cs) placed at the center of a slide on a slide warming table (ca. 75°C). The heat from the warming table rapidly evaporated the TBA leaving a mixture of silicone oil and residue.

To produce an even distribution of pollen grains under the cover slip, a clean dissecting needle was used to further blend the pollen and the silicone oil. The silicone oil-residue mixture clinging to the needle was wiped off on the underside of the cover slip which was promptly placed downward over the preparation. After making three slides from each of the residues, TBA was removed from what remained of the residue by a 100 percent ethyl alcohol wash. After centrifuging, the residue-ethyl alcohol mixture was pipetted back into the appropriate vials. Because of the noxious character of vaporized TBA, it is necessary to carry out these procedures in a fume hood. The volume of TBA-residue mixture in the graduated centrifuge tube and the number of drops of this used to make each slide were recorded.

Since the same pipette was used to mount every residue, the volume of one drop delivered by this pipette was presumably constant for all preparations. It was found, after 20 trials, that the pipette delivered 48.95 drops per ml. When counting, the number of traverses completed across a cover slip was recorded. Since in most cases the basic



sum was reached before the entire area was examined, the following equation was used to determine the total number of pollen and spores under the cover slip: number of traverses / total number of possible traverses = sum of terrestrial pollen and spores / x, where x is the number of grains per slide or per y drops of residue-TBA mixture. Multiplying x by a factor, z ml of residue-TBA mixture in the centrifuge tube  $\cdot 48.95 / y$  drops delivered to the slide, gives the number of grains per cc of wet sediment.

Although many potential sources of error are present in this technique, it is considered to give reasonably reliable results for the amount of time expended. To test the accuracy of the mounting technique, I determined the number of arboreal pollen grains for an equal number of traverses in each of two or three slides prepared from the same residue. These data, listed in Table 17, show that the method delivers similar numbers of pollen grains to individual slides in a series.

One of the most serious causes of error during counting occurs when the residue is concentrated under some sector of the cover slip. If, for example, the counts were made only in a zone of high concentration, fewer traverses would be necessary to reach a given sum than if the residue were evenly dispersed under the whole cover slip area, and thus, the calculated estimate of the number of grains per unit volume would be greater than was actually true. Visual

TABLE 17.

DATA FOR CHECK ON MOUNTING TECHNIQUE USED IN  
THE DETERMINATION OF ABSOLUTE  
POLLEN FREQUENCY

SAMPLE NUMBER	NUMBER AP	NUMBER OF TRAVERSES <sup>1</sup>
Pb 7020-1	262	22
Pb 7020-2	236	22
Pb 7156-1	116	44
Pb 7156-2	117	44
Pb 7156-3	122	44
Pb 7157-1	264	44
Pb 7157-2	261	44
Pb 7180-1	266	22
Pb 7180-2	272	22
Pb 7906-1	159	44
Pb 7906-2	156	44
Pb 7906-3	160	44
Pb 7907-1	188	44
Pb 7907-2	185	44
Pb 7907-3	207	44

<sup>1</sup>Using a magnification of 250 diameters 44 traverses are generally possible with little or no overlap across a 22 sq cover slip.

inspection and adjustment in the location of the traverses was used to overcome this potential source of error, and in many cases parts of several slides were also counted to obtain a representative sample of the residue.

Counts were uniformly made using equispaced traverses controlled by a mechanical stage. The distance between the traverses was initially chosen with reference to the density of the pollen under the cover slip. The lower the density, the closer together were the traverses. Counting was done routinely at a magnification of 250 diameters using a Leitz Ortholux microscope. Grains difficult to identify were examined using a 95 x oil immersion lens. As an aid to the identification of the pollen encountered in the preparations, a large collection of reference slides was assembled, and the standard pollen identification manuals were also frequently used (Erdtman, 1943, 1957, 1965, 1966; Faegri and Iversen, 1964; Wodehouse, 1935).

At least 500 pollen grains of trees were counted in nearly all samples. The percentage base used to calculate the relative pollen frequencies at a given level was the sum of arboreal pollen (AP) and nonarboreal pollen (NAP) at that level, as this figure best represents the regional upland pollen rain (Wright and Patten, 1963). The percentage base varied from spectrum to spectrum with the greatest differences occurring in the uppermost post-settlement and in the basal inorganic sediments where NPA is abundant. Relative

frequencies of other pollen taxa including mostly bog plants, aquatics and pteridophytes--everything to the right of the sums column in the pollen diagrams--were calculated using the sum of the first percentage base and the total number of pollen and spores of the miscellaneous taxa at a given level as a new percentage base.

Pollen grains and spores which were well-preserved but which could not be identified due to inadequacies in the pollen reference collection were classified as unfamiliar. Grains in the unknown category were in part corroded or broken, in part obscured by debris and in other ways rendered undeterminable.

#### SITES ASSOCIATED WITH THE VALLEY HEADS MORRAINE

##### Protection Bog

This basin is a large, fairly shallow ice-block kettle now nearly completely filled with sediment. Peat comprises the upper 3 to 4 m and the bog plant communities which currently occupy the surface continue to add to the deposit. The kettle occurs at an elevation of 1410 feet in an area of morainic topography of Valley Heads age somewhat north of the head of the Chaffee outwash plain. To the east, north and west the surrounding hills rise 300 to 400 feet. The bog is located in the Town of Holland near the southeast corner of Erie County, 0.2 mi west of the Erie-Wyoming County line, 1.8 mi northeast of Protection at 42° 37' 10" N Lat and

78° 28' W Long. It is shown as a wooded marsh in the northwest sector of the Arcade 7½' quadrangle. The bog and much of the surrounding land is currently owned by the County of Erie whose Bureau of Forestry administers the area as its Plantation #5.

The bog surface is uniformly covered with vegetation (see Plate 1, Fig. A) and there is no standing water except for a temporary lagg along the north edge of the mat. As measured by planimetry on an aerial photograph, the original lake occupied an area of about 22 acres. Of this, 15 acres are now nonforested and covered mainly by ericaceous shrubs with occasional clumps of tamaracks. The basin has an irregular outline with the long axis trending east-west. There is a prominent bay extending northward and smaller bays, which are now covered with deciduous swamp forest, occur at the east and west ends of the basin. The steepest slopes above the basin are found on the north and south sides. An intermittent shallow stream occurs at the east end, but the basin has no permanent outlet or inlet. The stream, which discharges into a tributary of Buffalo Creek, apparently functions only at the peak of the spring runoff as it is nearly dry during the summer.

In spite of the advanced stage of basin infilling, most of the major vegetation zones characteristic of bog succession are still evident. On the north, east and west sides a prominent and almost impenetrable, high shrub zone occurs.

Plate 1

Figure A. Protection bog, view looking southeast, August 23, 1967.

Figure B. Houghton bog, view looking east, August 26, 1967.



Vaccinium corymbosum, Pyrus melanocarpa and Nemopanthus mucronata are the major species. Rhododendron nudiflorum is also present but is less frequent. The western one-third of the open mat is occupied by a low shrub heath in which Cassandra calyculata is dominant. Andromeda glaucophylla, Kalmia polifolia and Vaccinium myrtilloides are other shrubs which occur in this zone. Eriophorum virginicum and Sarracenia purpurea are typical herbs. Sphagnum capillaceum, S. magellanicum and S. recurvum form a continuous carpet beneath the shrubs and at places Polytrichum juniperinum var. gracilius and Sphagnum fuscum have built up hummocks. Larix laricina and Pinus strobus seedlings are present throughout the low shrub zone. An island of Larix laricina trees 4 to 6 inches in diameter occurs near the middle of the mat and extends eastward and southward. Large Pinus strobus trees are present on humified peat along the west and northwest sides near the hinge line. Picea mariana does not occur at this bog.

Much of the upland around the basin was formerly under cultivation, although conifer stands planted during reforestation projects and secondary forests developing on abandoned fields currently occupy much of the area. The woodlot to the east and southeast of the bog is the least modified of any nearby forest remnant. On muck in the lower areas Acer rubrum, Betula alleghaniensis, Carpinus caroliniana, Prunus serotina and Tsuga canadensis are the principle trees.



Typical herbs in this area include Clintonia borealis, Coptis groenlandica, Oxalis acetosella, Medeola virginiana and Trillium undulatum. Upslope on better drained soil, Acer saccharum and Fagus grandifolia are abundant and they occur with Fraxinus americana, Tilia americana and Tsuga canadensis. Plantations of Pinus resinosa, P. strobus and Larix decidua interspersed with untilled fields occur south, east and north of the bog. To the west and northwest, contiguous with the bog, is a narrow zone of open swamp forest in which Acer rubrum and Ulmus americana are the dominant trees. Populus grandidentata and Crataegus sp. are common at disturbed sites and abandoned fields around the bog.

#### Sediment Stratigraphy

The bog was sampled on August 24, 1967 near the center of the basin. The Hiller sampler was used from the surface downward to 6 m but, because of the compactness of the sediments, it was necessary to substitute the Davis head attached to the Livingstone extension rods to sample beyond this depth. The stratigraphy at the sampling point is (Diagram 1):

- 0.00-0.10 m : peat, with sphagnum leaves; humified, dark brown;
- 0.10-0.90 m : peat, undifferentiated but with sphagnum leaves; reddish brown;
- 0.90-3.25 m : peat, undifferentiated but with sedge leaf fragments and other plant debris; coarse near the top but gradually becoming finer downward; reddish;

- 3.25-6.30 m : gyttja; soft, somewhat gelatinous, brown at top, gradually becoming stiffer and rubbery downward, with Najas seeds from 4.75 to 5.50 m; silt and clay admixture beginning at 5.60 m; mostly brown or reddish brown;
- 6.30-6.33 m : silty-clay, with some medium sand at bottom; bluish-gray. The sediments could not be penetrated further with equipment used.

### Houghton Bog

Located 12 mi southwest of Protection bog, Houghton bog occupies an ice-block depression in a pitted outwash plain which extends southward from the Valley Heads moraine past the village of Springville to Cattaraugus Creek. Houghton bog is one of the larger of the many basins which dot this plain. Most of the depressions have filled with sediment, but several open lakes are also present. Of these, Dead Man's Lake is the largest. It occurs in a deep kettle hole just northwest of East Concord and is surrounded by an extensive bog mat. Most of the smaller basins lack bog plant communities. The outwash fan forms a minor divide separating drainage in a general northward direction to Eighteen Mile Creek and the West Branch of Cazenovia Creek from drainage southward to Cattaraugus Creek.

Houghton bog is situated in the Town of Concord, 2.3 mi north of Springville between US 219 and Sharp Street at 42° 32' 30" N Lat and 78° 40' 13" W Long and is shown as an area of wooded marsh on the springville 7½' quadrangle. The basin occurs in a forest remnant about 45 acres in size

which is completely surrounded by tilled and fallow fields. Little of the original forest remains within a 3 mi radius of the bog. The basin measured on an aerial photograph, covers about 18 acres. The shoreline occurs between the 1400 and 1410 foot contour lines. Except for about 5 acres occupied by an open mat (see Plate 1, Fig. B) the depression is now entirely forested. The bog is owned by the Nature Sanctuary Society of Western New York, Inc. which attempts to maintain it in an unmodified condition.

The long axis of the basin has a north-south orientation. Two shallow bays extend beyond the main depression to the north and south (Brosius, 1953). These must have rapidly filled with sediment for the upper layer is strongly humified and now supports a swamp forest. The 5 acre bog mat extends entirely across the surface in a northwest-southeast direction. The mat is thinnest near the southeast end where the weight of a man is sufficient to cause water to seep upward. Elsewhere the mat is firm. No permanent outlet or inlet is present, although a low area which apparently is the route for excess spring runoff extends southward to join a tributary of Spring Brook. This temporary drainage channel is dry in the summer and its bed is mostly filled with water-saturated muck. The slopes immediately above the basin are gentle. The surface of the outwash plain is rolling and uneven and in general no more than 20-30

feet above the mat surface. The surrounding hills rise about 300 feet above the surface of the plain.

The bog is surrounded by a strip of forest of variable width. On the slope above the mat the main tree species are Acer saccharum, Betula alleghaniensis, Fagus grandifolia, Prunus serotina, Tsuga canadensis and Ulmus americana.

Adjacent to the north and northeast bog margin occurs a somewhat larger woodlot. This stand was heavily logged in the past and is now characterized by trees of small diameter, mostly Acer saccharum and Fagus grandifolia. A few Prunus serotina trees are also present, and Tsuga canadensis seedlings were noted. On the wetter, organic-rich soil between the hinge line and the open mat, a swamp forest of Acer rubrum, A. saccharinum, Betula alleghaniensis, Pinus strobus, Prunus serotina, Tsuga canadensis and Ulmus americana occurs. At places in the swamp forest, Taxus canadensis forms a dense cover. Pinus strobus is particularly abundant along the south and west margins of the bog mat.

A narrow high shrub zone of Nemopanthus mucronata, Pyrus melanocarpa and Viburnum cassinoides occurs between the swamp forest and the open mat. Cassandra calyculata is the dominant shrub throughout most of the open mat, but Kalmia polifolia and Vaccinium myrtilloides and V. oxycoccus are also present. Carex canescens, C. pauciflora, C. trisperma, Rhynchospora alba, Sarracenia purpurea and various bog orchids are restricted to certain parts of the mat. The main Sphagnum

species include S. capillaceum var. tenellum, S. fuscum, S. magellanicum and S. teres; S. cuspidatum occurs in the wetter areas near the southeast end. Pinus strobus seedlings are abundant on the grounded mat, but Larix laricina is restricted to the southeast and northeast corners of the mat. Picea mariana does not occur at Houghton bog.

### Sediment Stratigraphy

Because of the water pocket beneath the mat, two series of samples were collected at this site. The first, designated as section B, was taken on September 1, 1966 somewhat east of the center of the open mat using a Hiller sampler between 4.00 and 8.00 and a Livingstone sampler with a 2 inch tube beyond 8.00 m. The stratigraphy at this point is:

#### Section B (Diagrams 3 and 4)

- 0.00-0.75 m : peat, fibrous, with sphagnum leaves, with water; no samples taken;
- 0.75-4.00 m : finely comminuted plant debris in water, few seeds present near bottom; no samples taken;
- 4.00-9.43 m : gyttja, soft & gelatinous at top with small amount of plant debris, gradually becoming stiffer and more rubbery downward; brownish throughout;
- 9.43-9.95 m : marl, with dark brown and reddish laminae; mollusca and charophyte oogonia abundant, strongly calcareous; whitish gray;
- 9.95-10.04m : clayey silt, dense with gravel near bottom, carbonized wood fragments present sporadically; mostly dark gray but somewhat brownish; sharp contact with marl above. Further penetration impossible.

Section A was collected on October 17, 1966 with the Hiller sampler near a small stand of tamarack located one-half the distance toward the center of the basin 185 feet S 10° E of the sampling point for section B. The stratigraphy of section A is:

Section A (Diagram 2)

- 0.00-0.10 m : peat, humified; dark brown;
- 0.10-0.60 m : peat, undifferentiated but with sphagnum leaves; light reddish brown;
- 0.60-0.85 m : peat, undifferentiated but with sedge leaf fragments; somewhat coarse grading downward into finer texture; gray to dark gray;
- 0.85-4.00 m : gyttja, soft, with some sedge leaf debris near top, becoming stiffer downward; gray.

Pollen Stratigraphy

In the following discussion the pollen diagrams have been divided into zones using the letter designations that Deevey (1939) first applied to his New England pollen profiles. These have found wide usage in the northeast. Zone C, the uppermost, is characterized by an assemblage of hardwoods and hemlock and can generally be subdivided into three main parts. Below this in order are zone B which is dominated by pine pollen and zone A in which abundant spruce pollen is found. The T zone (Leopold, 1956b) records an interval beneath the A zone in which NAP percentages are high.

I am aware of the recent trend of describing pollen assemblage zones from bog and lake sediments in accord with the Code of Stratigraphic Nomenclature (see Cushing, 1967) rather than extending the use of letter zone designations

developed in one region to distant geographical areas. But I feel, as does Livingstone (1968), that zones are "to be regarded as temporary divisions of convenience, to be used as reference points in discussions of the underlying trends in the pollen curves . . . [and that they] . . . should not be enshrined under the protection of a code involving strict rules of description and priority" (p. 95).

There are chronological reasons, and perhaps climatic ones as well, for extending Deevey's zones to western New York. It should be understood, however, that floristically and vegetationally the zones are not the same in New England and western New York or, for that matter, nearly anywhere else they are used. This is clearly brought out by Deevey (1957) in a summary table in which he compares pollen sequences from northern Maine, southern Connecticut and Michigan by subdividing them into A, B and C zones.

Because of the close similarity between the pollen diagrams for Protection bog (see Diagram 1) and Houghton bog (see Diagrams 2 and 3), they will be discussed together. Minor pollen types not included in the diagrams are listed in Appendices B, C and D.

Zone A. In the lowermost spectra at both bogs 40 to 50 percent of the sum is comprised of Picea pollen. It is about five times more abundant than pollen of any other individual type. Although both records may be truncated at the bottom, there is no indication of a T zone beneath the A

zone at either site. At Protection bog, however, the abrupt decline in the spruce curve, which below the maximum at 6.265 m is coordinated with a 25 percent NAP high, may, in part, record the transition from herb to spruce dominated vegetation. The number of terrestrial pollen and spores rises rapidly from about 18,000 to 140,000 grains/ml of wet sediment between 6.325 and 6.195 m. Assuming a constant rate of sedimentation across this interval, the change parallels that reported for Rogers Lake, Connecticut during the T to A zone transition (Davis, 1967b).

At Houghton bog a similar change occurs, but it is not as readily interpreted (see Diagram 4). The deepest sediment sampled at this location was a dark gray silty clay, apparently barren of pollen. Upward, passing abruptly into marl, the number of grains per unit volume was at first very low, 2000 to 3000 grains/ml (see Fig. 7), but rose to 60,000 grains/ml in the first gyttja sample immediately above. Because of the change in sediment stratigraphy, it is unlikely that the rate of sedimentation was constant from the clay upward through the marl to the base of the gyttja. It seems possible instead that, in relation to the accumulation rate of the gyttja, the marl was deposited rapidly, resulting in a lower number of pollen and spores per unit volume.

Unfortunately close interval radiocarbon dating is the only method at present which can be used to determine accurately the sedimentation rate, and the necessary age



determinations are not available for Houghton bog. At Rogers Lake (Davis and Deevey, 1964; Davis, 1967b), Seth's Pond, Massachusetts and Silver Lake, Ohio (Ogden, 1966), however, fairly uniform rates have been demonstrated. These involve about a two- to threefold increase from lateglacial time through nearly all of the postglacial except the most recent.

At Protection bog, subdivision of the A zone into a Picea-Abies subzone is suggested by the prominent peak in the Abies curve near the top of the zone. The greatest percentage of Abies pollen at Houghton bog also occurs in the upper part of the A zone. Larix, although not encountered in A zone sediments at Houghton bog, accounts for about 5 percent of the sum in the middle portion of the A zone at Protection bog, decreases upward and finally drops out of the counts in zone B. Pinus pollen regularly comprises 10 to 15 percent of the total in the lower levels of both bogs, but upward, its percentage gradually increases until the maximum is reached in zone B.

Three different categories of Pinus pollen were counted. The basic separation was between grains which could be identified as belonging to the softwood pines, subg. Haploxyylon, which in east-central North America includes only Pinus strobus, and the hardwood pines, subg. Diploxyylon, which in this region includes P. banksiana and P. resinosa. The most readily observed differences between the pollen of

these two subgenera is that the germinal furrow, located on the distal face between the bladders, is verrucose in Haploxylon pines, whereas in Diploxylon pines it is smooth (Ueno, 1958). The third category, Pinus undifferentiated, contains grains that could not be oriented to permit observation of the furrow, those grains in which the exine between the bladders was missing and reassembled grains, the number of which was determined by keeping track of the larger fragments and then dividing the sum of these by an appropriate figure to reduce the sum to the number of whole grains. Diagram 1 shows that diploxylon pine pollen was the major type identified in zone A. This also is illustrated in Diagram 3, but less prominently. The sum of the three categories is graphed as Pinus total.

Ulmus pollen is found in low percentages near the bottom of zone A but gradually increases to about 7 percent near the top of the zone at Protection bog. From 1 to 2 percent Ulmus occurs at an equivalent stratigraphic position at Houghton bog. About 5 percent of Carpinus and/or Ostrya pollen is present in all A zone spectra. At both bogs there is a small but definite peak near the A to B zone transition. Low percentages of Corylus pollen occur in all A zone spectra at both bogs. Betula pollen is regularly present in A zone sediments, although in fairly low percentages. At Protection bog there is a gradual increase in percentage upward and near the beginning of the B zone a maximum is reached

which persists throughout the lower part of this zone. A similar but sharper peak is present at Houghton bog.

Populus pollen accounts for 2 to 3 percent of the total at Protection bog in zone A.

Low percentages of 3-colpate Fraxinus pollen occur in the A zone of Protection bog. Pollen of this type, which at most sites was tabulated separately from Fraxinus pollen with 4 and 5 colpi is, judging from reference slide examinations, produced mainly by F. nigra. Fraxinus americana and F. pennsylvanica, on the other hand, typically have quadricolpate pollen, although a few tricolpate grains are occasionally found in reference slide preparations of these species, as are some quadricolpate grains in reference slides of F. nigra. Fraxinus pollen was not differentiated in this way at Houghton bog, but it is reasonable to assume that 4-colpate grains are as poorly represented in the A zone at this site as they are at Protection bog.

The pollen of many taxa characteristic of the Hemlock-white pine-northern hardwoods and Beech-sugar maple forest regions appear in zone A. At Protection bog, 2 to 3 percent of Tsuga pollen occurs in the upper part of this zone, and at Houghton bog, 1 percent or less is found in the same stratigraphic position. At one or both sites, sporadic grains of Castanea, Fagus, Fraxinus 4-colpate, Juglans cinerea, Liquidambar and Platanus were also encountered. At Protection bog about 1 percent of Acer saccharum pollen is

present in A zone spectra and trace percentages of undifferentiated Acer grains also occur at Houghton bog. One percent Carya pollen and about 10 percent of Quercus pollen occurs throughout this zone at both bogs.

The presence of such pollen is somewhat difficult to explain ecologically, since at the time A zone sediments were deposited the region was presumably cool and moist and dominated by spruce forests. One possibility which has found favor with a number of workers is that such pollen is of secondary origin having been eroded from the surrounding till, into which it had become incorporated from older deposits. It then subsequently entered the basin carried with the mineral sediments that characterize the lower portions of these deposits. As small quantities of deciduous tree pollen have been found in surface samples in regions far removed from the place of origin of such pollen, a certain percentage may have been blown to the sites from distant sources as well.

With the exception of the top 20 cm of the sediment column, the A zone contains the highest percentages of non-arboreal pollen anywhere in the diagrams. At both bogs the pollen produced by unknown members of the Cyperaceae and Gramineae amounts to 5 to 8 percent of the total. Associated with them is the pollen of Ambrosia, Artemisia, Rumex, Thalictrum, periporate grains belonging to species in either the Chenopodiaceae or Amaranthaceae (Cheno-Am), and other

herbaceous taxa listed in Appendix 2 and 4. Significant percentages of pollen belonging to unknown members of the Asteroideae (Compositae) were regularly present in the A zone. In all diagrams these are graphed under the heading high-spine Compositae. From 1 to 5 percent of Alnus and Salix pollen occurred in this zone at both bogs. Low percentages of Myrica pollen were found in the A zone of Houghton bog upward to the base of zone B.

An age determination of  $11,800 \pm 730$  B.P. (I-3290) on wood near the bottom of the marl at Houghton bog affords a minimum date for the beginning of the A zone at this site. This is a good correlation with a comparable date of  $12,000 \pm 300$  B.P. (W-507; Rubin and Alexander, 1960) on wood from a marly silt deposited in a depression near Cheery Tavern Crossroads on the Chaffee outwash plain 10 mi to the east. Both provide minimum dates for the formation of the Valley Heads moraine in this region. Mollusks found in the marl at the Cheery Tavern site indicate the sediment was deposited near the margin of a heavily vegetated pond. Pollen analysis and the fossil snails suggest a climate somewhat cooler than the present at the time of deposition (Daily, 1961). Remains of a mastodon were also uncovered at this site.

The Mollusca which occurred in the marl at Houghton bog were not identified, but charophyte oospores removed from the residue after HCl treatment and part of the original

core were sent to Fay Kenoyer Daily for study. The collection contained only Chara sejuncta A. Br. (letter, April 11, 1968), a species which often grows in ponds with mud bottoms (Daily, 1961). Wood (1965) treats it as a variety of Chara zeylandica and reports that it occurs from Massachusetts to the Great Lakes southward to the West Indies, Brazil and Uruguay. Its New York State distribution is listed in Wood and Muenscher (1956).

Zone B. Pine pollen is by far the predominant type in zone B at both bogs, although substantial percentages of Quercus pollen are also present. The boundary separating A and B zones was drawn where Quercus pollen begins to increase. This also is at about the middle of the Picea decline marking the demise of spruce forests in the area. Pine pollen accounts for about 50 percent of the total in this zone, oak pollen for an additional 20 percent. The identification of high percentages of Pinus subg. Haploxylon suggests that Pinus strobus was the dominant pine surrounding the site when the B sediments were deposited. At Protection bog a Pinus strobus cone was found in stiff gyttja at a depth of 5.75 m near the beginning of zone B in the 2 inch diameter core collected for radiocarbon assay. This establishes the presence of white pine immediately adjacent to the basin during early B zone time.

Small but significant percentages of Ulmus and Carpinus-Ostrya occur in the B zone and a slight increase is

shown in the amount of birch pollen present across the A to B zone transition. About 2 percent of the total pollen in the B zone is contributed by nonarbooreal species. This level continues upward throughout both diagrams until the pre- to post-settlement boundary is reached.

Diagram 4 in which the number of grains per ml of wet sediment is plotted shows that the greatest numbers of pollen grains in the B zone were contributed by Pinus and Quercus. Pinus reaches a maximum of 176,000 grains/ml at 9.25 m. At Protection bog the B zone Pinus peak has been dated at  $9030 \pm 150$  B.P. (I-3551).

Zone C-1. The boundary between zones B and C-1 was drawn at the middle of the Tsuga increase. Pine pollen at this point still accounts for about 30 percent of the total but it subsequently decreases to 7 percent in the lower third of the C-1 zone and to about 3 percent at the end. Abies disappears in the beginning of zone C-1. The percentage of Quercus remains high and amounts to nearly 20 percent of the total at Protection bog. Its decline is gradual at this site and, with a slight lag, parallels that of Pinus, although at the end of the C-1 zone it is still 10 percent of the total. A similar pattern in the curve for this species occurs at Houghton bog. The lower third of C-1 is dominated by the pollen of Tsuga, Quercus and Pinus. Upward, the latter decrease in abundance and are replaced in part by

Fagus which at the end of zone C-1 forms 35 percent of the total at Protection bog and about 10 percent at Houghton bog.

At the beginning of the C-1 zone at Houghton bog are peaks in the curves for Fraxinus and Juglans. Fraxinus is strongly represented through much of the zone, and at Protection bog the highest C zone percentages of Fraxinus 4-colpate occur in the C-1. Betula increases somewhat over its percentage in lower levels at both bogs and reaches a peak in the lower half of the zone. Acer, Ulmus, Carpinus, Ostrya and Carya are represented in all C-1 spectra in amounts ranging from 5 to 10 percent. Both Acer rubrum (incl. A. saccharinum) and A. saccharum were present at Protection bog in this zone. Smaller percentages of Tilia and Corylus occur throughout. At Protection bog there is a Tilia maximum of modest size at the beginning of zone C-1.

Castanea first appears in the lower half of the C-1 zone at Houghton bog and, although sporadic grains occur in the same zone and at lower levels at Protection bog, Castanea was not regularly encountered in the counts until just above zone C-1 at this site. The highest percentages in the Platanus curve occur near the middle of this zone at Houghton bog and a similar but smaller peak occurs at about the same stratigraphic position at Protection bog, although in both cases fairly high percentages persist into the lower part of zone C-2.



As shown in Diagram 4, the largest number of pollen grains of any one type per ml in the C-1 zone at Houghton bog was contributed by Tsuga. Tsuga replaces Pinus and Quercus as the major contributor to the pollen rain upward from zone B to zone C-1.

Zone C-2. The middle of the prominent Tsuga decline was chosen to mark the C-1/C-2 boundary and at Protection bog this point has been dated at  $4390 \pm 110$  B.P. (I-3550). Associated with the decreasing Tsuga percentages at both bogs are increases in Acer, Betula, Carya, Fagus and Quercus curves. At Protection bog where species identifications of Acer pollen were made, A. saccharum percentages are larger and increase more than those of A. rubrum (incl. A. saccharinum). The number of Tsuga grains per ml decreases from 30,000 to 5000 across the C-1/C-2 transition. Small increases in the number of grains per volume for Fagus, Acer, Quercus and Betula are evident.

At Protection bog there is a small decrease in the percentage of Fagus pollen at about the middle of zone C-2. This probably does not reflect a decrease of Fagus in the surrounding forest, as the decrease is mainly compensated for by an increase in Cyperaceae pollen which is most likely of local origin. Other than the two spectra at Protection bog in which Cyperaceae pollen accounts for about 7 percent of the total, NAP percentages average less than 3 percent of the sum.

Zone C-3. It is difficult to place the C-2/C-3 boundary, but at both sites it was drawn after the decline in Quercus which was taken to mark the end of zone C-2. Tsuga percentages increase across this interval. At Protection bog these changes are dated at  $1270 \pm 95$  B.P. (I-3549).

It cannot be conclusively determined whether sediments of the same age are present in Diagram 3 for Houghton bog because of the obvious absence of the upper spectra. Diagram 2 was prepared to overcome this deficiency. The exact relationship between these two perhaps can be determined only by radiocarbon dating, but an examination of the pollen curves in relation to the complete diagram for Protection bog indicates that zones C-3, C-2 and part of C-1 are present in Diagram 2. In the absence of dates, however, the boundaries have been drawn to indicate their questionable positions. The best markers in Diagram 2 are the low in the Tsuga curve and the corresponding highs in the Carya, Fagus and Quercus curves. The percentages are about the same magnitude at the edge and at the center of the basin.

Zone C-3 has been divided into two subzones. In subzone C-3a, the lowest, Tsuga increases to 25 percent and Fagus correspondingly decreases at both sites. At Protection bog Quercus, Betula, Carya and Acer saccharum, which decrease slightly at the C-2/C-3 transition, increase somewhat toward

the end of the C-3a. These changes are not evident at Houghton bog.

The C-3a/C-3b boundary records the influx of settlers to the area and the associated forest clearance. The change is quite abrupt and about 50 percent of the total pollen in subzone C-3b above the boundary is contributed by nonarboreal species, mainly those associated with agriculture. Since the percentage base includes both AP and NAP, decreases in tree taxa percentages are directly related to the large numbers of NAP.

At both sites Ambrosia accounts for about 25 percent of the total. Other important herbaceous taxa include Gramineae (incl. Ceralia), Rumex and Plantago. The latter is perhaps the best zone marker, since it appears abruptly at the pre- to post-settlement boundary. Occasional grains which are found in the C zone below this level are best interpreted as contaminants, although species of Plantago were presumably native at this time to the region surrounding the bogs. Cheno-Am pollen also occurs in the C-3b and the small increases in Artemisia and high spine Compositae may be attributed to introduced weedy species. Zea occurred in this zone at both bogs and Fagopyrum was found in the surface spectrum at Houghton bog. Clay and silt sized mineral particles, presumably blown into the basin, were abundant in the C-3b subzone at both bogs.

Populus and Picea pollen reappear in upper C-3 spectra. Increases in the percentages of Acer, Betula, Larix and Pinus occur at one or both sites between 2.5 and 7.5 cm levels and the surface. In spite of the absence of mature trees in nearby forests, a few Castanea grains were found in the surface samples at both bogs.

#### LOCKPORT SITE

Several years ago a rich deposit of plant debris was discovered on property belonging to Neil Malloy between Ewings Road and Eighteen Mile Creek, 4.5 mi north and a few degrees west of the center of Lockport in Niagara County at 43° 14' 6" N Lat and 78° 42' 30" W Long (see Fig. 2). Although somewhat north of the region on which this study concentrates, I have included the results of my research on the site because of the added information it provides on the lateglacial vegetation of western New York.

The plant material lay beneath about 3 m of sorted sand and gravel which at the present time is being actively quarried by Malloy. Numerous animal fossils have been found at the site including a well-preserved mammoth tooth and abundant gastropods. Richard L. McCarthy of Lockport has obtained an age determination of 12,000  $\pm$  100 B.P. (I-838, Buckley et al., 1968) on a sample of spruce wood from the organic bed.

I visited the locality with McCarthy on October 16, 1966 at which time the water table was low enough to permit access to the organic bed. The overlying gravels had been completely removed and the organic material which was still in place lay beneath several cm of inorganic sediment deposited largely out of a shallow pond which covers the bottom of the excavation every spring. At the sampling point the organic deposit was about 15 cm thick. Using a shovel, over 5 liters was readily collected and the contents of this sample will be discussed in following paragraphs. At the time the water table was just at the top of the deposit, and any hole being dug rapidly filled with water.

The principal constituent of the deposit is wood. Large fragments of branches, stems and roots are present intermingled with abundant smaller woody debris 1 cm or less in length. The larger pieces have rounded corners and other evidence of having been water transported. Spruce needles, mosses, seeds and other plant remains also occur, and very little inorganic sediment is intermixed. Judging from exploratory digging elsewhere, the organic bed is of limited distribution.

At 50 m N 20° W of the sampling point a residual "island" of sediment was left in place when the surrounding sands and gravels were stripped away. According to McCarthy, sediments of similar lithology occurred above the organic bed. The section was measured as follows:

0- 15 cm : soil, A zone;  
 15- 53 cm : sandy loam, with cobbles, reddish;  
 53-100 cm : sandy loam, yellowish;  
 100-104 cm : pebble lens;  
 104-112 cm : sandy loam, yellowish;  
 112-135 cm : sand, fine to medium, with dark stain;  
 135-174 cm : sand, medium to coarse, carbonate  
 cementation into stringers trending north-  
 south;  
 174-198 cm : gravel, with silt lenses, grading from lt  
 brown to reddish brown at base;  
 198-262 cm : sand, fine to medium with pebbles and  
 cobbles, yellow brown to olive;  
 262-277 cm : sand, coarse, dark gray with yellow brown  
 patches;  
 277-282 cm : silty clay, pink;  
 282-295 cm : sand, coarse, dark gray with yellow brown  
 patches;  
 295-300 cm : silty clay with coarse sand, pink;  
 300-306 cm : sand, fine, dark gray;  
 306 cm : water table;  
 306-311 cm : silty clay;  
 311- cm : sand, fine.

No organic layer was found at this point.

On April 11, 1968 I again visited the site and at this time a backhoe was being used to dig a small pit 350 m north of the organic bed. The overlaying sand and gravels had also been removed from this new site. The excavation had begun in medium sand and had proceeded downward through fine sand with silt and clay to a depth of 2.5 m. A sample of the silty-clay sand, 1.8 m below the surface, was collected for pollen analysis.

It seems clear that the plant material was deposited after having been abraded in moving water, but how this relates to the Late Wisconsin geological history of the area is not precisely known. Several possibilities exist. The age of the Lockport organic deposit corresponds closely to

dated wood samples from Lake Iroquois sediments found at 340 ft A.T. near Lewiston in western Niagara County (see Karrow et al., 1961). The Lockport deposit is located 1.75 mi lakeward from the Iroquois strand, more or less equi-distant between two strand extensions which course southward toward the city. The Iroquois beach is about 400 ft A.T. in this area and the deposit occurs 50 ft below this. In view of these facts, it is likely that the organic material was deposited under comparable conditions at both sites.

The ice front at this time was some distance north of the sites and drainage was to the east through the Rome outlet to the Hudson River. Lake Tonawanda which was trapped between the Onondaga and Niagara escarpments in northwestern New York during the lowering of early Lake Algonquin was draining through five spillways. The two westernmost outlets located at the present cities of Lockport and Lewiston carried the most water and functioned the longest. Separate deltas were built up north of these spillways and, as shown on the map of Kindle and Taylor (1913), the Lockport organic deposit occurs at the edge of a stony delta deposit which grades lakeward into lacustrine sand.

A subaerial delta with shifting stream courses easily accounts for the burial of organic debris carried down the spillway or derived from the near shore vegetation. It is likely that this would have occurred in the early history of Lake Iroquois at a time when the lake was north of the main

strand, perhaps building the weakly expressed Newfane beaches of Kindle and Taylor (ibid.). Subsequent ice retreat and isostatic uplift raised the lake to the level of the main beach, inundating and planing most of the delta and the Newfane beaches. It is also possible, however, that the organic debris became buried along the shoreline during these adjustments in lake level and the gravel and sand above represents off-shore beach deposits. In either case there is no evidence at present which suggests that the two events were greatly separated in time.

The spillways gradually became extinct westward with further uplift and the draining of Lake Tonawanda. As ice retreated north of the St. Lawrence River valley, permitting drainage along its axis, Lake Iroquois came to an end. It was followed by a low stage presumably contemporaneous with the Champlain Sea episode, although marine waters did not invade the Ontario basin because of the low sea level at this time. Isostatic rebound subsequently tilted the basin roughly toward the west causing the lake level to rise initiating Lake Ontario.

The sample of the organic bed was washed with water through a series of three sieves with 1190, 500 and 177 mu screens arranged in decreasing size downward. The residues retained by each were then examined under a dissecting microscope and potentially identifiable fossils were removed and placed in vials. Thirty gms of the wet silty clay were



macerated with treatments in 10 percent HCl, 72 percent HF,  $\text{ZnCl}_2$  (heavy liquid separation) and acetolysis. About 240 grains were present per gram of wet sediment.

The plant macrofossils in the deposit are of several types. Seeds are infrequent, but of the many species represented I have been able to identify only a few. These are Abies balsamea, a single trigonous Carex achene, Eleocharis spp., Hippuris vulgaris, Menyanthes trifoliata, Potentilla anserina and Potamogeton spp. Branch tips with needles of Picea sp. or spp., cones of Picea mariana, spruce seed wings, leaves or floral bracts of Myriophyllum, a bracket fungus, a microscopic vesiculate fungus similar to that described by Rosendahl (1943) as Rhizophagites butleri, megaspores of Selaginella selaginoides, charophyte oospores identified by Fay Kenoyer Daily (letter, April 11, 1968) as Chara sejuncta and Tolypella glomerata and thirty different moss taxa have also been identified.

The mosses are the most useful macrofossils for making inferences about the type of plant communities present in the area 12,000 years ago. The moss assemblage is a mixed one indicating that a number of different communities contributed fossils to the deposit. This implies that the plants did not grow in place where they were found, but rather became intermingled prior to their burial, a fact which is independently confirmed by the abraded nature of the large pieces of wood in the deposit.

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The identified moss species are listed in Table 18, and as none of them is extinct, knowledge of their current autecological requirements enables inferences to be made about the habitats present near Lockport 12,000 years ago. These are listed in an idealized transect beginning at the lake shore and proceeding inland, although, instead of the zonation which this implies, a habitat mosaic may have been present. A fairly good analogue for this vegetation exists today at places in the Straits of Mackinac region of Michigan where rich fens (Sjörs, 1961) occur between sandy beaches and Picea glauca stands. Many of the moss species which are found in or near the fens in this area are considered boreal forest or subarctic disjuncts. The Lockport moss assemblage is comprised mostly of calciphiles, and presumably the nearby Niagara escarpment and local deposits of calcareous till provided a ready source of carbonates.

A dry, sandy beach, perhaps near the lakeshore or some distance inland, but in any case above the zone of perpetual wave disturbance, is the first habitat indicated. Behind the beach, between dunes and elsewhere, rich fens occurred in shallow ponds enriched with carbonates. On drier, gentle slopes adjacent to the fen a somewhat shaded habitat characterized by shrubs and perhaps occasional spruce trees occurred, and this likely graded further inland into a forest of spruce and balsam fir, perhaps with occasional tamaracks. Exposed areas of the Niagara escarpment ca. 5 mi southward



TABLE 18  
LOCKPORT SITE BRYOPHYTE FOSSILS BY HABITAT TYPE

Taxa	Sandy Calcareous Strand	Beach Pool or Fen	Fen Edge, Moist + Shaded	Forest	Rock Outcrop or Talus
<u>Abietinella abietina</u> (Hedw.) Fleisch.*	+	-	+	-	+
<u>Ceratodon purpureus</u> (Hedw.) Brid.*	+	-	+	-	-
<u>Ditrichum flexicaule</u> (Schwaegr.) Hampe	+	-	+	-	+
<u>Tortella inclinata</u> (Hedw. f.) Limpr.	+	-	-	-	+
<u>Tortula ruralis</u> (Hedw.) Gaertn., Meyer & Scherb.	+	-	-	-	+
<u>Aulacomnium palustre</u> (Hedw.) Schwaegr.*	-	+	+	R	-
<u>Bryum pseudotriquetrum</u> (Hedw.) Gaertn., Meyer & Scherb.*	-	+	+	+	-
<u>Campylium stellatum</u> (Hedw.) C. Jens.*	-	+	+	-	-
<u>Meesia</u> cf. <u>trifaria</u> Crum, Steere & Anderson	-	+	-	-	-
<u>Drepanocladus aduncus</u> (Hedw.) Warnst.*	-	+	-	-	-
<u>D. fluitans</u> (Hedw.) Warnst.	-	+	-	-	-
<u>D. vernicosus</u> (Lindb. ex Hartm.) Warnst.*	-	+	-	-	-
<u>Scorpidium turgescens</u> (T. Jens.) Loeske	-	+	-	-	-
<u>Tomenthypnum nitens</u> (Hedw.) Loeske*	-	+	+	-	-
<u>Aulacomnium acuminatum</u> (Lindb. & H. Arnell) Par.	-	-	?	-	+
<u>A. turgidum</u> (Wahlenb.) Schwaegr.	-	-	+	-	+
<u>Bryoerythrophyllum recurvirostrum</u> (Hedw.) Chen	-	-	+	R	+
<u>Campylium chrysophyllum</u> (Brid.) J. Lange*	-	-	+	+	-
<u>Dicranella schreberiana</u> (Hedw.) Schimp.	-	-	+	-	-
<u>Distichium capillaceum</u> (Hedw.) B.S.G. or <u>inclinatum</u> (Hedw.) B.S.G.	-	-	+	-	+
<u>Fissidens osmundioides</u> Hedw.	-	-	+	-	+
<u>Hylacomnium splendens</u> (Hedw.) B.S.G.	-	-	+	+	-
<u>Meesia uliginosa</u> Hedw.	-	-	+	R	R
<u>Mnium punctatum</u> Hedw.* or <u>pseudopunctatum</u> Bruch & Schimp.	-	-	+	+	-
<u>Polytrichum juniperinum</u> Hedw.*	-	-	+	-	-
<u>Dicranum fuscescens</u> Turn.*	-	-	-	+	+

+ = characteristic of this habitat; - = not characteristic; R = rare; ? = probably expected in this habitat.

\*Currently found in Lockport area (Ketchledge, 1957).

provided habitats for those species which today occur in rocky situations. Certain species are found in more than one habitat, but others are of more restricted occurrence. Twenty-six species are listed in Table 18 and additional species of Bryum and Campylium and species of Brachythecium and Sphagnum were also found.

According to Ketchledge (1957), 46 percent of the species occur in the Lockport area today, although some are not of widespread occurrence and are considered rare in the area. Careful collecting would probably increase the percentage somewhat. Nearly all of the species are characteristic of the boreal forest and the region northward. For example, 88 percent of them are listed by Steere (1947) as found in the Canadian eastern arctic which encompasses the area from the Ungava Peninsula to the north end of Ellesmere Island.

The two species of greatest phytogeographical interest are Aulacomnium acuminatum and A. turgidum. Steere (ibid.) considers the former to be an important component of the high arctic vegetation. It is a circumpolar species widespread in the North American arctic and extends into the subarctic in the western half of the continent. The most southern station, a major range disjunction, occurs in the Thunder Bay District of Ontario near the north shore of Lake Superior between Nipigon and Port Arthur (Williams, 1968). Aulacomnium turgidum is also a circumpolar species which

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occurs throughout arctic subarctic North America. Although very rare in northeastern United States, it is found southward through the White Mountains to the Adirondacks.

Macrofossils of various animals were also found in the organic bed. Beetle exoskeleton fragments were common. Ostracod valves, statoblasts of fresh water bryozoa and several snail shells were present. I have not attempted to identify these fossils, but the beetle remains have the greatest potential for contributing paleoecological data.

The pollen spectrum from the site is given in Table 19. Of the total pollen 41 percent is comprised of non-arboreal species, principally members of the Cyperaceae. Picea accounts for 38 percent of the AP, Pinus for 13.6 percent and Larix about 1 percent. About 5 percent of the total was contributed by Quercus, Betula and Fraxinus 3-colpate. Single grains of Acer, Carya, Juglans cinerea and Ulmus were also found. Microspores of Selaginella selaginoides were present and complement the presence of the megaspores of this species found in the organic bed. A number of blackened pre-Pleistocene spores were also found.

#### SITES ASSOCIATED WITH PRE-VALLEY HEADS MORAINES

##### Allenberg Bog

Situated in Cattaraugus County in the Town of Napoli, a few miles north of the Wisconsin drift limit, this bog occupies a deep, northeast-southwest trending basin about 10



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TABLE 19

POLLEN SPECTRUM FROM A SILTY-CLAY LACUSTRINE  
DEPOSIT OF LAKE IROQUOIS AGE, LOCKPORT SITE,  
NIAGARA COUNTY, NEW YORK

	No. Grains	Percent
<b>TREES</b>		
<u>Picea</u>	129	38.1
<u>Larix</u>	4	1.2
<u>Pinus</u> undifferentiated	41	12.1
<u>P.</u> Diploxylon	5	1.5
<u>Acer</u>	1	0.3
<u>Juglans</u> cinera	1	0.3
<u>Carya</u> *	1	0.3
<u>Quercus</u>	8	2.4
<u>Ulmus</u>	1	0.3
<u>Betula</u>	5	1.5
<u>Fraxinus</u> 3-colpate	4	1.2
<b>SHRUBS</b>		
<u>Alnus</u>	3	0.9
<u>Salix</u>	6	1.8
<b>HERBS</b>		
Cyperaceae	115	33.9
Gramineae	2	0.6
<u>Ambrosia</u>	6	1.8
<u>Artemisia</u>	4	1.2
High spine Compositae	3	0.9
PERCENTAGE BASE (SUM AP + NAP)	339	
PERCENT AP	59.0	
PERCENT NAP	41.0	
<b>MISC.</b>		
Polypodiaceae	6	1.3
<u>Selaginella</u> <u>selaginoides</u>	4	0.8
<u>Sphagnum</u>	1	0.2
Fungus spores	74	15.5
<u>Pediastrum</u>	3	0.6
Dinoflagellate cysts	10	2.1
pre-Pleistocene spores	7	1.5
Ostracoda	3	0.6
Broken Abietineae	8	1.7
Unknown	23	4.8
PERCENTAGE BASE (339 + SUM MISC.)	478	

\*Badly corroded.

acres in extent located at the outer edge of an area mapped as Kent (Binghamton) moraine by MacClintock and Apfel (1944). It is approximately 30 mi southwest of Houghton and Protection bogs and is shown on the southeastern quarter of the New Albion quadrangle at  $42^{\circ} 15' 4''$  N Lat and  $78^{\circ} 52' 57''$  W Long as a small lake with a marsh on the southwest side, 2.7 mi south of New Albion and 1.2 mi north of the Pigeon Valley cemetery. The lake, which occurs near the northeast end of the basin, is about 40 m in diameter.

Less than one-half mile north of Allenberg bog is Waterman swamp, a roughly triangular tract of swamp and bog forest about 300 acres in extent. The swamp probably began as a lake ponded between drift deposits to the south and north. Allenberg bog does not seem to have been connected originally to the lake, and at present is separated from it by a hill and other intervening high ground. Since both occur at 1620 ft A.T., however, a possible connection between them may have been present around the south and east edge of the upland. Black pond, a small bog lake, is located at the west end of the swamp.

Both occur in a valley above which hills to the east and west rise 250 to 300 ft. In the vicinity of Allenberg bog the valley floor is slightly higher in elevation than the area to the south permitting drainage in this direction through Cold Spring creek. Waterman swamp is the headwaters of Little Valley creek, which, as an outlet, functions

mostly in the spring carrying waters charged with humic acids to the northeast away from the swamp. The two streams eventually empty into the Allegheny River. The swamp, Allenberg bog and some of the surrounding land are currently owned by the Buffalo Audubon Society which maintains the area as a wildlife sanctuary.

The vegetation of the region has been described by Gordon (1940) and Schick and Eaton (1963). Most of Waterman swamp is characterized by the latter as an elm-ash-rhododendron swamp. On the several knolls which rise above the level of the swamp Pinus strobus is particularly abundant, and Betula alleghaniensis and Tsuga canadensis are common associates. Rhododendron maximum and Viburnum alnifolium are typical understory shrubs in this area. Below the 1720 ft contour Abies balsamea, Fraxinus nigra, Larix laricina, Picea mariana, Pyrus americana and Ulmus americana are frequent. At certain places dense thickets of Nemopanthus mucronata and Vaccinium sp. occur. Large Abies, Larix and Picea trees, 18, 21 and 16 inches d.b.h. respectively, have been found at the southeastern corner of the swamp. Black pond is surrounded on all sides by an invading Cassandra calyculata heath, but an extensive sedge mat is absent. Small Picea, Larix and Pinus strobus trees are scattered across the heath.

At Allenberg bog the zonation of plant communities around the lake is fairly distinct (see Plate 2, Fig. A). The photographs in Gordon (1940) taken in the mid-1930's

Plate 2

Figure A. Allenberg bog, view looking northwest, August 28, 1967.

Figure B. Genesee Valley Peat Works, view looking northwest, September 2, 1967.



show a narrow low shrub zone separating the lake from the bog forest. Beavers, sometime after these pictures were taken, dammed the outlet and raised the water level high enough to kill most of the trees and many other plants then inhabiting the mat. They cut a shallow channel through the peat to the lake and constructed houses near the north- and southeast ends of the basin. The beavers were last seen in 1951 and the disappearance of the dam has since allowed the water level to return to normal. The pollen stratigraphy seems not to have been disturbed by their activity.

Nuphar microphyllum and Nymphaea odorata have been reported from the edge of the open water, although currently only the former is present. A narrow quaking mat of Carex limosa and Sphagnum spp. is located along the south and southwest margin of the lake, but northward becomes grounded. Here Cassandra calyculata and Decodon verticillatus are invading the open water directly. A discontinuous low shrub zone interspersed with dead trees occurs across the southwest two-thirds of the bog. Andromeda glaucophylla, Carex spp., Cassandra, Decodon, Eriophorum virginicum, Ledum groenlandicum, Rubus hispidus and Vaccinium macrocarpon are the main species present. Xyris caroliniana, an apparent coastal plain disjunct, has been found near the south end of the bog mat.

Around the periphery of the basin, particularly along the north edge, Larix laricina and Picea mariana occur.

Nearer the upland, they are found with Acer rubrum, Betula alleghaniensis, Fraxinus nigra, Pinus strobus and Tsuga canadensis. The understory shrubs in this area are Viburnum cassinoides and Pyrus melanocarpa. Rhododendron maximum is present along the west edge above the hinge line.

The upland vegetation has been described as a Tsuga canadensis-Fagus grandifolia forest with an admixture of Acer saccharum (Gordon, 1940). Other upland trees include Juglans cinerea, Ulmus rubra, Fraxinus americana, Prunus serotina, Acer pensylvanicum, A. rubrum and Betula alleghaniensis. The typical forest herbs are Dryopteris spinulosa var. intermedia, Lycopodium lucidulum, Mitchella repens, Medeola virginiana, Oxalis montana, Trillium undulatum, Viola incognita and V. rotundifolia. Oak forest does not occur in the nearby upland.

Cultivated fields surround the entire area and approach within 0.25 mi on the west and northeast sides of Allenberg bog. However, about one-half of the area in a 3 mi radius of the bog is forested. A narrow strip of cut-over forest occurs on the east and west sides and a similar but more extensive forested area occurs immediately to the south. Much of Waterman swamp has been heavily logged. Secondary forests on abandoned farmland are abundant in the area, but mature conifer plantations are rare. Southeast of Allenberg bog the New York State Conservation Department has



flooded about 30 acres for use as a waterfowl breeding preserve.

### Sediment Stratigraphy

Sediments from Allenberg bog were collected in three series. Section A was taken on October 17, 1966 with a Hiller sampler southwest of the bog lake from solid peat peripheral to the sedge mat. The stratigraphy at this point is:

#### Section A (Diagram 5)

- 0.00-0.15 m : peat, sphagnum leaves abundant, humified; dark brown;
- 0.15-3.00 m : peat, undifferentiated, fibrous at top grading into medium to fine dissected peat downward, sphagnum leaves abundant above 1.5 m, Drepanocladus fluitans from 1.7 to 3.0 m; reddish brown throughout.

Section B was collected on October 15, 1966, again with the Hiller sampler, at a point 60 m N 39° E of section A. Sampling was discontinued at 12.5 m because insufficient extension rods were available to reach beyond this depth. At this point the stratigraphy is:

#### Section B (Diagram 6)

- 0.00-0.70 m : peat, fibrous, not compacted, watery; no samples taken;
- 0.70-4.50 m : water, some fine plant debris; no samples taken;
- 4.50-6.25 m : peat, undifferentiated, finely dissected; brown;
- 6.25-7.20 m : peat, undifferentiated, finely dissected but with Drepanocladus fluitans; brown;
- 7.20-7.93 m : peat, with abundant sedge leaf fragments, gyttja percentage increases downward; brown;

- 7.93-11.90m : gyttja, soft gelatinous at top, becoming stiffer downward; dark brown;  
 11.90-12.50m : gyttja with silt and clay; dark brown.

Section C was taken through a Cassandra heath on April 12, 1968, 1.5 m west of the site where section B was collected. At this time more extension rods were available and the Hiller sampler was used to a depth of 14.5 m. The Davis head coupled to the Livingstone rods enabled further sampling to 15.17 m. The stratigraphy of this section is:

Section C (Diagram 7 and 8)

- 11.50-12.30 m : gyttja, soft; dark brown;  
 12.30-14.90 m : gyttja, with increasing amounts of clays and fine sand, some plant debris present; dark brown above, becoming light brown to gray to light gray at bottom;  
 14.90-15.17 m : clay, stiff and dense, with dark brown stains, small specks of vivianite present; bluish gray;  
 15.17- m : not sampled further because of the difficulty of withdrawing the sampler from the sediments.

Pollen Stratigraphy

Zone T. The lowest sediments sampled at Allenberg bog, including the basal clay and a portion of the clay-gyttja above, contain a pollen assemblage rich in NAP (see Diagram 7 and Appendix G). At 14.87 m, just above the base of the T/A zone boundary as it was placed in the diagram, 28 percent of the sum was contributed by nonarboreal species. In the next lower spectrum NAP increases to over 51 percent, and at 15.165 m it reaches a maximum of 55 percent.

The largest NAP contributor to the zone is the Cyperaceae which accounts for over 20 percent of the total. Also present is about 10 percent Gramineae pollen. From 5 to 7 percent of Artemisia pollen occurs, and Ambrosia, Thalictrum and high-spine Compositae pollen are found regularly but in lower percentages in all T zone spectra. Of the less common pollen types listed in Diagram 7 and Appendix G, pollen belonging to the Caryophyllaceae, Chenopodiaceae, Cichoriodeae and Labiatae and to Plantago, Ranunculus and Rumex appear most regularly. Microspores of Selaginella selaginoides were found at 14.985 and 15.085 m. Pollen from the shrubs Alnus, Myrica and Salix aggregate 15 percent of the total.

The most frequent AP type in the T zone, Picea, accounts for nearly 20 percent of the total. About 10 percent of Pinus pollen is present, and in general half of this is of the Diploxylon type. Very low percentages of Pinus Haploxylon pollen also occur. Quercus pollen is uniformly present in amounts which range from 5 to 8 percent. A high in the Quercus curve occurs near the top of the T zone and carries over to the lower A zone spectra where a peak occurs. Increasing percentages of Fraxinus 3-colpate pollen are found from the lowest spectrum upward across the T/A zone transition where a maximum of 9 percent occurs. Abies, Betula, Carpinus-Ostrya and Ulmus are weakly represented and a few grains of Acer saccharum, Carya, Corylus, Fraxinus

4-colpate, Juglans cinerea, Larix and Populus occur in some or all of the spectra.

Diagram 8, which shows the number of grains per ml of wet sediment, was prepared for the same spectra graphed in Diagram 7. The number of grains in the three lowest samples is relatively small and ranges from 26,000 to 40,000 per ml (see Fig. 8). In the sediments above, the absolute number rises gradually to about 200,000 at 14.425 m near the bottom of the A zone, and it fluctuates near this figure to the end of the zone at which point the number of grains again increases until the maximum of about 380,000 grains is reached at 12.425 m. Assuming that the rate of sedimentation was constant, Diagram 8 shows that in relation to the A zone relatively few pollen grains of any type were deposited during the accumulation of T zone sediments. The change upward into the A zone is marked not only by an increase in the percentage of spruce pollen, but also by a six-fold increase in the numbers of spruce grains being deposited. Contrary to the implication of the relative percentage diagram, larger numbers of Cyperaceae pollen occur above the T zone than within it.

Zone A. Spruce pollen dominates slightly over 2 m of sediments at Allenberg bog. It accounts for about 40 percent of the total in nearly all spectra except those near the bottom of the zone, where at one level over 60 percent was found. This peak is associated with lows in the Pinus

total and Pinus Diploxylon curves and high (but not the highest) percentages of Quercus and Fraxinus 3-colpate. The absolute pollen frequency diagram, however, does not show these fluctuations, although lower numbers of Pinus grains occur below the level of the Picea peak than above it.

Except near the T/A transition, Pinus accounts for about 20 to 25 percent of the total in all A zone spectra. Nearly half can be assigned to the Diploxylon type. Haploxylon grains also occur and, in the upper two thirds of the zone, they account for about 5 percent of the total, but nearer the bottom, lower percentages are found.

With the exception of somewhat higher percentages in the lower part of the zone, Quercus averages about 7 percent of the total in all A zone spectra. Highs in Carpinus-Ostrya, Fraxinus 3-colpate and Polypodiaceae curves are also present near the bottom of the zone. Two peaks in the Abies curve occur near the beginning and end of the zone at 13.075 and 14.425 m. From 2 to 5 percent of Ulmus, Betula, Corylus and Populus pollen are present throughout. Larix, although poorly represented in the lowest A zone spectra, increases to about 5 percent just below the middle of the zone and remains near this level upward to zone B.

NAP percentages above the T/A zone transition are about one-third of what they were in the T zone. Alnus, Cyperaceae and Gramineae have the highest percentages. Salix is more weakly represented in this zone than below and

finally drops out upward in zone B (see Diagram 7) or near the bottom of zone C-1 (see Diagram 6). High-spine Compositae, Ambrosia and Artemisia are present in nearly all spectra and the curve for the latter has three highs at various points throughout the zone.

The relative and absolute pollen frequency diagrams agree closely across the A zone.

Zone B. The A zone to the B zone change is shown in Diagrams 6 and 7. In spite of the close proximity of the sample series, the B zone begins 30 cm lower in Diagram 7. However, the percentages in both match well. Just the top of the A zone occurs in Diagram 6.

The A/B zone transition is marked by several important changes in pollen percentages. In a span of 25 cm Picea decreases from 35 to 5 percent, and it finally drops out near the end of zone B. The boundary between the two zones was drawn at the middle of the Picea decline which also corresponds to about the middle of the Pinus increase. This transition is characterized by peaks in the Betula, Fraxinus 3-colpate, Larix and Populus curves. Quercus percentages steadily increase in the lower half of the B zone and reach a high of 25 percent near the end of this zone. Associated with this is an increase in Carpinus-Ostrya percentages which remain high but decrease somewhat in the lower part of zone C-1 over a peak reached near the end of zone B.

NAP percentages decrease at the A/B zone transition and are low throughout the B zone. Small but steady percentages of Alnus, Cyperaceae, Ambrosia, Artemisia, high-spine Compositae and Thalictrum occur. In no B zone spectrum do NAP percentages rise above 2 to 3 percent of the total.

Both the absolute and relative frequency curves are similar across the B zone. The high numbers of total pine pollen which occur in a broader interval than is evident in the corresponding relative frequency curve help to define the zone. The two taxa which contributed the greatest numbers of grains in the B zone of Allenberg bog, as was the case in the two Valley Heads bogs discussed previously, are Pinus and Quercus. The total number of Pinus grains at 12.425 m, the peak of the pine curve, was 145,000. Quercus at the same level was represented by 91,000 grains.

The Betula, Carpinus-Ostrya, Fraxinus 3-colpate and Populus highs shown in the relative frequency diagram also appear when the data are plotted on an absolute basis. If the sedimentation rate was constant across the A/B zone transition, these peaks occurred at a time of high pollen delivery to the basin which presumably reflects a greater abundance of the plants producing these pollen types in the region neighboring the basin.

Zone C-1. A complete C-1 zone is shown in Diagram 6, but in Diagram 7 only the lower third of it is present. The

B/C-1 transition is marked by rapidly increasing percentages of Tsuga pollen coordinated with decreasing percentages of Pinus grains. However, the Pinus decline is not as abrupt as the increase in Tsuga and there is a small interval across which the percentages of both are high. Quercus remains strongly represented across the transition and high percentages persist through the lower third of the zone. Near 11 m, Quercus decreases from 20 to 10 percent, while Fagus and Betula percentages increase. Quercus continues to decline upward through the C-1 until just below the 9 m level where only 7 percent occurs, its lowest postglacial percentage at this site. Fagus is weakly represented in B and lower C-1 spectra, but it begins to increase above 11.675 m, after Tsuga becomes stabilized at near 30 percent of the sum. Near the middle of the zone, Fagus accounts for 13 percent of the total, but in the upper one-third of the zone, it comprises 27 percent. The curves for Acer saccharum, Betula and Juglans cinerea show highs near the middle of the zone.

Although Fraxinus 4-colpate and Tilia first appear in the B zone, the former has a maximum in the lower third of the C-1, while in the same interval the latter has two highs, one near the beginning and one near the end of the zone. From 3 to 5 percent Fraxinus 3-colpate pollen occurs regularly in the lower two-thirds of the C-1. In the rest of the zone only about 1 percent is present. A parallel change also occurs in the Carpinus-Ostrya curve. Ulmus is uniformly



present in all C-1 spectra and accounts for about 7 percent of the sum. The C zone maximum for Platanus is reached at the end of the C-1. Carya pollen, which is found in low percentages at the beginning of the C-1, increases slightly in percentage upward in the zone. Except for sporadic grains in lower levels, Castanea occurs regularly from the upper one-third of the zone to the topmost spectrum.

Total NAP percentages vary from 1.2 to 3.6 in zone C-1. Cyperaceae and high spine Compositae are most consistently present. Less frequently counted pollen types are graphed in Diagrams 6 and 7 or listed in Appendices F and G.

As in zone B, the relative and absolute frequency curves parallel one another (cf. Diagrams 7 and 8). In that portion of the C-1 studied the largest numbers of grains belonged to Tsuga and Quercus. Pinus is also an important component of lower C-1 spectra.

Zone C-2. The boundary between this zone and C-1 is easily placed at about the midpoint of the Tsuga decline, but the upper boundary of the C-2 is more difficult to locate. The gradually increasing Tsuga percentages which characterize the C-2/C-3 transition in the Valley Heads bogs are not evident in Diagram 6, although they do occur in Diagram 5. Tsuga percentages increase somewhat in the upper 0.5 m of Diagram 6, and for this reason the zone boundary was placed just below this level. A case might also be made for locating it beneath the 8 m level at which point Quercus and Betula

percentages have decreased somewhat over their previous highs. However, this creates an unusually thin C-2 zone, especially when taking into account the amount of sediment above this level and a comparison between Diagram 6 and the complete Protection bog profile. A similar comparison suggests that a part of the C-2 zone may be represented in Diagram 5.

At the C-1/C-2 transition Tsuga pollen drops from 38 to 7 percent in 50 cm. A small decrease in Ulmus percentages is also apparent across this interval. These reductions are mainly compensated for by increases in percentages of Acer saccharum, Betula and Quercus and to a lesser degree by Carya, Fagus, Fraxinus 3- and 4-colpate, Pinus undifferentiated and Pinus Haploxylon. The Fagus curve shows a gradual increase from 22 percent near the end of the C-1 to 30 percent just below the C-2/C-3 boundary at a depth of 6 m. Higher percentages of Acer saccharum, Betula and Quercus are maintained throughout the C-2 than occur in the upper C-1 spectra. Castanea is weakly represented across the C-1/C-2 transition but reaches its maximum of 4 percent at 7.175 m, well into zone C-2.

Two Tsuga highs, each about 15 percent, occur in the middle of the C-2. These represent an increase over the 7 percent Tsuga low present near the beginning of the C-2 and the 9 percent low which occurs near the end of the zone. After a sporadic presence in much of the C-1, Larix regularly

appears from the beginning of the C-1 to the uppermost spectrum in Diagram 6. Similarly, Picea pollen, after an absence from all C-1 spectra except the lowest, occurs in low percentages from near the beginning of the C-2 upward.

Total NAP percentages remain small throughout the C-2. One or two percent of Alnus, Ambrosia, Artemisia, Cyperaceae and Gramineae pollen is most regularly present. The peak in the Cyperaceae curve just above the 7 m level may be associated with intrabasinal succession, since sedge peat, which is evidence of the presence of a sedge mat at the surface, occurs just below it. The associated Ambrosia high is more difficult to explain, although contamination during sampling may be the cause.

Zone C-3. The complete C-3 zone is shown in Diagram 5; percentages of minor pollen types are listed in Appendix E. At Allenberg bog the increasing Tsuga percentages of this zone are associated with decreasing Fagus values. As in the Valley Heads bogs, the upper NAP rich sediments are placed in subzone C-3b. The remainder of the zone, where NAP percentages are minimal, belongs to the C-3a.

Except for minor fluctuations, the percentages of most pollen types remain more or less constant across the C-3a. The percentage of Betula pollen increases below the C-3a/C-3b boundary and remains higher in the C-3b than in the C-3a. Together Picea and Larix account for about 4 percent of the sum in most C-3 spectra. NAP percentages are

low in the C-3a subzone and average about 3 percent of the total. Alnus, Ambrosia, Cyperaceae and high spine Compositae are most regularly present.

The higher percentages of Cyperaceae in the lower half of the C-3a than in the upper seem to be related to intrabasinal succession. Upward from the lowest spectrum in Diagram 5, the aquatics Brasenia, Nuphar and Nymphaea abruptly drop out of the counts. Above the level of their disappearance, Cyperaceae percentages increase and above this, increases occur in the curves for Ericaceae and Osmundaceae. These changes match those expected during succession from open water to an ericaceous shrub association of the type which occurs at the surface today. Pollen typical of the terminal stage, a bog forest, does not replace the Ericaceae upward, but the occurrence of Larix and Picea pollen throughout zone C-3 is evidence for its presence somewhere on the bog mat. A few spruce needles recovered from the peat in the lower C-3b spectra imply the presence of spruce trees near the sampling point at the time this part of the zone accumulated. These were no doubt produced by black spruce which is found on the bog mat today.

The C-3a/C-3b transition is abrupt and clearly marked by a decrease in AP and an increase in NAP. The largest reductions in tree pollen percentages occur in Fagus, Pinus Haploxyton, Quercus and Tsuga. Acer saccharum percentages drop somewhat but generally remain high, as do those for

Betula. Only Acer rubrum/saccharinum and Populus show a marked increase in C-3b spectra.

At 2.5 cm beneath the surface total NAP reaches 57 percent of the sum, the highest in the C-3b subzone at Allenberg bog. Pollen from herbs which today grow mostly in disturbed habitats is abundant. As in the Valley Heads bogs, Ambrosia has higher percentages than any other NAP type. Pollen from Cheno-Ams, Cichorioideae, Gramineae p.p., Plantago and Rumex, probably produced by weedy species, also occurs. Fagopyrum, Gramineae p.p. (incl. Cereal) and Zea pollen, representing cultivated plants, was present but in much lower percentages than the weeds. Highs in the Cyperaceae, Ericaceae, high-spine Compositae, Nemopanthus and Polypodiaceae curves probably reflect conditions on the bog mat favorable to the growth of local species.

#### Pollen Size-Frequency Measurements

In certain cases size is a useful species character in pollen which on other morphological grounds can be identified only to genus (Cain, 1940; Cain and Cain, 1948; Leopold, 1956a). For this reason measurements were made on as many well-preserved Betula, Picea and Pinus Diploxylon grains as possible while counting the Allenberg bog sections. Silicone oil is a particularly effective mounting medium in such studies because gentle tapping of the cover slip rotates grains permitting access to the length chosen to be measured.

The data collected have been plotted in size-frequency graphs (Figs. 4, 5 and 6).

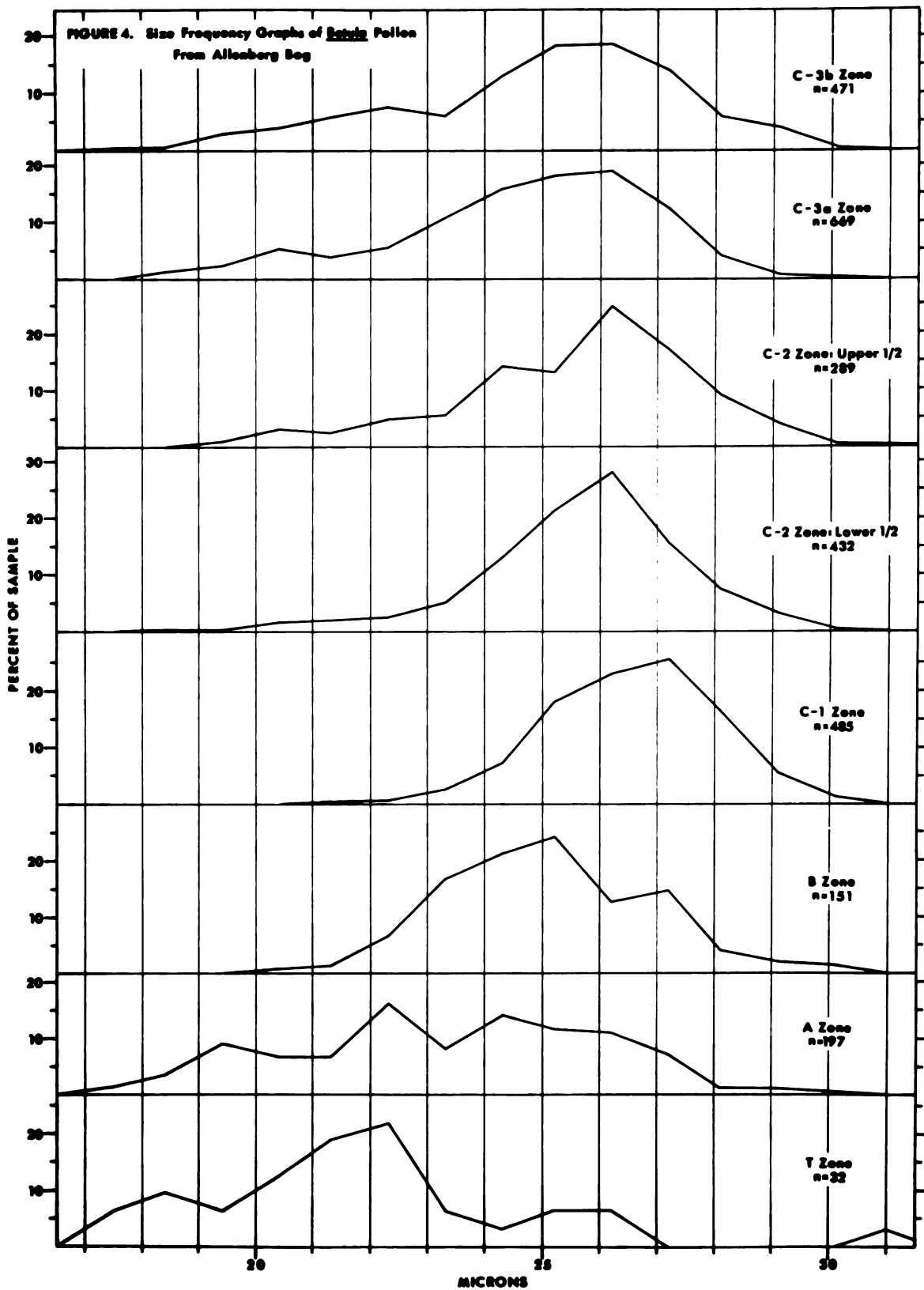
Some difficulties in using size-frequency data have been reviewed by Whitehead (1964). The maceration procedure employed to isolate pollen from sediments, the nature of these sediments and the medium in which the pollen is mounted for microscopic study apparently affect grain size. When these sources of variability are coupled to the fact that in only a few cases has an analysis been made of the geographical variation in pollen size of a given species, not to mention the absence of an evaluation of differences within populations or within a single individual, fossil size-frequency data must be interpreted cautiously.

Certain of these factors have been studied but less variability was found than anticipated. For example, Faegri and Deuse (1960) exposed Betula tortuosa pollen to different lengths of treatment in boiling 10 percent KOH and did not find a significant size change with longer treatment, although they did observe an increase in size when acetolysis followed exposure to KOH. These authors have also shown negligible changes over a period of 5.5 years in pollen preparations mounted in water, glycerol and glycerine jelly. Clausen (1960), who studied freshly gathered pollen from different parts of Betula catkins located on different parts of two birch species, was unable to demonstrate any significant size variations within a single species. Similar studies

need to be extended to all species identified on size characteristics alone, but, if the same maceration procedure and mounting medium is used for the fossil samples and the modern preparations employed to identify peak frequencies within a fossil spectrum, variability caused by these factors can be minimized.

Betula. The most extensive study of size variation in pollen of the North American species of Betula has been published by Leopold (1956a). Birch pollen is triporate and the dimension usually measured extends from the tip of a pore across the grain to the edge of the exine in the interporal area on the opposite side. This, the maximum diameter of the grain, can be measured at three places. The grain diameter:pore depth ratio, used recently by Birks (1968) to identify Betula nana pollen, may also be useful for working with temperate North American species.

Measurements collected from individual spectra were lumped by zones or major portions thereof to increase sample size and to produce graphs that were characteristic of the main subdivisions of the diagram (see Fig. 4). As only one mode occurs in nearly all parts of the C zone, one or possibly two birch species with pollen grains of similar size seem to have been dominant during C zone time. Today only Betula lenta and B. alleghaniensis occur in the region (Zenkert, 1934) and, although the former is not listed by Schick and Eaton (1963) as growing within the Allenberg bog-Waterman





swamp area itself, it is reasonable to conclude that these species contributed most of the birch pollen to C-3b spectra. The gross volume data collected by the U. S. Forest Service show both species to be about equally abundant in Cattaraugus County (Northeastern Forest Experiment Station, 1967). Because nearly identical modes occur throughout zone C, B. lenta and B. alleghaniensis are likely to have been the only species present.

The highest size-frequencies occur over a 1 to 2 mu interval with the mode at 26 mu in the C-3b, C-3a and the upper and lower halves of the C-2, but in the C-1 the mode shifts to 27 mu. Leopold (1956a) has reported the mode for Betula lenta pollen to be 28 mu in acetolyzed samples and to be near 24 mu in those treated only with KOH. In B. alleghaniensis the mode for KOH treated samples is 28 mu but it is 45 mu for acetolyzed ones. My samples were exposed to both KOH and acetolysis, so it is expected that their modal classes would be near the larger figures. The fact that they are smaller may be related to the shrinkage phenomenon reported to occur during fossilization in peat by Buell (1946) and others. The shift in the position of the mode in zone C-1 to slightly larger grains may indicate the presence of Betula papyrifera, a species which, although now rare in western New York, may have been more abundant in the past.

The modes shift to smaller size classes in zone B and below. The presence of at least some grains greater

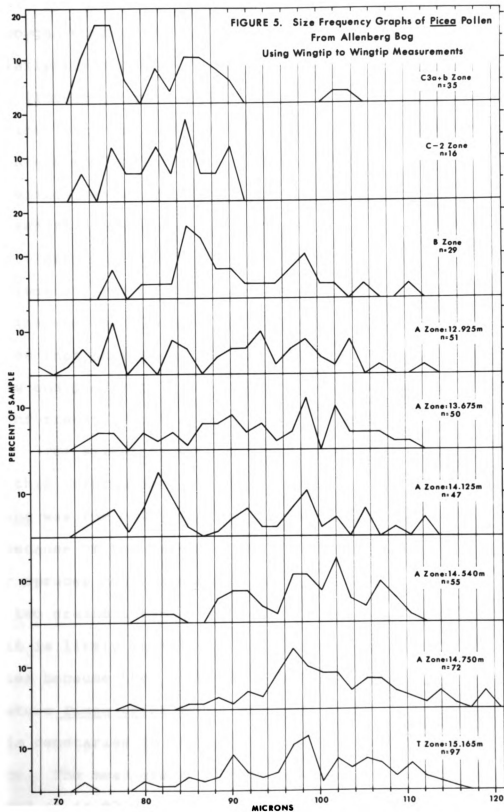
than 25 mu suggests that Betula lenta, B. alleghaniensis and perhaps B. papyrifera grew at an unspecifiable distance from the basin during the period of time represented by these zones. However, it is difficult to identify the main birch species contributing pollen to zone B sediments because none of the taxa studied by Leopold (1956a) has modes at 25 mu. Perhaps some aspect of the depositional environment caused pollen from the three tree species to shrink more in zone B than in those zones above or possibly another species was present. If so, it may have been the shrub Betula pumila which has been found only once in western New York within the area of glacial lake Tonawanda, but likely had a wider distribution in the past. Leopold (1956a) considers the pollen of this species to be smaller than that of the tree birches mentioned above, but the mode at 30 mu for the aceto-lyzed sample she reports does not match the mode in the fossil material. Betula pumila pollen treated only with KOH is smaller, however, and six samples prepared this way have a mean size of 24 mu.

The modes at 22 mu in the A and T zones can be identified with more certainty. Leopold (1956a) has found Betula glandulosa, an arctic-alpine species found as far south as the Adirondack mountains in eastern North America (Fernald, 1950), to have small pollen with modes at 20, 22 and 23 mu in the three acetolyzed modern samples she studied. These

comfortably overlap the mode for fossil grains in both zones at Allenberg bog.

Picea. The technique of using the size-frequency graph at the surface to interpret those beneath can also be used in reference to Picea (see Fig. 5). There are three spruce species that could have been members of the late- and postglacial vegetation of western New York, Picea glauca, P. mariana and P. rubens. The last named is now found in mountain forests stretching from the southern Appalachians to New Brunswick and Nova Scotia (Fowells, 1965) but, in spite of some evidence that it may have occurred as far west as Michigan during A zone time in this area (Cain, 1948), the distributional history of the taxon is largely unknown.

A number of recent workers have consistently separated the pollen of Picea glauca and P. mariana. Most use only size characteristics, but there seem also to be morphological differences between these species (ibid.). Size-frequency measurements indicate that the smaller grains generally belong to P. mariana and larger ones to P. glauca (Cain, 1948; Davis and Goodlett, 1960; Heusser, 1960). West (1960) has used 100  $\mu$  based on wingtip to wingtip measurements as the point of separation between them in his work in eastern Wisconsin. Unpublished measurements of this dimension made by James H. Anderson of Michigan State University (personal comm.) on three collections of P. glauca treated with 10 percent KOH and acetolyzed have the following



means: 116 mu (Arnold Arboretum, Massachusetts), 104 mu (Cheboygan County, Michigan) and 99 mu (Neultin Lake, N.W.T.). Similarly treated samples of P. mariana have smaller means: 85 mu (Ingham County, Michigan) and 79 mu (Thunder Bay District, Ontario). Since these data indicate that a total length greater or lesser than 100 mu is a reasonable point of division between the pollen of these species, this figure was used in the present study.

Maximum internal diameter (excluding the wings) measurements of five collections of Picea rubens pollen show that the average of the means is about 3 mu greater in this species than an average of the same dimension in P. glauca (Davis and Goodlett, 1960). Wingtip to wingtip measurements are unfortunately not available for P. rubens.

The size-frequency graphs are readily interpreted with this information. We can be fairly certain that Picea mariana was the only species present in zones C-3a + b and C-2 because of the probable absence of habitats for the two other spruces near Allenberg bog during the past 4000 years. Only two grains larger than 100 mu were found in these zones, and it is likely that these originated from introduced species because they occurred in post-settlement spectra. As mature Picea abies trees are common near farm dwellings and in cemeteries in the area, this species is a possible source. The mean grain size in the C-3a + b is 81 mu; in the C-2 it is 82 mu. Spruce pollen is practically absent in

zone C-1 at Allenberg bog. It also occurs in low percentages in the C-1 at the other sites included in this study.

In zone B the mean grain size is 91  $\mu$ , but 87 percent of the grains are still less than 100  $\mu$  in length. Progressively lower in the bog, the mean size is larger and a maximum of 101  $\mu$  is present at 14.750 m near the bottom of zone A. At this level 53 percent of the grains are greater than 100  $\mu$ . At 15.175 m in zone T the mean size decreases slightly to 98  $\mu$  but 43 percent of the sample is greater than 100  $\mu$ . In the lower spectra the maximum wingtip to wingtip length found was 120  $\mu$ . Whether such grains belong to Picea rubens cannot be determined, but occasional grains of P. glauca attain this size.

Pinus. Early work on size-frequency distributions in Pinus pollen suggested the feasibility of species identification on this basis. Cain (1940), for example, found three modes in a size-frequency curve of fossil pine pollen extracted from the Spartanburg buried soils on the Piedmont of western South Carolina. He related the smallest mode to P. banksiana and the larger ones to P. glabra and P. rigida or P. palustris. In a study of pine pollen from sediments in a southeastern Michigan lake, Cain and Cain (1948) found bimodal and trimodal distributions which they considered evidence for the occurrence of P. banksiana, P. resinosa and P. strobus.

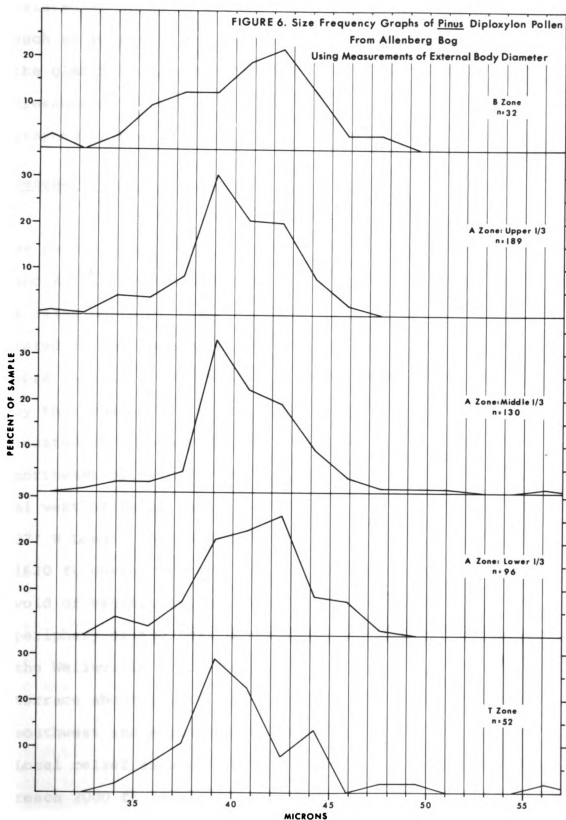
The presence of a verrucose furrow (Ueno, 1958) allows pollen from the only member of the subg. Haploxyton in eastern North America, Pinus strobus, to be tabulated separately from the smooth furrowed pollen of the subg. Diploxyton. Size measurements of Diploxyton pine pollen can thus be directed at identifying the occurrence of species exclusive of P. strobus.

Whitehead (1960) has studied pollen of all Pinus species occurring in eastern North America and has published the most complete size-frequency data available. Our maceration techniques were similar, so his data should be comparable to mine. Whitehead found that, of the three Diploxyton pines expected in western New York pollen profiles on the basis of modern distribution patterns, P. banksiana, P. resinosa and P. rigida, the last named has the largest grains with a mean size of 44.95  $\mu$  based on 9 collections. Pinus banksiana and P. resinosa pollen grains are smaller. The mean size of P. banksiana based on 24 different samples was 37.01  $\mu$ , while the latter, based on half as many, was 40.11  $\mu$ . Whitehead concludes, "it is . . . doubtful if one could separate grains of Pinus banksiana and P. resinosa in size-frequency analysis even though the means differ by 3.10  $\mu$  . . . [and] . . . a size-frequency curve for fossil grains to which both species contributed would be perfectly unimodal" (p. 772). His measurements are of internal body diameter.

My own measurements of fossil *Diploxylon* pine pollen from Allenberg bog are graphed in Fig. 6. Since I measured the external body diameter, 2  $\mu$  should be subtracted from my data to obtain figures which are equivalent to those of Whitehead (ibid.). In zone B the modal class at 42.5  $\mu$  minus the 2  $\mu$  correction factor gives a figure which compares well with the mean size of *Pinus resinosa* pollen as determined by Whitehead. In the upper two-thirds of zone A the mode for the Allenberg data shifts to 37  $\mu$  (39  $\mu$ ) suggesting dominance by *P. banksiana*. A fairly prominent shoulder at 40.5  $\mu$  (42.5  $\mu$ ) corresponding to the mode in the B zone also occurs in these graphs. In the lower third of zone A the mode again shifts to the larger size class. None of my size-frequency graphs is strictly bimodal, but the correlation in size implies the presence of both species in zones A and B.

In zone T, two modes occur, one at 37  $\mu$  (39  $\mu$ ) and another at 42  $\mu$  (44  $\mu$ ). The lesser corresponds to the two upper A zone modes and presumably reflects the presence of *Pinus banksiana*, while the greater has no precise counterpart elsewhere in Fig. 6. Since the T zone was apparently a time of low pollen delivery to the basin by the regional vegetation, the probability of finding far-travelled pollen types in T zone spectra is greater than elsewhere in the profile because they would not have been masked by nearby pollen producers. Perhaps the higher frequency of larger grains is





related to input by one of several possible pine species, such as P. rigida, which occurred at some distance south of the glacial boundary. However, no clear evidence of the presence of P. rigida is shown in the pre-C zone samples graphed in Fig. 6.

#### Genesee Valley Peat Works

This site occurs in an area mapped by Connally (1964) as part of the pre-Kent Olean moraine. Similarly, MacClintock and Apfel (1944) and Muller (1960) place the Kent terminal moraine north of the locality. The peat, which has accumulated in what seems to have been originally a shallow 10 acre lake in a pitted valley train, is being actively mined by the owner, Paul Button of Belmont, New York. The site is located in Allegany County in the Town of Amity, 2.6 mi northeast of Belmont on the north side of NYS 244 about 0.3 mi west of Baker Valley Rd at 42° 15' 10" N Lat and 78° 59' 37" W Long. The surface of the peat deposit lies near the 1620 ft contour line. The peat works is shown as an area devoid of vegetation, but with three small ponds that mark the periphery of the peat deposit, on the northwest quarter of the Wellsville North quadrangle. The basin occurs on a flat terrace about 100 ft above Phillips Creek which flows to the southwest and empties 3 mi downstream into the Genesee River. Local relief is about 350 ft and many of the surrounding hills reach 2000 ft in elevation.

The peat deposit was wooded when Button purchased it in 1951 and at this time no outlet or inlet existed. He removed the trees and built a dike at the west end of the basin to flood it for use as a trout pond. During the ensuing years the stumps and root mat became freed from the underlying peat and Button decided to drain the pond and begin to excavate the peat. The surface was bulldozed clear, a channel was cut through the drift at the west end to facilitate drainage and the peat along the south rim of the basin was removed and dragged up onto the land for drying (see Plate 2, Fig. B). Mining has continued along this edge. The peat after being screened is sold in nearby cities for use in gardening.

According to Button the bog surface was covered with a forest of Acer rubrum, Betula alleghaniensis, Pinus strobus and Tsuga canadensis. At the basin edge Prunus serotina and Ulmus sp. occurred. Apparently Picea mariana and Larix laricina were absent. In a somewhat open area near the east end, cranberries (either Vaccinium macrocarpon or V. oxycoccus) grew and Arisaema sp. and Cypripedium acaule and C. calceolus were mentioned as noteworthy for their abundance on the forested mat.

At the present time the site is entirely surrounded by fields or secondary forests. To the north and contiguous with the basin margin is a highly disturbed forest remnant, long cut over and now dominated by trees of small diameter.

The following species were noted in the summer of 1967:

Acer rubrum, Crataegus sp., Pinus strobus, Populus grandidentata, Prunus pennsylvanica, P. serotina, Quercus alba and Tsuga canadensis. Cultivated land occurs on the east and south sides and a plantation of small conifers in an abandoned field is located immediately to the west of the basin. In general a large percentage of the surrounding hill tops are forested but valley floors and lower slopes are usually under cultivation. Oak-rich forests are more abundant in this area than to the west in Cattaraugus and southern Erie Counties.

#### Sediment Stratigraphy

The deposit was sampled on September 12, 1966 near the west end of the basin at a point where Button said that the maximum depth occurred. The Hiller borer was used from the surface to 3.25 m. The Livingstone sampler equipped with a 1 in diameter barrel was employed beyond this depth. The stratigraphy at the sampling point is:

- 0.00-0.50 m : peat, undifferentiated, humified; dark brown, no samples taken because of disturbance;
- 0.50-3.00 m : peat, undifferentiated, mostly coarse near top, finer at bottom, well compacted, Meesia trifaria layers at 2.63 and 2.83 m; dark brown and humified at top, reddish brown commencing at 0.75 m;
- 3.00-3.25 m : peat, mostly sedge leaf debris, with Meesia trifaria layer at 3.18 m; light brown;
- 3.25-3.35 m : gyttja; brown;
- 3.35-4.16 m : gyttja, with silt and clay;

- 4.16-4.80 m : silty-clay, compact, with shale fragments and quartz sand and granules throughout but most abundant near bottom, layer of gastropod shells at 4.60 m, small vivianite nodules from 4.70 m, mostly greenish gray;
- 4.80- m : further sampling not possible because of the compactness of the sediment.

### Pollen Stratigraphy

The pollen zonation at the Genesee Valley Peat Works is basically similar to that found in the three bog deposits discussed previously. However, several important differences are apparent: the tripartite C zone does not occur, pine pollen is predominant over an exceptionally broad interval and very high NAP percentages are associated with rather low percentages of spruce pollen in the sediments beneath zone B. These divergences from the basic pattern have made the placement of zone boundaries difficult and the two shown on Diagram 9 have been placed with question.

The precise age of the Olean drift on which the present site is located is unknown, but it generally is considered to be older than the Kent glaciation, dated at 23,250 B.P. near Cleveland, Ohio (White, 1968), which in turn predates the deposition of the Valley Heads moraine. The temporal equivalence of the A and B zones at the Genesee Valley site and similar zones elsewhere in southwestern New York cannot be exact because of the differences in the times of basin origin. Radiocarbon dates for all the boundaries

are needed to determine the precise relationship between the Genesee Valley profile and the others.

Zone A. Spruce pollen reaches a maximum of 29 percent in one level near the bottom of the zone, but in general its percentages are half what they are at the other sites in the study area. Spruce gradually decreases in abundance upward and is replaced mainly by Pinus. About 5 percent Pinus Diploxylon occurs; Pinus Haploxylon pollen was only sparsely represented. Also present in A zone spectra is 2 percent Abies pollen.

Pollen from broadleaf deciduous trees consistently occurs in the A zone. Fraxinus and Quercus each account for about 8 percent of the sum, and lesser, but nonetheless substantial, percentages of Betula and Carpinus-Ostrya also were found. In addition Acer, Carya, Corylus, Fagus, Juglans, Ulmus and Tsuga pollen occur, but in very low percentages. Typically, these taxa amount to 15-20 percent of the total.

The most unusual aspect of the A zone is the high percentages of NAP. In similar stratigraphic positions at the other sites, total NAP reached only 10 percent, but here it uniformly accounts for over 30 percent of the sum and reaches 48 percent in the bottom spectrum. Near the A/B transition between 3.45 and 3.19 m, NAP decreases from 33 to 5 percent. Pollen from a variety of herbs was identified throughout zone A. Cyperaceae, Gramineae, high spine Compositae and Salix have by far the highest percentages and

total grass and sedge pollen varies from 25 to 30 percent. Lesser amounts of Alnus, Ambrosia, Artemisia, Cheno-Ams, Myrica, Plantago, Rosaceae, Thalictrum and Umbelliferae occur and, of the minor types listed in Diagram 9 and Appendix H, the most significant ecologically are grains similar to Empetrum sp., Dryas spp. and Saxifraga spp. which were found in spectra below 4.5 m.

The number of pollen and spores per ml of sediment does not help to further define the A zone. Below 3.19 m the grain number varies from 42,000 per ml at 4.8 m to 85,000 at 3.45 m, with most spectra having about 50,000 grains. The increase in the number of pollen and spores upward is not great enough to overcome the decrease in spruce percentages, so similar curves are obtained whether the data are plotted on an absolute basis or not.

Zone B. The A/B zone boundary was located at the middle of the increase in the Pinus total curve. Greater Pinus percentages are compensated for by a decrease in Picea and nonarboreal pollen. Both Pinus Haploxylon and Pinus Diploxylon grains are present and, while the former continues to occur in abundance upward, the latter falls to less than 1 percent near the middle of the zone and stays at this level until it drops completely out of the counts in the C-1. In some spectra, total Pinus accounts for 70 percent of the sum. Abies percentages reach a peak just below the middle of zone B.

High percentages of Quercus pollen which occur with pine in zone B at the other sites are not present until near the end of the zone. In the bottom half Quercus was found in slightly lower percentages than were present throughout zone A, but above the middle of zone B Quercus increases from 7 to about 15 percent.

The B/C-1 boundary was placed at the middle of the interval where total Pinus percentages decrease and Tsuga percentages reciprocally increase. The abrupt rise in the Tsuga curve marks the beginning of zone C-1 at this site as well as at the others in southwestern New York. A slight increase in percentages of Ulmus and Carpinus-Ostrya is apparent near the end of zone B, but percentages of other AP types remain fairly constant across the zone.

NAP percentages in zone B are about one-fourth of what they were in lower spectra. Cyperaceae and Salix pollen are the two most abundant types, but it is likely that these were produced by the local rather than the regional vegetation.

Intrabasinal succession is well-defined by peak pollen frequencies of bog and lake indicator species encountered at various levels in the sediments, which by themselves are evidence for such change. Pollen from Sagittaria and Sparganium, two shallow water, near-strand aquatics, occur in the lowest spectrum and upward for over 1.5 m. They imply that the water was probably too deep during most of



this interval to permit other aquatics to grow near the sampling point.

Somewhat higher in the sediments, Potamogeton makes its first appearance and later Brasenia occurs in abundance. These are rooted, open water aquatics which generally grow in shallow ponds. Both have their peak frequencies higher in the section, near the level where Sagittaria and Sparganium drop out of the counts.

Potentilla palustris and Potamogeton first appear together, but the peak percentage of the former is slightly above that of the latter, a situation perhaps caused by the occurrence of the Potentilla at the leading edge of an advancing bog mat. High percentages of Cyperaceae pollen occur in these levels and in those immediately above, at which point both Potentilla and Potamogeton have nearly dropped out of the counts.

The Cyperaceae high occurs precisely between the last occurrence of Potentilla palustris and the first occurrence of Ericaceae pollen. In absolute numbers of pollen per ml of sediment, sedge pollen is more than twice as abundant in this part of the profile than in the A zone. Within this interval occur three separate horizons of the moss Meesia trifaria, a predominantly boreal forest species with disjunct stations throughout the lake states. It grows in bogs and swampy woods and is often found in somewhat calcareous habitats.

Upward, Cyperaceae percentages decrease and percentages of Ericaceae and Polypodiaceae rise. Ericaceae reach a peak near the top of the profile and, slightly above this, maximum Osmundaceae percentages occur.

These changes record the presence of several distinct plant communities which probably occurred in response largely to the degree of basin infilling. In a developmental sequence open water, sedge mat, ericaceous shrub heath and lastly bog forest are the main ones indicated. The bog forest is the least clearly defined, but evidence of its presence is afforded by the high percentages of Osmundaceae spores similar to those produced by Osmunda cinnamomea and O. regalis, species which are characteristic of this habitat.

Zone C-1. The entire C zone is truncated and no subdivisions, as they are defined in the previous profiles, can be discerned. The Tsuga and Fagus curves suggest that only the C-1 is present. The two-step Tsuga curve is unparalleled elsewhere in the study area. High Pinus percentages persist well above the B/C-1 boundary and Pinus Haploxylon pollen is the predominant type present. Between 0.5 and 1 m Pinus drops below 10 percent of the total.

Pollen from deciduous tree species show a gradual increase in the upper C-1 spectra. Acer, Betula, Carya, Fagus, Fraxinus, Juglans, Tilia and Ulmus have higher percentages at the end of the zone than at the beginning. The temporary decrease in the Betula, Fagus and Quercus curves

at 1.41 m is associated with a reciprocal increase in Pinus. This probably reflects a short term change during which Pinus became more abundant locally perhaps due to disturbance.

Total NAP percentages are low and account for less than 2 percent of the sum in all C-1 spectra except at 0.67 m where Nemopanthus, Rhus, Salix and Viburnum pollen, probably from species growing on the bog mat, contributed over 12 percent to the sum.

## INTERPRETATION

### ZONE T

Among the sites included in this study, pre-A zone spectra with total NAP amounting to 50 percent or more of the sum occur only at Allenberg bog, although the lowest spectra in the two Valley Heads bogs contain enough non-arboreal pollen to suggest that they are transitional between the NAP-rich T zone and the comparatively NAP-poor A zone. The large nonarboreal pollen content in what I have called the A zone at the Genesee Valley Peat Works site is difficult to interpret and will be discussed under the heading, Zone A. T zones, or Herb Pollen Zones as they have come to be called more recently, have been found in various parts of glaciated eastern North America (Sirkin, 1967), Michigan (Anderson, 1954) and Minnesota (Cushing, 1967).

High NAP frequencies in basal lake sediments were overlooked by North American pollen analysts until Deevey (1951) demonstrated abundant sedge and grass pollen in clays from several lakes in northern Maine. A band of marly sediment within the clay contained lower NAP percentages and greater relative numbers of spruce and birch pollen than the clay above or below. The similarity in both pollen and

sediment stratigraphy between these changes and those associated with the European Younger Dryas--Allerød--older Dryas sequence indicates that the marl was deposited during the warmer Two Creeks interval. High NAP percentages above the marl were evidence of tundra vegetation occurring in response to the probable colder climate that prevailed during the subsequent Valdres glaciation; those below presumably recorded a similar type of vegetation developed during some phase of the Port Huron (Mankato) glaciation.

In southern Connecticut lake sediments determined by radiocarbon analysis to predate Two Creeks time, Leopold (1956b; Leopold and Scott, 1958) found similar fluctuations in pollen percentages. The youngest of these so-called "Pre-Durham" oscillations (T-3) is characterized by abundant herb and birch pollen. It succeeds spectra with low herb and relatively high spruce percentages (T-2), which in turn overlies sediments containing high herb pollen percentages (T-1). These fluctuations were correlated with the European Older Dryas--Bølling--Oldest Dryas sequence (Deevey, 1958) and were interpreted (Leopold, 1956b) as evidence of birch park-tundra developed during a pause or readvancement of the Port Huron ice (T-3), preceded by spruce park-tundra representing a period of climatic amelioration (T-2) which followed another interval of tundra vegetation (T-1).

Zone A spectra from southern New England have been internally divided into subzones, the "Durham" oscillations,

interpreted as responses to the Two Creeks--Valders climatic changes. These will be discussed later.

No "Pre-Durham" oscillations are present in the T zone at Allenberg bog, but the pollen assemblage compares fairly well with the T-3 from New England. Davis (1967a) has contrasted the basal herb zone pollen assemblages from various sites in New England, Wisconsin and Minnesota. Assemblages from Allenberg bog have much in common with comparable spectra from both of these regions, but in general, New England sites have less spruce and more sedge pollen than occurs in the Allenberg bog T zone. At the Minnesota and Wisconsin locations more spruce but about the same percentage of sedge pollen occurs.

Similar herb-rich spectra have been reported from only two sites in upstate New York: Crusoe Lake near Syracuse in north-central New York (Cox and Lewis, 1965) and Kernochan bog southwest of the Catskill Mountains near the Pennsylvania border (Stingelin, 1965). Erratic fluctuations of tree and herb pollen percentages in the basal gravelly clay at the former site and the unknown age of the sediments make interpretation difficult, but the authors tentatively suggest correlation with Deevey's Maine zonation. From 15 to 45 percent NAP occurs in a 2.5 m section of silty clay differentiated as zone T at Kernochan bog. The entire interval is interpreted as evidence of a period during which the vegetation near this site was taiga-like. It is of interest

that Quercus pollen is almost completely absent from the bottom 1.5 m of the section.

In recent years pollen diagrams have been most effectively interpreted by relating the current pollen rain from regions of known vegetation to fossil pollen assemblages. If fossil and modern pollen assemblages are similar, a high probability exists that the vegetation producing them was also similar and, as an extension of this, it can be further reasoned that the climate controlling the vegetation was alike at both points in time. The pollen content of uppermost lake sediments, moss polsters and other superficial pollen traps has been determined at many localities across northern North America, but the pollen rain of much of this region still remains imperfectly known. Nevertheless, Davis' (1967a) use of the analogue technique has produced several informative correlations.

None of the surface counts she illustrates are exactly like the Allenberg bog assemblage, although some spectra from the tundra and boreal forest regions of Labrador are similar. Of the sites in arctic and boreal Canada studied by Ritchie and Lichti-Federovich (1967), the pollen rain at Fort Churchill, Manitoba in the forest-tundra ecotone is perhaps the closest to the Allenberg bog T zone assemblage. Major pollen types found at the surface at Fort Churchill include: Picea--13 percent, Pinus--25 percent, Betula--11 percent, Gramineae--6 percent and Cyperaceae--24 percent.

Lesser amounts of Larix, Alnus, Salix, Myrica and pollen from a number of herbaceous species were also found. At this particular site only 0.1 percent Artemisia pollen occurs, but at other sampling localities in the same vegetation type up to 17 percent was counted. Unfortunately, the modern pollen rain in the tundra and tundra-forest ecotone, as it is currently known, is too similar to permit differentiation of these vegetation types in the fossil record (Davis, 1967a). Hopefully, as more data become available, better correlations should be possible.

The occurrence of an open, park-tundra vegetation surrounding Allenberg bog during the deposition of zone T might be questioned in light of the nearly equal representation of AP and NAP. However, the presence of 20 percent Picea and 10 percent Pinus pollen indicates that species belonging to these genera grew within pollen dispersal distance but not necessarily close to the basin. Ritchie and Lichti-Federovich (1967) report finding 4 to 35 percent spruce pollen in various parts of the subarctic where spruce trees occur in widely scattered stands surrounded by heaths and dwarf-birch tundra. In the high-arctic, still farther away from the region of provenance, less than 3 percent was encountered. Similarly, Hafsten (1961) working in the southwestern U.S., found about 10 percent Pinus pollen 150 mi from its nearest source, and Ritchie and Lichti-Federovich (1967) report over 10 percent pine pollen at the surface in



the three high-arctic sites they investigated. These findings are evidence that a considerable quantity of pine and spruce pollen is normally blown into areas where the parent plants either do not occur or are of patchy distribution. The presence of other tree pollen types in zone T can be similarly explained.

Pollen contributed to a given part of a profile is derived from both nearby and distant sources, but because the absolute pollen frequency data indicate a low delivery rate of pollen and spores to the basin during the T zone interval, the area contributing to the pollen rain may have been much larger at this time than during any subsequent period. Fewer than 1000 grains/  $\text{cm}^2$  / year were deposited in zone T at Rogers Lake, Connecticut in sediments older than 12,000 B.P. (Davis, 1967b). The absence of radiocarbon dates at Allenberg bog makes similar calculations impossible, but the number of grains/ml of sediment is nearly equal in pre-A zone levels at both sites.

With a relatively low number of grains reaching the basin every year, the few grains that are occasionally shed in the air by local entomophilous species and those derived from distant sources would have an increased chance of being expressed in the counts. This is borne out by data collected by Ritchie and Lichti-Federovich (1967). They found about 1400 grains/  $\text{cm}^2$  / year being deposited at Fort Churchill in the region which provides a close modern analogue to the

Allenberg bog T zone fossil pollen assemblage. Pollen from both entomophilous taxa and species which grow many hundreds of miles away are represented in their counts. With this phenomenon in mind, species represented in the T zone at Allenberg bog can be discussed.

Among the arboreal pollen types identified in zone T, those of temperate thermophilic species are incongruous in a pollen assemblage which otherwise indicates the vegetation surrounding the site was similar to that in the boreal forest-tundra ecotone. The pollen types in question include Fraxinus nigra (from 3 to 5 percent), Quercus (from 3 to 8 percent) and a few grains of Carpinus-Ostrya, Carya, Corylus, Fraxinus americana and/or F. pennsylvanica, Juglans cinerea and Ulmus. Such pollen frequently occurs out of place in lateglacial T and A zone spectra throughout glaciated eastern North America. Its presence has been explained by claiming redeposition from older sediments (Andersen, 1954) and long-distance wind transport (Deevey, 1951). A third alternative, that species producing these types actually grew nearby, seems less likely at least during the deposition of T or Herb Pollen Zones.

I know of no source near Allenberg bog for rebedded grains. Furthermore, pollen in the T zone at this site is extremely well-preserved and shows little evidence of abrasion. A strong case can be made, however, for wind transport of exotic grains using recently published data of

Ritchie and Lichti-Federovich (1967). They measured the pollen rain at Fort Churchill with a Hirst spore trap for six days in early May, a time when local plants had not begun to flower. During each 24 hour period at least one Quercus grain was trapped and a maximum of four grains were collected on one of the six days. Other types were recovered less frequently, but often were more abundant. For example, 17 Ulmus grains, 15 Corylus grains and 5 Fraxinus grains (pollen with 3 and 4 colpi were not separated) were trapped in one 24 hour period. All of the exotic pollen types occurring in the Allenberg bog T zone except Carpinus-Ostrya were found capable of being carried to Fort Churchill from sources 500 to 1000 mi away.

Calculated as a percent of the sum of all other pollen and spore types trapped by the Hirst sampler, however, such pollen amounts to only 0.6 percent of the total. Since by comparison higher percentages of Quercus and Fraxinus occur at Allenberg bog, pollen producing trees of these taxa perhaps grew much closer to the site than did species of Carya, Corylus, Juglans and Ulmus. The nearness of Allenberg bog to the unglaciated Salamanca reentrant and other ice-free areas further south suggests that black ash and certain oak species may have occupied favorable habitats several tens of miles beyond the terminal moraine. Of the ash species in eastern North America, Fraxinus nigra currently has the most northern distribution, so it seems likely that it would be

able to survive closest to the ice front. Similarly, Quercus macrocarpa and Q. rubra, which are found northward to the edge of the boreal forest, are the most probable members of the lateglacial T zone vegetation near Allenberg bog.

Davis (1958) has pointed out that T zone herb pollen assemblages are mixtures of taxa which have both northern and southern affinities. The Allenberg bog samples yielded pollen from Artemisia, Caryophyllaceae, Rosaceae, Ranunculus, Salix, Cichorioideae and Asteroideae (= high-spine Compositae p.p.), all of which have species in both arctic and temperate regions. Other pollen types identified in T zone sediments are from taxa which are mainly temperate in distribution. At Allenberg bog these include Ambrosia, Chenopodiaceae-Amaranthaceae, Labiatae and Umbelliferae. Taxa found exclusively in arctic and subarctic regions have not been identified in the basal layers at Allenberg bog. However, the presence of Betula glandulosa is indicated by the size-frequency measurements of birch pollen. This is an arctic-alpine species which today is widespread in the North American subarctic with an extension southward in eastern North America to the Adirondack Mountains (Fernald, 1950). Microspores of Selaginella selaginoides were also found in zone T sediments at this site. Currently, this species grows at exposed, calcareous sites in the boreal forest and subarctic across North America as far south as the upper Great Lakes

and the mountains of southern New England (Hultén, 1958). The occurrence of this species, and pollen from other taxa with high light requirements, give support to the interpretation of an open vegetation.

In the absence of radiocarbon dates, it cannot be determined if the semi-treeless landscape which occurred adjacent to Allenberg bog was a successional stage transitional to a spruce forest or whether it was a climatically controlled group of communities equivalent to several of the many expressions of tundra vegetation. In southern New England where tundra persisted several millenia prior to 12,000 B.P. (Davis, 1967b), the treeless interval probably represented a period during which the climate was too severe to allow the development of a spruce forest near the site. Trees may also have been absent because they had not migrated to the region. In view of the length of time involved, however, climatic control is the most acceptable hypothesis, even though both factors may have interacted.

The Allenberg bog T zone pollen assemblage seems clearly to imply the occurrence of park-tundra vegetation at some time prior to the development of A zone spruce forests in the region. Size-frequency measurements indicate that Picea glauca was the main spruce species present, although P. mariana undoubtedly also occurred. Evidence suggests that spruce trees were either sparsely scattered across the landscape or occurred some tens of miles away. The presence

of Pinus banksiana and/or P. resinosa is also indicated, but these species may have grown much further south of the site, perhaps even a distance of several hundred miles. Plant communities rich in sedges, grasses and heliophytic herbs must have dominated much of the surrounding region. Few truly tundra species were apparently present, although a dwarf arctic birch, Betula glandulosa, and Selaginella selaginoides, both of which are northern species, are represented in the deposit.

The vegetation may also have been prairie-like. The occurrence of Ambrosia and Cheno-Am pollen supports this conclusion but the maxima in Artemisia, Cyperaceae and Gramineae curves, which also would support such an inference if prairie species could be identified, can be taken as evidence of either prairie or park-tundra vegetation. Since both ragweed and Chemo-Am pollen could have been wind carried to the basin from a distant source, however, the park-tundra interpretation remains the strongest.

#### ZONE A

One of the most consistent stratigraphic features in basal lake and bog sediments across glaciated eastern North America is a zone in which spruce pollen accounts for 30 to 70 percent of the sum. The occurrence in New York State of a spruce zone, or A zone as Deevey (1939) named it, was early established by McCulloch (1939) from a bog near

Syracuse. Later workers have confirmed its presence and have since found similar zones in sedimentary basins throughout central and eastern New York (Cox, 1959; Durkee, 1960). An A zone was also found in each of the four southwestern New York bogs I studied, but since this zone varies from site to site, it will be discussed separately in reference to each of the localities.

#### Genesee Valley Peat Works

Low spruce percentages and the high values of total NAP set the Genesee Valley Peat Works A zone apart from the others. At this locality most A zone spectra contain less than 25 percent spruce pollen and the maximum value of 29 percent was reached in only one sample. By comparison, from 40 to 65 percent spruce was counted in equivalent stratigraphic positions at the three other sites. Associated with spruce in the Peat Works sediments are unusually high percentages of Cyperaceae, Gramineae, high-spine Compositae (= Asterioideae p.p.), Salix and other NAP types. Replotting A zone spectra on an absolute basis does not greatly change the form of the curves. Although the overall pollen stratigraphy of the entire diagram is basically similar to the other profiles from the region, the unusual character of the spruce zone makes its meaning difficult to determine. In the paragraphs that follow two alternative explanations are proposed and evaluated in light of the evidence at hand.

Taken at face value, the nearly equal representation of AP and NAP throughout zone A at the Genesee Valley site, but particularly near the bottom where Pinus percentages are low, implies that the regional vegetation was open and perhaps similar to that which occurred in Cattaraugus County during the deposition of zone T at Allenberg bog. Widely spaced spruce stands interspersed with herb communities is one possible interpretation of the data based on the assumption that A zone pollen assemblages from the Peat Works fully represented the regional vegetation. The slightly larger spruce percentages in the lower part of the zone indicate that spruce trees were more abundant around the site early in the depositional history of the basin. Pine pollen increases at the expense of spruce higher in zone A suggesting that pines became more frequent in the surrounding vegetation with the passage of time. Pinus banksiana and/or P. resinosa seem to have been the only species present because Haploxyton grains are only sparsely represented. Since much of the pine pollen at the lowest levels could have been blown in from a distance, the actual abundance of pine in the vegetation around the site must remain conjectural for this part of the profile.

An open spruce-pine woodland interpretation is hard to accept, however, because there is no evidence in the profile that a more closed forest was present later in the history of the region adjacent to the basin. Such a change



would be expected to have occurred on the basis of pollen studies elsewhere. A climate too cold to permit the development of a spruce forest may have been the controlling factor in the lower part of zone A where pollen tentatively identified as Dryas spp., Empetrum nigrum and Saxifraga spp. was found. The proximity of an ice front may have induced conditions favorable to tundra communities and might at the same time have kept Picea from becoming more dominant in the landscape. High frequencies of sedge, grass and forb pollen would be expected in vegetation of this type. A warming trend and other factors that aided the colonization of the region by Pinus banksiana and/or P. resinosa may have occurred in the upper 1.25 m of the A zone. The NAP contribution remained more or less constant during this interval implying the persistence of an open vegetation.

Since the Peat Works is situated on the Tazewell or pre-Tazewell Olean drift (Muller, 1965), the lower part of the profile, if complete, may antedate most other pollen records in eastern North America. The other sites I investigated in southwestern New York had their inception during subsequent glacial advances and therefore provide no parallel data. However, in eastern North America several additional deposits on Olean drift have been studied. Highland Lake southwest of the Catskill mountains (Cox, 1959) is truncated basally, as is the Cranberry bog profile from eastern Pennsylvania (fide Stingelin, 1965; Gehris, 1965), but the

long sedimentary record at Kernochan bog, located near Highland Lake about 150 mi east of central Allegany County, contains a sequence that is similar to the Genesee Valley profile. The shape of the spruce silhouettes at both sites is almost identical, but at Kernochan bog, below the point where spruce reached its A zone maximum of 35 percent, there is a long interval of lower spruce percentages and high Pinus and NAP values which are absent from the Genesee Valley site. Above this level the pine and spruce curves at both sites are essentially identical, but at Kernochan bog NAP values are about half those at the Genesee Valley site.

The parallel nature of the spruce and pine curves in the Kernochan bog and the Genesee Valley profiles indicates that the sequence may have regional significance. This raises the interesting possibility that, for an unknown period following the Tazewell (?) glaciation and perhaps contemporaneous with subsequent ice advances, a more or less open pine-spruce woodland existed in the Allegheny Upland of southern New York. Pollen analyses of sediments below a radiocarbon date of  $13,630 \pm 230$  years B.P. (Y-479; Martin, 1958b) in unglaciated southeastern Pennsylvania have produced spectra somewhat similar to A zone samples at the Genesee Valley Peat Works, but without C-14 dates at this site the contemporaneity of the deposits cannot be proved. The main differences at the Pennsylvania locality include larger total NAP percentages (50 to 75 percent) and a weaker

expression of Picea (ca. 5 percent); Pinus comprises from 15 to 25 percent of the total. In light of the uncertain age of the various drift sheets east of the Salamanca reentrant and of the Genesee Valley and Kernochan bog pollen profiles and in the absence of radiocarbon dated profiles between these two localities, the open spruce-pine woodland hypothesis is presented as one of several explanations of existing data.

The vegetation inferences in the preceding discussion are based in part on the assumption that the fossil spectra represented the regional pollen rain. An alternate interpretation is possible, however, if the NAP was derived mainly from a source near the basin. In this case the regional vegetation contributing to A zone sediments was probably not an open woodland. As a correction for local overrepresentation, a portion of the data were recalculated using the total number of arboreal pollen at a given level for the percentage base rather than the sum of AP and NAP. The new curves still show the same trends because the total NAP contribution was more or less constant throughout the interval. However, what is different is the percentage of the main arboreal components in the counts. In such a calculation spruce attains a maximum of nearly 50 percent and the overall transition from the spruce dominated basal sediments to pine dominated sediments above is not unlike the A/B zone transition at the other sites in western New York with the

exception that it is more gradual. The new data indicate that the tree cover was more dense and was perhaps similar in overall aspect to the boreal forest of northern Ontario and central Quebec. If this were so, the previous hypothesis would have to be modified to accomodate the new vegetation interpretation. Pending C-14 dating, therefore, the possible existence of a denser pine-spruce forest on the glaciated Allegheny Upland of southern New York during pre-Cary times must also be considered.

There are several lines of evidence pointing toward local over-representation. The slopes above and leading to the center of the basin are gentle and the depression itself is large and relatively shallow. Therefore, an abundance of habitats for marsh plants could have existed around the margin of the basin during its early history. The presence of Sagittaria and Sparganium pollen throughout zone A is confirmation that marshy shallows existed in or near the basin. Both genera are not represented in the counts higher in the deposit, probably because littoral habitats were eliminated by the development of a bog mat. Other parts of the valley floor on which the depression is located may have supported marsh communities but bedrock highs are abundant in the area and well-drained upland sites must also have been a regular feature of the landscape.

An incomplete knowledge of the current pollen rain in many sections of northern North America again hampers the

search for a modern analogue of the A zone vegetation near the Peat Works. If pollen spectra from this zone represent the regional pollen rain, they cannot be matched with any of the surface samples reviewed by Davis (1967a), because modern pollen assemblages in which Carpinus-Ostrya, Fraxinus, Quercus and Ulmus pollen are minor but significant components of spectra otherwise dominated by Picea, Pinus and NAP are unknown. The anomalous occurrence of pollen from these thermophilic taxa is not without precedent. I have already discussed the possibility of their having been derived from a southern source by wind transport.

The spectra may also be contaminated by redeposited pollen. I have not demonstrated that rebedding has occurred, since a source of older pollen is unknown in the area, but the presence of Fagus grains in the silty clay at the bottom of the deposit and their absence from the more organic sediment immediately above, suggests that pollen eroded from the surrounding drift may have been carried into the basin along with the inorganic sediments. Andersen (1954) has asserted that the optimum time for redeposition is during an ice advance when frost activity would be continuously exposing potential pollen-bearing deposits. This is also the time of maximum inorganic sedimentation because the basin would be relatively free of living organisms. Thus the occurrence of Fagus grains together with pollen of Dryas, Empetrum and Saxifraga might be explained by claiming a climate favorable

to solifluction. If there were some way to determine objectively what part of the spectra were composed of redeposited and extra-regional pollen, subtractions could be made, and the modified fossil spectra might compare more favorably with one or more of the surface pollen assemblages now known.

### Allenberg Bog

At Allenberg bog the A zone overlies an interval which I interpret as a record of a more or less treeless landscape with herb communities covering much of the region surrounding the basin. Above this, a rapid increase in spruce percentages occurs and high spruce values are maintained for about 2 m of sediment. Fluctuations in the relative numbers of subdominant AP types, however, allow the interval to be divided into several subzones that are reminiscent of those reported from southern New England by Leopold (1956b; Leopold and Scott, 1958) and Davis (1958). The correspondence of the subzones in the two areas is not exact and, to my mind, the percentage changes in the Allenberg bog profile are not evidence of a modification in forest composition or density induced by advance and withdrawal of an ice sheet as the New England workers have claimed for their area. Davis (1967b; Davis and Deevey, 1964) has demonstrated that at Rogers Lake, Connecticut, the fluctuations in relative pollen frequency which have been

taken as evidence of vegetation change, can be interpreted differently when the data are replotted on the basis of numbers of grains deposited per unit area per year.

Four divisions of the A zone are recognized at sites studied by Davis (1958) in central Massachusetts. The A zone sequence in her Tom Swamp profile is the closest to what I have found at Allenberg bog. The Tom Swamp Picea curve shows an increase in the lowest subzone, the A-1, while Pinus values decrease slightly over the same interval. These changes are also present across a comparable stratigraphic interval in the Allenberg bog profile. However, the high values for Betula and Populus pollen (ca. 10 percent each) which characterize the A-1 at the former site are absent from the latter and without other stratigraphic markers, an A-1 cannot be as readily defined at Allenberg bog.

At Tom Swamp Betula and Populus drop to 5 percent or less of the total in the next highest subzone, the A-2, and a pronounced maximum in the relative numbers of Picea occurs. Somewhat lower Quercus percentages are found in this subzone than are present in the A-1 or in the A-3 above. The spruce peak at Allenberg bog occurs between 14.70 and 14.92 m and, in contrast to the New England locality, is found with maximum percentages of Quercus and Fraxinus nigra. The Allenberg Quercus curve shows no important fluctuations below the Picea peak, but the maximum A zone percentage of Fraxinus nigra pollen occurs just beneath it.

The New England A-3 subzone has somewhat lower Picea percentages and increased values for Pinus, Quercus and other AP types. At Allenberg bog spectra between 14.22 and 14.70 m can be assigned to subzone A-3. Higher relative percentages of Carpinus-Ostrya occur in this interval than elsewhere in zone A, although the maximum for this pollen type is reached just above the Picea peak. Spruce percentages increase in the A-4 which at Allenberg bog encompasses sediment between 12.80 and 14.22 m or about the upper two-thirds of zone A. Pinus values are lower at the middle of the A-4 than they are in the A-3, but the curve of the sum of the three pine categories increases gradually across the upper part of the A-4. In further contrast to the New England diagrams Carpinus-Ostrya, Fraxinus nigra and Quercus percentages do not decline in the A-4.

The interpretation of the New England A zone sequence was based on the Late Wisconsin glacial chronology as it was known in the mid-1950's (see Beetham and Niering, 1961; Davis, 1965b). As the climate improved following the retreat of the Port Huron ice, subzones A-1 and A-2 were deposited in which spruce percentages increase and attain a maximum. The lower relative numbers of Picea and the increased percentages of Pinus and deciduous tree pollen types implied further warming during the A-3. Several radiocarbon age determinations permitted correlation of the A-3 with the Two Creeks Interstade, then dated at about 11,000 years B.P.



(see Leopold, 1956b). The return to higher spruce percentages in the A-4 and drops in oak and pine values were taken as a record of a spruce dominated forest developed during the colder climate which presumably prevailed during the ensuing Valders Stade. The more recent dating of the Two Creeks forest at  $11,850 \pm 140$  years B.P. (Broecker and Farrand, 1963) makes its correlation with the New England A-3 doubtful.

The similarity between the New England and Allenberg bog profiles may be fortuitous. The lower part of the A zone at Allenberg bog is perhaps not temporally equivalent to spectra with comparable pollen assemblages in the New England diagrams where the zone is broadly contemporaneous with the Valders and Two Creeks events. Accepting 23,250 years B.P. as the age of the Kent drift (White, 1968) upon which Allenberg bog is located, not only the Valders--Two Creeks climatic changes may have influenced the vegetation surrounding the site but also those associated with the preceding Port Huron and Cary glaciations. Records of these events in the pollen profile may be in part preserved beneath the A zone lower in the incompletely sampled clay deposit, but the A zone itself seems not to show any well-defined changes that might be related to them. At Houghton bog, 25 mi northeast of the Allenberg site, wood from near the bottom of zone A dated at  $11,880 \pm 730$  years B.P. (I-3290) is of Two Creeks age. The sample occurs with Picea dominated pollen spectra which are similar to those in the upper part

of zone A at Allenberg bog. Between the dated level and the end of the spruce zone at Houghton bog, which encompasses the time of the Valders readvance, changes in pollen percentages similar to those just reviewed from the southern New England profiles do not occur. Therefore, the vegetation in southwestern New York State does not seem to have been affected by climatic changes accompanying the Valders readvance. The maximum southward extension of Valders ice was more than 100 mi north of southwestern New York. Valders ice apparently never reached the Lake Ontario basin (Karrow et al., 1961) which was then occupied by Glacial Lake Iroquois.

Replotting section C of the Allenberg bog profile on an absolute basis permits an alternate interpretation to be made (cf. Diagrams 7 and 8). Variations in numbers of different pollen types per unit volume through time is meaningful only if the sedimentation rate was more or less constant across the interval being considered. At Rogers Lake, Connecticut, the only site in eastern North America where data on the pre-Valders sedimentation rate has been obtained, Davis and Deevey (1964) reported a constant rate of 0.036 cm per year (later corrected to 0.037; Davis, 1967b) between 14,000 and 10,000 years B.P. In certain parts of a profile deposition rates for each pollen type are potentially the most useful data for assessing vegetation change. If the accumulation rate of the sediment was constant, however, variations in the absolute numbers of pollen types with depth

will show the same trends. It would have been preferable to determine directly the sedimentation rate at Allenberg bog with close interval C-14 dating but in the absence of the necessary age determinations, the following discussion is based on the assumption that the time taken to accumulate a unit volume of sediment was the same in all divisions of zone A.

At Rogers Lake the spruce dominated A zone begins at 12,000 years B.P. and ends about 9,500 years B.P. Quercus pollen is present during the entire interval but 10,500 years ago it fell from about 15 to 5 percent. A similar but less pronounced change also occurs in the Caprinus-Ostrya and Fraxinus curves at this site. These changes, clearly expressed in the relative frequency diagram, are not maintained when the data are converted to the numbers of pollen and spores accumulating per unit area per year. The pollen input from Quercus and other temperate deciduous trees remained relatively constant during the entire interval and the maximum and minimum of oak pollen at 11,000 and 10,000 years, respectively, that occur in the percentage diagram no longer exist. Davis (1967b) concludes that percentage change in Quercus is a reflection of increasing deposition rates for coniferous tree pollen 10,000 years ago and is not due to a climatic oscillation correlated with the Allerød--Younger Dryas sequence.

The same reasoning can be used to explain fluctuations in the percentages of Quercus and Fraxinus nigra near the bottom of zone A at Allenberg bog. In the interval across which the percentages for these taxa are high, the number of grains per ml of sediment increases (see Fig. 8). Between 14.540 and 14.425 m the pollen and spore total stabilizes near 200,000 grains per ml where it remains until the end of zone A. The increase is due mainly to a greater number of spruce and pine pollen being deposited in the basin and this indicates an increase in the number of spruce and pine trees in the region. By 14.425 m the maximum attainable density of the spruce-pine forest may have been reached and, significantly, above this level no important changes are evident in Quercus and Fraxinus nigra percentages. The higher relative pollen frequencies just above the T/A zone boundary may reflect the openness of the developing spruce forest when fewer numbers of Picea pollen relative to Quercus pollen were being deposited. If the input of Quercus remained constant, as was the case according to Diagram 8, an increase in the absolute numbers of spruce and pine pollen being deposited would depress the percentage values for Quercus.

Allenberg bog upper A zone spectra, with the exception of somewhat higher percentages of Carpinus-Ostrya and Fraxinus, agree fairly well with southern New England spectra from equivalent stratigraphic positions. Davis (1967a) considers the New England fossil pollen assemblages

to be similar to surface samples deposited today at about 53° N Lat in northern Quebec in the Nichicun Lake area west of Schefferville. This region has been characterized as an open, park-like woodland in which closed black spruce forests with an admixture of larch are present at wet lowland localities, while black and white spruce with balsam fir occur in open stands interspersed with lichen communities on the better drained upland sites (Terasmae and Mott, 1965). Davis (1967a) suggests that the lower part of the New England A zone represents tundra-forest transitional vegetation which developed into a boreal woodland later in the zone. She further suggests that such a change is evidence of gradual climatic warming. The data from Allenberg bog would seem to fit this interpretation, but it is to be treated as tentative until confirmatory information is obtained from other sites in southwestern New York State.

The gradual increase in the number of Quercus grains in the sediment from zone T to the beginning of zone A may represent northward migration of oaks to positions nearer the basin. The occurrence of from 5 to 7 percent oak pollen throughout the upper part of zone A suggests that oaks were present somewhere within 100 mi or less of the bog. Quercus percentages of this magnitude are not known to be deposited in the boreal forest or in the more open subarctic woodland to the north, which on other evidence are the closest analogues of the fossil vegetation. In eastern North America

at about 46° N Lat, near the northern distributional limit of the genus, similar percentages occur. But since this is located in the mixed coniferous-deciduous forest of mid-Ontario, significant percentages of Acer, Ulmus and other temperate AP types are present also. Similar percentages of these types are absent from the A zone of Allenberg bog. Less than 1 percent Quercus pollen, calculated using the sum AP as the percentage base, was found by King and Kapp (1963) at the southern edge of the boreal forest north of Georgian Bay.

A relatively high representation of temperate tree pollen in existing vegetation dominated by spruce and larch has been found by Janssen (1967) at Myrtle Lake on the Lake Agassiz plain of north-central Minnesota. By comparing an estimate of the regional forest composition derived from the General Land Office Survey notes with pollen deposited on the surface at a number of points along transects at the lake, he showed Picea and Larix to have high importance values in the surrounding vegetation, but to be relatively poorly represented in the surface pollen spectra. On the other hand, Fraxinus, Quercus and Ulmus pollen were distinctly over-represented in reference to the regional vegetation. If spruce and larch had a similarly low 'delivery capacity' during lateglacial time, they would be under-represented in pollen profiles, while higher percentages for certain extra-regional deciduous trees with greater 'delivery capacity'

would be expected in spite of the probability that they composed only a minor part of the regional vegetation. It would seem, therefore, that the problem is defining the area contributing pollen to a given basin. During the deposition of the lateglacial spruce zone at Allenberg bog, judging from studies on the current pollen rain, it may have included the area within a 100 mi radius of the site.

Using 100  $\mu$  as the dividing point between the smaller pollen of Picea mariana and the larger P. glauca grains, size-frequency measurements of A zone spruce pollen at Allenberg bog confirm the presence of both species (Fig. 5). Picea rubens may or may not have been present also. At 14.750 m near the bottom of the zone, the mean size of measured spruce grains was 101  $\mu$ ; wingtip to wingtip measurements were greater than 100  $\mu$  in 53 percent of the sample. Higher in the profile the mean size decreases until near the end of the zone, at 12,925 m, it was 89.2  $\mu$  and only 17.6 percent of the measured sample was over 100  $\mu$ . This implies a gradual loss of P. glauca upward and perhaps replacement by P. mariana.

Most of the pine pollen in the Allenberg A zone is the Diploxylon type. The configuration of the modes in the size-frequency curves for this pollen type (Fig. 6) indicates that both Pinus banksiana and P. resinosa contributed to zone A sediments. In view of the similarity in pollen size of these species (Whitehead, 1964), however, it will be

necessary to find macrofossils to establish conclusively the presence of either one. The occurrence of about 20 percent of pine pollen throughout the zone definitely establishes that one or both of the Diploxylon pines grew near the basin. This is in contrast to the situation in the western Great Lakes region where significant amounts of pine pollen are not found in the profile until near the end or following the spruce zone (Wright, 1964; 1968b). Judging from present-day habitat preferences, both P. banksiana and P. resinosa grew on dry sandy soils, although the former was probably restricted to the driest sites. The low relative frequency of Haploxylon pine pollen further implies that P. strobus was not a part of the regional vegetation, because the relatively small amount of Haploxylon pine pollen present in the counts could have been blown to the basin from afar.

The broad size class spread and the occurrence of several modes in the A zone size-frequency curve for Betula indicates that more than one species was present near Allenberg bog (Fig. 4). The smallest grains, 20  $\mu$  or less in size, may have been derived from the arctic-alpine dwarf birch, B. glandulosa. This species was apparently also present in the underlying T zone. The modal classes centering near 22 and 24  $\mu$ , however, have no exact modern counterparts among the taxa investigated by Leopold (1956a), which include 9 of the 11 species native to northeastern North America. Although it could be postulated that extinct



species contributed to the modes, it is more likely that the maceration technique or some aspect of the fossilization process modified the grain size of extant taxa. In the upper part of zone C, for example, where the only contributors to the regional pollen rain were B. lenta and B. alleghaniensis, the modal class in the size-frequency curve is smaller than that reported for pollen from herbarium specimens of either species (ibid.). On the basis of modern distribution patterns and pollen size-frequency characteristics, speculation leads to two additional birches that may have been members of the lateglacial flora near Allenberg bog. One of these, B. populifolia, is a species with small pollen (mode 27 mu in three acetolyzed preparations; ibid.). Davis (1958) suggests that it may have occurred in the New England A zone vegetation where it likely occupied disturbed sites. Betula papyrifera is the other expected species because it now grows mainly in the boreal forest. However, its relatively large pollen (mode 33 mu in one acetolyzed preparation; Leopold, 1956a) does not correspond to any measurements of fossil grains at Allenberg bog.

Reviewing briefly the nature of the vegetation in the A zone of Allenberg bog, as it has been interpreted here, the lower third of the zone seems to record the development of a more or less open boreal woodland, similar to that which today occurs in the subarctic of northern Quebec. This appears to have persisted throughout most of the zone

because few meaningful changes occur in the A zone above 14.5 m. The woodland was preceded by a transitional vegetation type in which spruce and pine greatly increased in abundance. These changes may have been in response to a warming trend in the climate, as the A zone overlies an interval of tundra-like vegetation apparently dominated by herbaceous communities with spruce probably infrequent in the entire region. Without information on the duration of the tundra, however, a simple successional change may be represented instead. The density of Picea and Pinus in various parts of zone A must remain conjectural until additional surface samples prove that the pollen rain in an open woodland is different from that in a more closed forest. If the landscape contributing to the regional pollen rain was incompletely covered by stands of Picea glauca and P. mariana, the latter being more abundant at wetter sites, various non-tree communities dominated by sedges, grasses, Artemisia, other Compositae and additional herbs occupied the openings. An alternate interpretation would have most of the herbs at the basin margin. Alnus and Myrica were certainly present at pond and lake edges and in other wet habitats. Salix was also part of the vegetation, but it is not known whether dwarf or shrub species are represented. Pinus banksiana and/or P. resinosa grew at dry sandy sites in the vicinity, and both Abies balsamea and Larix laricina were members of the regional vegetation, although it is not possible to tell in what

proportion they occurred in the forest because their pollen is usually under-represented. Carpinus caroliniana and/or Ostrya virginiana, Fraxinus nigra and Quercus spp. probably occurred within 100 mi of the basin, but perhaps closer.

#### Houghton and Protection Bogs

The two sites that remain to be discussed are associated with the Valley Heads moraine. Both have relatively thin A zones in comparison to the long interval of spruce domination at Allenberg bog. In neither of them is there any clear indication of a zone with high NAP percentages. The lowest spectra in each do contain from 15 to 24 percent herb and shrub pollen but this is in association with high values (40 to 50 percent) for Picea. The absence of a T zone at both localities may be a sampling deficiency, although the samplers were pushed as deeply as possible. Pollen is present in the basal clay at Protection bog, but is absent from similar sediments at Houghton bog.

As has been mentioned already, the A zone pollen assemblages from the Valley Heads bogs compare favorably with the upper A zone spectra from Allenberg bog. The vegetation that presumably produced the assemblages has just been reviewed and little new information can be added here. In common with the other sites in southwestern New York, Carpinus-Ostrya, Fraxinus and Quercus pollen are apparent in the A zone of both profiles. Lesser amounts of Carya,

Corylus and Ulmus pollen also occur. Low relative numbers of Tsuga pollen first appear in the A zone of the two bogs and also near the beginning of this zone at the Allenberg site. It is probable that hemlock was an extra-regional species at this time because the few grains present could have been wind carried to the site from a distant source. All of these are minor pollen types, however, and the zone is clearly dominated by spruce and pine. Pinus banksiana and/or P. resinosa were present. Except for the pollen of the temperate tree species, the assemblages match the modern pollen rain accumulating today in the open, boreal woodland of subarctic northern Quebec and at certain points to the south within the boreal forest itself.

A maximum in the Abies curve occurs near the end of zone A in all four profiles, but is best developed at Protection bog. At this locality, and perhaps at the others as well, this increase may represent an actual increase in the number of balsam fir near the basins. The rapidly declining spruce percentages associated with the fir maximum imply an abrupt and perhaps catastrophic change in the vegetation. If balsam fir was growing suppressed in a spruce-dominated woodland at this time, deterioration of the spruce overstory might have released the fir seedlings and saplings growing in the understory. The period during which fir thrived must have been relatively short because its pollen drops out of the counts soon after the maximum is reached. At the present

time Abies balsamea persists under a dense forest cover but nearly full sunlight is needed for best development (Fowells, 1965). This behavior is in agreement with its known quick response to release.

High fir percentages near the end of the spruce zone occur over a wide area in the Northeast, although the peak is sometimes just within the zone and other times at its end (Cox, 1959; Deevey, 1943; and others). Deevey (1943) has suggested that the high fir values, which often occur with a spruce maximum at the New England sites he studied, may represent a vegetation response to the last glacial advance. As such it would correlate with subzone A-4 discussed previously. Since the Protection bog fir peak occurs in sediments accumulated about 10,500 years B.P. (by extrapolating from the two higher dates at this site assuming a constant sedimentation rate), considerably after the last or Valdres readvance, it seems best to view the peak as a successional event.

The radiocarbon dated Valley Heads profiles enable time stratigraphic correlations to be made between these sites and others in eastern North America. In New York State itself, few dated pollen spectra comparable in age to the lateglacial A zone assemblage at Houghton bog, the lower part of which has been dated at  $11,880 \pm 730$  (I-3290), have been published. I am aware of only one, the King Ferry site in the Finger Lakes region of central New York (Cox, 1959;

Brown in Deevey et al., 1959). There, spruce wood 11,410  $\pm$  410 years old (Y-460; Deevey et al., 1959) in close association with a mastodon skeleton was embedded in sediments dominated by spruce and pine pollen. Spruce accounted for over 80 percent of total AP; NAP, unfortunately, was not tallied. The microfossil flora was taken to record the presence of a boreal coniferous forest in central New York at this time (Brown in Deevey et al., 1959).

Spruce wood dated at 12,100  $\pm$  400 years B.P. (I-838; Buckley et al., 1968) from the Lockport site near the Glacial Lake Iroquois strand in central Niagara County is approximately the same age as the lower part of the Houghton bog A zone. I was able to extract pollen from a silty clay lake deposit associated with the organic bed from which the wood was taken and found the assemblage to agree, in a general way, with Houghton bog spectra of the same age. The main difference is the relative frequency of Cyperaceae pollen: 34 percent was found at the former site, while only 4 to 8 percent occurred at the latter. If all of the sedge pollen is considered to have been produced by the upland vegetation, it is likely that a considerably less dense spruce woodland occurred near Lockport than existed 50 mi to the south near Houghton bog. If, on the other hand, habitats near the strand were especially favorable to the aquatic lowland members of the family, local over-representation could explain the difference. The abundant seeds of Eleocharis spp.,

members of the Cyperaceae with pollen typical of the family (Sears, 1930), in the Lockport organic bed substantiates the case for a near-site origin of much of the 'sedge' pollen. Eleocharis species probably grew along the Lake Iroquois strand in beach pools and along the stream that passed through the Lockport spillway. Since pollen recovered from the lake sediments was carried there by both wind and moving water, near-site aquatic and semi-aquatic species shedding pollen into the water would have an excellent chance of being well represented in the counts.

The largest amount of wood in the Lockport deposit confirms the suspected dominance by forest communities. Cones of black spruce were positively identified and perhaps one other species of spruce is represented also. In addition spruce needles, seeds and twigs are exceptionally abundant in the deposit. A single seed of Abies balsamea and pollen of Larix laricina indicate that these trees occurred also. The rich moss assemblage that was found in the organic deposit permits recognition of several other communities. Rich fens must have been relatively common because both fen and fen edge mosses are frequent. Drier habitats, perhaps on beach ridges, were present, and species which may have grown on or among the calcareous rocks of the nearby Niagara escarpment also occur. Only one species which today typically grows in shaded spruce forests was identified. Others which sometimes grow in this habitat were also found, but

are less useful indicators because they occur at open sites as well. The absence of a dominant forest element in the moss flora probably means that the landscape along this part of the Iroquois strand was occupied by a patchwork of dry and wet site herb and moss communities and that spruce occurred some distance behind the beach. Most of the spruce macrofossils were probably carried to the site from inland by drainage through the spillway.

Nearly all of the fossil mosses are characteristic boreal forest species. Most range northward to the arctic tundra but many also occur in the Great Lakes states. For example, 92 percent of the assemblage presently grows in the Straits of Mackinac region of Michigan where the present zonation of the strand vegetation is similar to that which apparently existed in northwestern New York State 12,000 years ago. An important difference, however, is that a temperate coniferous-deciduous forest occurs today in the upland of northern Michigan but was absent from western New York at this time. The mosses of greatest phytogeographic interest are Aulacomnium acuminatum and A. turgidum whose present North American ranges center in the arctic and subarctic. The southernmost station for the former is along the north shore of Lake Superior, an area well-known for its relict arctic-alpine plants. Aulacomnium turgidum has a greater number of occurrences along the southern edge of its range but it also is found widely in the subarctic and



arctic. In the East disjunct stations are known from the high peak region in the Adirondack mountains of New York and from the White Mountains of New Hampshire.

The presence of these taxa indicates that arctic-alpine vascular plants also may have grown near the Lake Iroquois strand at Lockport 12,000 years ago and raise the possibility that limited areas of tundra may have occurred in the region. It is possible, of course, that at this time both mosses were relicts from a period of 'tundra' vegetation which may have existed in the area 500 to 1000 years prior to their burial. The presence of the two taxa along the strand could be explained, therefore, by postulating microhabitats favorable to their survival. Since fossils of other tundra plants have not been found in the deposit and forest species are clearly present and abundant, this seems to be the better hypothesis.

Beyond New York State, but within glaciated eastern North America, spruce-rich forests were widely distributed 12,000 years ago. Their presence in southern New England (see Davis, 1965) has already been mentioned. To the west in southern Ontario an age determination of  $11,950 \pm 350$  years B.P. dates the beginning of organic sedimentation and the upper part of the A zone at Crieff Kettle bog near Hamilton (Karrow, 1963). Spruce pollen accounts for about 80 percent of total AP in the A zone (Terasmae in Karrow, 1963) and the proportion of white to black spruce pollen is

approximately 6 to 1. Abies, Betula, Pinus banksiana and Quercus are the other main tree pollen types present. From 15 to 45 percent NAP occurs in the zone (calculation based on sum AP) and Ambrosia, Artemisia, other Compositae, Cyperaceae and Gramineae are the principal types identified. Dryas pollen occurs near the bottom of the zone.

The correspondence of the Houghton bog date and the newly determined age of the Two Creeks forest bed (11,850  $\pm$  100 years B.P.; Broecker and Farrand, 1963) has been noted. West's (1961) reanalysis of the type Two Creeks locality along the shore of Lake Michigan at the base of the Door peninsula, Wisconsin, produced spectra dominated by up to 90 percent spruce pollen (calculation based on sum AP + NAP) in all levels except the bottom. At this level Shepherdia canadensis, a heliophytic shrub that may have been one of the first colonizers of surfaces freed for plant occupation in the area, attained over 95 percent of the total. One out of every 6 spruce grains was identified as Picea mariana. Spruce forest was also present in southeastern Minnesota at this time (the Picea-Larix Assemblage Zone of Cushing, 1967).

It seems clear that the spruce dominated vegetation 12,000 years ago was not uniform in composition between New England and Minnesota. The most obvious difference is the presence of high values for Pinus pollen in western New York and New England at this time and their absence from sites in Michigan, Wisconsin and Minnesota. Apparently pines were a

part of the lateglacial A zone vegetation in the East but did not occur in the contemporaneous vegetation of the Midwest. The available data (Wright, 1964; 1968b) indicate that the Appalachian region served as a full- and late-glacial survivium for the three main pine species, Pinus banksiana, P. resinosa and P. strobus, which participated in the revegetation of the glaciated Northeast. The relative numbers of temperate deciduous tree pollen types also vary from site to site within the region. An accurate assessment of the variability in terms of climate depends in part on a detailed knowledge of the pollen rain in existing boreal forest and woodland, the forest-tundra transition and the tundra itself. This is not available at the present time. It also must be kept in mind that modern analogues for certain lateglacial pollen assemblages may never be found because the vegetation which produced them may have been a mixture of species brought together by differential migration rates and may thus represent chance combinations of species which coexisted for varying periods of time following the withdrawal and disappearance of the ice.

South of the glacial boundary the vegetation in several parts of Pennsylvania 12,000 years ago was apparently much different from that found at this time near Houghton bog in western New York. At Bear Meadows in central Pennsylvania (Kovar, 1964; Stingelin, 1965) pollen analysis of sediments below a radiocarbon date of  $10,320 \pm 290$  years B.P.

(Westerfeld, 1961) produced spectra dominated by pine pollen (60 to 70 percent) and associated with relatively low values for spruce (10 to 15 percent). NAP generally totaled 10 percent of the sum. Similar spectra have been obtained by Paul S. Martin from sediments below a C-14 date of  $11,300 \pm 1000$  years B.P. (Y-727; Guilday et al., 1964) at the New Paris Sinkhole No. 4, in south-central Pennsylvania, 65 mi from Bear Meadows and 100 mi from the glacial boundary crossing northwestern Pennsylvania. The 3 m of cave filling beneath the dated horizon is dominated by Pinus pollen which accounts for about 60 percent of the AP plus NAP sum. From 6 to 15 percent Picea pollen occurs in the same interval and the rest of the sum, from 20 to 30 percent, is comprised of Compositae, Cichorioideae, Cyperaceae and Gramineae pollen. Both categories of Compositae pollen likely were produced by near- and on-site herbs. Some grass and sedge pollen may have had a similar origin. The vegetation producing this assemblage may have resembled an open boreal woodland with spruce and jack (?) pine separated by open ground (ibid.). Above the dated level Pinus remains dominant but Picea drops to less than 5 percent of the sum and Betulaceae, Quercus and other temperate arboreal pollen taxa become strongly represented. This apparently records the movement of temperate forest elements into the area.

Sediments below the date contain bones of a large number of vertebrates whose modern ranges center southeast

and west of Hudson Bay in boreal Canada. Of particular interest are the remains of at least three Labrador collared lemmings, a species that today occurs mainly within the tundra of northern Quebec. Also found were the bones of the thirteen-lined ground squirrel and the sharp-tailed grouse, two prairie species whose occurrence substantiates the contention (Schmidt, 1938; see also Benninghoff, 1964) that an eastward extension of prairie elements occurred in late- rather than postglacial time.

If the vegetation in central and southern Pennsylvania indeed was an open, boreal woodland like that existing beyond the north edge of the boreal forest today, an interpretation which is in part substantiated by the fossil vertebrates, the presence of a more closed spruce-pine forest to the north on glaciated terrain is difficult to understand because this zonation is the reverse of the current arrangement of these vegetation types in North America. Existing data are too sparse to establish the presence of the boreal forest in the region south of Pennsylvania and a taiga-tundra in a wide band between the ice margin and the forest during the full-glacial 18,000 years ago as has been claimed by Martin (1958a). If such a zonation existed, however, the low relative numbers of spruce pollen in Pennsylvania about 11,500 years ago might have been produced by the stragglers of the spruce migration that participated in this phase of the revegetation of the glaciated region to the north. The apparent

abundance of pine trees in Pennsylvania at this time as shown by the work of Martin (Guilday et al., 1964 and Kovar, 1964), indicates that certain species of this genus may have dominated the landscape northward toward New York State. A floristic boundary separating spruce- and pine-rich forests must have existed somewhere between the two areas. If pines indeed were dominant behind the spruce forest during A zone time, this would help to explain the rapid development of the B or pine zone following the disappearance of spruce from the region. In western New York Pinus strobus was the principal B zone pine. It would be interesting to determine whether it was present in central Pennsylvania during the lateglacial. The presence or absence of a verrucose furrow, a characteristic which allows white pine pollen to be separated from pollen produced by the other pines in eastern North America makes such differentiation possible.

The end of the A zone at both Houghton and Protection bogs can be dated by extrapolation. At the former locality, assuming that the pine peak occurred at the same time as it did at nearby Protection bog and that the sedimentation rate was constant, the mid-point of the Picea decline is about 9500 years B.P. Since the basal marl at Houghton bog may have accumulated at a more rapid rate than the silty gyttja at Protection bog, this date may be somewhat too young. The same type of calculation applied to data from Protection bog yields an age of 10,500 years B.P. for the same point in the

spruce decline. Both age determinations are in accord with those listed by Ogden (1967) who has concluded that the approximate synchronicity in the extinction of the spruce forest across the mid-latitudes of eastern North America points toward a sudden climatic change at this time.

#### ZONE B

As the spruce dominated A zone vegetation near the two Valley Heads sites disappeared about 10,500 to 9500 years ago, the pollen record indicates that pines became increasingly abundant in the region. At Houghton, Protection and Allenberg bogs the transition was abrupt. In contrast, spruce percentages at the Genesee Valley Peat Works gradually decline, although Pinus values increase rapidly. This is achieved mainly at the expense of various nonarboreal pollen types. High Pinus values are maintained upward in the section well into spectra which seem to be equivalent to those in zone C-1 at the three other sites. Although Pinus drops to about 7 percent of the sum in the Genesee Valley profile above a depth of 1 m, that portion of the diagram in which percentages of both Pinus and Tsuga are high may be strongly influenced by on-site pine trees. Pinus strobus pollen was the main type identified from this interval and the occurrence of white pine cones at various levels in the peat implies that white pine was growing locally. For this reason the end of zone B was drawn near 2.25 m at the

mid-point of the Tsuga increase, even though above this level Pinus percentages are still high. The A to B zone transition has not been dated at either Allenberg bog or the Genesee Valley Peat Works but, considering the proximity of all four sites, the disappearance of spruce may have been synchronous across the entire region.

The interval over which maximum pine percentages occur in Protection bog sediments has been dated at  $9030 \pm 150$  years B.P. (I-3551). This age determination compares well with a date of  $9310 \pm 150$  years B.P. from an equivalent stratigraphic position at Crystal Lake in northwestern Pennsylvania (Walker and Hartman, 1960) where the entire postglacial pollen sequence parallels my profiles from western New York. The dated sample at Crystal Lake was taken from the level at which maximum Pinus values occur, although at this depth Picea still amounts to 10 percent of the sum. In southern New England maximum relative and absolute members of pine pollen have been found in sediments about 9000 years old (Davis, 1967b; see also Davis, 1965b).

The ecological meaning of zone B has been discussed at length by Dansereau (1953) who presents a number of hypotheses to explain the widespread occurrence of maximum pine values following the disappearance of the A zone spruce forests. This publication appeared at a time when specific identifications of Pinus pollen were less certain than they are now. A part of the difficulty in interpreting zone B



lies in the well-known over-representation of pine pollen in sediments. With this in mind, Davis (1963, 1965b) has applied correction factors derived from a comparison of surface pollen accumulation and vegetation composition to a profile from northern Vermont. Her data indicate that maximum B zone pine percentages are an artifact caused by the low pollen productivity of the rest of the B zone vegetation. Pine trees were thought to have been rare in the region surrounding the basin in spite of the high relative pine pollen frequencies. This interpretation was later revised, however, when absolute pollen frequency data from Rogers Lake in southern Connecticut became available (Davis, 1967b). The deposition rate of oak, pine and other arboreal pollen types was found to actually increase in zone B, and at certain levels the rate for pine was 18 times higher than later in postglacial time, implying that pines were truly abundant in the region during B zone time. My absolute pollen frequency determinations from Allenberg and Houghton bogs corroborate these findings, providing the sedimentation rate was uniform across zone B at these sites.

One or both of the Diploxylon pines, Pinus banksiana or P. resinosa, appear to have been members of the regional vegetation that contributed pollen to zone A sediments in western New York. Fairly high values for the Diploxylon species persist through the lower part of zone B at all sites, but by the end of the zone B time, only 1 to 3 percent

occurs. Similar values are found in early post-settlement spectra before extensive plantings of Diploxylon pines were made in the area. At this time presumably only P. resinosa, which is today restricted to stations along the Genesee River (Zenkert, 1934), was contributing Diploxylon pine pollen to the sediments. Utilizing data given by Whitehead (1964), a shift of the mode to a larger size class, as seen in the size-frequency graphs of Pinus Diploxylon pollen from Allenberg bog (Fig. 6), suggests that P. resinosa was the principal B zone Diploxylon pine, whereas both P. banksiana and P. resinosa may have been members of the zone A vegetation. However, the closeness in pollen size of these two species, as Whitehead has emphasized, makes positive identification impossible. Diploxylon pines were infrequent in the regional vegetation at the west end of New York State after about 9000 years B.P., while they appear to have been more abundant before this date throughout the state (see Cox, 1959). Prior to 10,500 years B.P., red or jack pine or both were absent from Minnesota, but about this time they arrived at the southeast corner of the state, having migrated, probably around the northern end of the Great Lakes, from their survivium in the Appalachian Highlands of eastern North America (Wright, 1968b; Yeatman, 1967). Jack pine does not seem to have persisted in other refugia south or west of the Great Lakes.

The relatively few Pinus strobus grains which occur in the lower half of zone A indicate that white pine was not initially near any of the basins. However, as the deposition of zone A progressed, P. strobus percentages increased, indicating that white pine became more abundant regionally. This is most clearly seen in the Allenberg bog section C diagram. It is certain, however, that white pine was present near Protection bog during the A to B zone transition because a white pine cone was recovered from silty-clay gyttja at a depth of 5.75 m. Based on an extrapolation from the two higher radiocarbon dates at this site, assuming a constant sedimentation rate, the cone was deposited approximately 10,000 years ago. Total pine pollen at 5.75 m accounted for 35 percent of the sum. Haploxylon and Diploxylon types each amounted to 6 percent but the remainder could not be identified to subgenus. Pine was associated with 18 percent spruce pollen at this level. A maximum of 25 percent P. strobus pollen is present higher in zone B. At the other sites in southwestern New York, white pine also appears to have been one of the principal species which replaced spruce. Pinus strobus arrived in eastern Minnesota 7000 years ago from the east (Wright, 1968b). Its further migration toward the west was limited by the eastward expansion of the prairie and oak savanna which began 8000 years ago in the upper Midwest. The expansion ceased 4000 years ago and white pine began again to migrate westward reaching the northwest part of

Minnesota about 2700 years B.P. This is presently the western edge of its distribution in North America. White pine in western New York 10,500 years ago supports Wright's contention that the species survived full-glacial conditions in eastern North America.

Studies in the Allegheny National Forest of northwestern Pennsylvania (Hough and Forbes, 1943), indicate that Pinus strobus may have played a successional role in the change from spruce to pine forests. In this area today occur even-aged pine stands whose origin, in many cases, has been traced to an event that opened a part of the forest to seeding from nearby mature individuals. Understory white pines are absent because its seedlings do not survive in the shade. It is easy to visualize white pine seeding into openings created in the deteriorating spruce forest 10,500 years ago. We know that mature, seed-producing white pines were established at this time near Protection bog and probably elsewhere in the region. They seem to have coexisted temporarily with spruce whose actual abundance in the total vegetation at this time is not precisely known. Size-frequency measurements indicate that Picea mariana was the main spruce near Allenberg bog at the end of zone A. Because this is principally a lowland, wet-site species, the upland Picea glauca forests, which according to the pollen size data were present earlier in the A zone, may have been replaced by other communities. Considering the narrow interval

across which spruce drops from high to low values, spruce forests must have rapidly disappeared, freeing more and more surfaces for occupation by pine and other B zone species. Wright (1964) has suggested that spruce regeneration at this time was limited by summer temperatures which exceeded the tolerance of the species.

The total duration of zone B in western New York seems to have been between 1500 and 2000 years, extrapolating from the Protection bog age determinations. This is equivalent to about four white pine lifetimes, if we accept 450 years as the normal life span of the species (see Fowells, 1965). The occupation of a given site by successive generations of white pine may mean that other species that would normally replace it in the region today, e.g. Tsuga canadensis, had not yet migrated to the area. Since hemlock pollen does not occur in large numbers until some time after the B zone peak at  $9030 \pm 150$  years B.P., this hypothesis seems to be supported by my data. There was at least a four millenium lag in the migration of hemlock northward from somewhere in the unglaciated Appalachians following ice withdrawal from the Valley Heads moraine 13,000 years ago. Rather than assuming a climatic control for the zone B vegetation, differential migration rates of species back onto glaciated terrain may explain the basic pattern of post-glacial pollen succession in this region.

In some of my profiles zone B can be divided into a lower pine-birch subzone and an upper pine-oak subzone. A birch peak in the lower part of the zone is best developed at Allenberg bog where it is associated with a high in Carpinus-Ostrya, Fraxinus nigra and Populus curves. These features are less apparent at the other sites, although at Houghton bog high percentages of Betula and Carpinus-Ostrya occur in the equivalent stratigraphic interval. Whether these changes had regional significance is doubtful, however, because they are less clearly defined at nearby Protection bog where no peak is discernable in the Betula curve. Ulmus is well represented at most sites suggesting that elms were an important part of the regional vegetation. In fact the magnitude of elm percentages in zone B is only slightly less than that present in later postglacial time.

The presence of high birch values is not unique to western New York. Similar findings from southern New England have been reported by Davis (1958) and by Whitehead and Bentley (1963). These authors refer to the interval as subzone B-1. Since the peak occurs across the A/B zone boundary, birches may have been locally important members of the vegetation that existed during the transition from spruce to pine domination. In western New York Carpinus caroliniana and/or Ostrya virginiana, Fraxinus nigra and Populus spp. appear to have been present during this interval as well. Davis (1967b) mentions that the New England B-1 pollen assemblages

compare well with modern surface samples from northern Minnesota and from central Canada near Lake Timagami. These localities are in the mixed coniferous-deciduous forest formation about 60 mi south of the boreal forest and indicate that the climate of southern New England during the B-1 was cooler and drier than it is at present. Slightly lower Betula percentages and higher Quercus and Ulmus values characterize the western New York State sites, but otherwise B-1 assemblages from this region agree with those from New England.

At Allenberg bog where size measurements are available for B zone birch pollen, the configuration of the size-frequency curve suggests the presence of two species (Fig. 6). However, these cannot be identified with the size data currently available from herbarium specimens of eastern North American birch species. Possibly B. populifolia, B. pumila or both were present, as these species have pollen intermediate in size between the small grains of the shrub birch, B. glandulosa, and the larger pollen of the tree species, B. lenta and B. alleghaniensis. If B. populifolia and B. pumila produced the mode at 25 mu, then the larger modal class near 27 mu may indicate the presence of one of the tree birches during the deposition of zone B. In zone C-1 the mode also occurs at 27 mu, but higher in the section it shifts to 26 mu. Although I can be certain that only B. lenta and B. alleghaniensis gave rise to the mode at 26 mu in the upper C

zone spectra, the meaning of the modes at 25 and 27 mu in zone B is obscure and I must conclude that, although other species seem to be represented, their identity is unknown.

The upper portion of zone B in western New York is dominated by Pinus strobus and Quercus pollen. In some of the profiles Betula, Carpinus-Ostrya, Fraxinus and Populus values are lower than they were near the bottom of zone B. Acer saccharum was likely established in the region by the end of zone B. Arrival of oaks and expansion of the area occupied by them at locations near the basins is indicated by rapidly increasing relative numbers of oak pollen, although before this time some oaks were probably growing within 50 to 100 miles of the basins. The species involved are unknown, and either macrofossil evidence or improved pollen identification techniques are needed for specific determinations. However, Quercus rubra is a good possibility because of its current 'northern' distribution and pioneer status, but others could have been present also.

The entire B zone would seem to record the development of a white pine-oak forest. However, it is likely that the vegetation was quite complex at this time. Because of its broad ecological tolerances, white pine probably occurred in lowland valleys with elm and black ash and in the upland with oaks and/or sugar maple. The former community may have been similar to the White pine-American elm swamp forest that originally occupied the axes of some of the major



valleys in Cattaraugus County (Gordon, 1940). Forest types containing white pine and oak species are also known from western New York at the present time. White pine and red, black and white oak originally occupied dry sites in about 2 percent of Monroe County (Shanks, 1966), and similar stands undoubtedly occurred elsewhere in the Erie-Ontario Lowland. Castanea dentata and, at certain places, Pinus rigida were additional important members of this community. The pollen rain of this forest type has not been determined and, considering the present distribution of vegetation in the lowland, it seems unlikely that a sample which was not influenced by pollen output from the surrounding mesophytic forests could be obtained for comparative purposes. In any case, neither Castanea nor Pinus rigida appears to have been a member of the B zone vegetation according to pollen data currently available. Forests containing white pine and oak species are also known from well-drained sites, usually S-facing slopes, in the Allegheny Upland.

The pine-oak subzone pollen assemblages seem to have no exact modern analogue, but Davis (1967a) has pointed out that they are closest to the modern pollen rain in southern Ontario near the boundary between the deciduous and coniferous-deciduous forest (see King and Kapp, 1963, sample 4). However, an important difference is the higher pine and oak percentages found in upper B zone spectra from southwestern New York State. Although the suggestion that an

analogue of the pine-oak subzone is not in existence today seems premature, it is possible that a unique assemblage of species brought together by differential migration rates was present in western New York 9000 years ago.

#### ZONE C-1

Post-zone B sediments contain a record of the development and persistence of forests which contain the same species that now dominate existing forest types in western New York. Hemlock is an important tree in this region today and its pollen record is especially interesting and significant. The C-1 is set apart from the zones above it by high relative numbers of hemlock pollen and gradually increasing beech values. These features are retained when the relative frequency data from Houghton and Allenberg bogs are re-plotted on an absolute basis. Tsuga percentages increase markedly at the B/C-1 boundary and total Pinus values, with P. strobus pollen predominating, reciprocally decline. Across a 30 cm interval at Protection bog Tsuga increases from 2 to 25 percent. Assuming that it took 26 years to deposit 1 cm of gyttja in the basin (the sedimentation rate between the two radiocarbon dates immediately higher in the section), about 800 years was needed to accumulate this thickness of sediment.

The abrupt nature of the increase and the weak expression of Tsuga in zone B suggests that the interval may

record the initial invasion and expansion of hemlock in the region. The low relative numbers of hemlock pollen found in zones A and B at most of the sites probably represent wind-blown grains. Unfortunately, detailed information on the dispersal of hemlock pollen is not available, but up to 7 percent has been found in surface sediments near Lansing, Michigan (Parmelee, 1947) at locations about 75 mi south of the limit of continuous hemlock distribution in the state as mapped by E. L. Little, Jr. (in Fowells, 1965). According to the R values which I have calculated using several estimates of forest composition, hemlock pollen is somewhat over-represented in both surface and pre-settlement spectra. This may also have been true during earlier postglacial time suggesting that hemlock trees were actually somewhat less abundant in the total vegetation than the pollen record implies.

The ultimate cause of the replacement of white pine by hemlock is speculative. Arrival of hemlock in the region during its migration northward onto glaciated terrain has already been mentioned as one possibility, but whether hemlock was migrating at its fullest potential during the time preceding its arrival in western New York or whether its movement was held in check by climate or soil development is not known. The latter would seem not to have been too critical because hemlock seeds are able to germinate on a wide variety of substrates: moist, well-decomposed litter, rotted

wood, mineral soil and moss mats on soil and rocks (Hough, 1960). Once hemlock was present, however, white pine replacement can be viewed as a successional event. Although in existing forests both white pine and hemlock are often periodic in occurrence, studies in the Allegheny National Forest (Hough and Forbes, 1943) have shown that when both are found together, white pine will drop out of the association as time passes because its seedlings do not become established under a dense canopy, while those of hemlock can.

At the present time hemlock occurs from the southern Appalachians northward across the glacial boundary to northern Maine, New Brunswick and Nova Scotia and westward to eastern Kentucky, central Ohio and through southern Ontario and the northern part of the southern and the entire northern peninsula of Michigan to northeastern Wisconsin (Little in Fowells, 1965). The pollen record for Tsuga is not identical across this entire region, however, and although the main difference is the absence of two hemlock maxima from certain areas, a feature which will be discussed more fully under the heading zone C-2, another variable is the magnitude of hemlock representation in sediments deposited immediately following the high B zone pine percentages. In glaciated eastern North America from northwestern Pennsylvania to northern Maine (see Cox, 1959; Davis, 1965b; Deevey, 1951; Krauss and Kent, 1944; Potzger and Otto, 1943; Terasmae in Karrow, 1963; Walker and Hartman, 1960)

maximum hemlock values appear early in the profiles. At several sites in the southern part of this region where radiocarbon dates are available, the appearance of hemlock can be estimated at between 9300 and 8500 years B.P. (Davis, 1967b; Walker and Hartman, 1960). Although hemlock first appears near Halifax, Nova Scotia about this time, maximum values were not reached until about 7100 years ago (Livingstone, 1968).

In general, at sites from eastern North America which fall within the present limits of the Hemlock-white pine-northern hardwood forest (Nichols, 1935), Tsuga accounts for 25 to 35 percent of the sum directly above zone B. However, in southern New England, south of the forest boundary but still within the total range of hemlock, maximum C-1 hemlock values reach only 10 percent (Davis, 1967b). To the west in the Hemlock-white pine-northern hardwood Forest region of Michigan and Wisconsin, Tsuga pollen is also weakly represented in the equivalent stratigraphic interval. Unfortunately few C-14 dated pollen profiles are available from either state but hemlock would seem to have reached the Douglas Lake region of Michigan (Wilson and Potzger, 1943) early in the period of oak-hardwood domination which may be temporally equivalent to zone C-1 in the East. About 5 percent or less occurred until some point later in postglacial time when an increase to 20 percent took place. In central Michigan hemlock is consistently a part of the pollen record

above a C-14 date of  $7982 \pm 250$  years B.P., but it accounts for only 5 percent or less of the sum (Gilliam et al., 1967). West's diagram (1961) from Seidal Lake in eastern Wisconsin shows similarly that Tsuga appeared fairly early during the period of oak domination that followed the Pinus maximum, but hemlock never exceeded about 3 percent of the total until much higher in the section. Increasing Tsuga percentages in later postglacial sediments from this lake (=C-3 in western New York?), parallels the same trend at sites in northern Michigan. This change can also be observed in profiles from many other sites in the region (Messenger, 1967; Potzger, 1946).

Hemlock appears to have entered Michigan from the east, north of Lake Erie, and not from the south across the Prairie Peninsula which apparently acted as an effective barrier to migration of hemlock, beech and perhaps other species from the central Appalachians (Benninghoff, 1964). For example, in the diagram from Silver Lake in western Ohio (Ogden, 1966), low relative numbers of hemlock pollen (<5 percent) first occur 9800 years ago, but at several points higher in the section it completely drops out of the counts. Whenever hemlock pollen is found, it comprises only 2 to 3 percent of the sum, indicating that Tsuga was never very abundant in western Ohio. In this region during postglacial time hemlock likely occurred intermittently in small, isolated stands, perhaps on N-facing slopes or in other suitable

edaphic situations. At the present time Silver Lake is about 50 mi west of the limit of continuous hemlock distribution in Ohio.

Although it seems that hemlock pollen and probably hemlock trees first appeared at about the same time in western New York, Michigan and northern Wisconsin, the period of hemlock dominance characteristic of my western New York profiles is absent from sites to the west. In western New York where the C-1 occurs between about 8500 and 4300 years B.P., the vegetation appears to have been remarkably stable. The only significant changes occur in the Fagus and Quercus curves. The former shows a long-term increase, while the latter undergoes a corresponding decline. However, during the same period, the prairie and oak savanna expanded eastward in Minnesota (Wright, 1968a). It has not yet been established whether Wisconsin and Michigan were affected by the drier and warmer climate that probably induced this vegetation change, but if they were this might explain the meager representation of hemlock pollen in sediments accumulated during this interval at sites in the northern part of these states. Hemlock is known to grow best in a humid, cool climate and to be sensitive to drought which, if excessive, will result in death of the trees. As a corollary to this hypothesis, it follows that western New York State, where hemlock pollen is abundantly represented between 8500 and 4300 years ago, was moister and cooler than the Midwest. In

short, it would seem that when Minnesota and perhaps surrounding areas were undergoing a 'xerothermic' interval, western New York was not.

Too few pollen profiles are available from the Erie-Ontario Lowland in central and western New York to determine conclusively whether the vegetation during zone C-1 time was the same on both sides of the tension zone which now exists in the area, or whether beech-maple and oak forests dominated the lowland vegetation as they did immediately preceding settlement of the region. In pre-settlement forests hemlock was apparently much less abundant than in the upland, and since the development of this difference should be apparent in the pollen record a weaker representation of hemlock pollen in the lowland than the upland during the C-1 might indicate that the tension zone was established fairly early in postglacial time. Little difference is apparent in the C-1 Tsuga values between available profiles from lowland and upland sites, however. For example, in the Bullhead Pond profile (Cox, 1959), from a small lake 20 mi south of Lake Ontario in central New York, Tsuga accounts for about 20 percent of the sum. Slightly higher percentages of hemlock pollen occurred at some of my upland sites, but the difference hardly seems significant. At Cicero Swamp (ibid.) and Pennville Hidden Lake (Durkee, 1960), about 40 mi further east but near the edge of the lowland deciduous forest region,



Tsuga reaches about 40 percent of the sum in zone C-1. In general, the pollen diagrams from both the upland and the lowland are enough alike to indicate that only minor differences occurred across the entire region, but further data are needed to more adequately treat this problem.

The forest vegetation which developed during zone C-1 in southwestern New York was very similar to that existing in the region just prior to colonial settlement. Upper C-1 spectra closely match pollen assemblages which accumulated in the region between 1000 and 200 years ago. This means that the regional vegetation, and very likely the climate, during both periods was the same. Tsuga and Fagus did not arrive in western New York at the same time, and communities containing hemlock must have been well-developed when beech entered the region and began to expand. The long-term increase in Fagus values, which took place mainly at the expense of Quercus, can be interpreted as a trend toward increased mesophytism in the total vegetation. The prominence of beech in postglacial sediments from western New York is scarcely surprising in view of the important position this species holds in the Allegheny National Forest where it ranks highest of all forest species in establishment capacity, survival and competition. Beech is also less dependent on special seedbeds, soil moisture or light than hemlock (Hough and Forbes, 1943). During zone B time, oak forest types may have occurred at a variety of sites, although at the present

time they are found mostly on S- and SW-facing slopes in southern Cattaraugus County and in limited areas to the north. The pollen record indicates that with the passage of time these forests shrank in size and were in part replaced by more mesophytic associations containing hemlock, beech, sugar maple and other northern hardwoods.

Overall, the C-1 vegetation was probably a mixture of forest types as complex as now occurs in the region. Pollen from most of the important tree species which at present exist in the area are represented in various magnitudes in the zone; those that are not, such as Prunus serotina and Magnolia acuminata, are mainly insect pollinated and therefore are rarely found as fossils. Both Tilia and Fraxinus americana and/or F. pennsylvanica (4 colpate Fraxinus grains) first appear at the beginning of the C-1 and are as well represented in this zone as higher in the profiles. Likewise, pollen from Platanus occidentalis was first encountered at about this time in the two Valley Heads bogs; however, to the south at Allenberg bog small percentages occur throughout zone B. High Platanus values are prominent in zone C-1 at Houghton bog where the outwash plain surrounding the bog may have been an especially favorable habitat for this species. Juglans cinerea first occurs in low relative numbers in the upper part of zone A and a few grains were encountered in zone B sediments, but at all sites the postglacial maximum is reached at some point within the C-1.

Ulmus and Betula continued to hold prominent positions in the vegetation of the region. At Allenberg and Protection bogs birch values are somewhat higher near the middle of the zone than at either beginning or end. Size-frequency measurements of birch pollen at the former location indicate that the tree birches, B. lenta and B. alleghaniensis were the main species present. Low relative numbers of Castanea dentata pollen first appear in zone C-1 at Allenberg and Houghton bogs, although it regularly occurs from near the beginning of the C-2 upward at Protection bog. Local habitat differences around the basins probably explain the disparity.

#### ZONE C-2

In southwestern New York zone C-2 is characterized by low hemlock percentages and increased values for broad-leaf deciduous tree taxa. It is an interval between two successive hemlock maxima. The zone is represented in the Houghton, Protection and Allenberg bog profiles but is absent from the Genesee Valley Peat Works diagram because the uppermost sediments at this site were not sampled due to disturbance by bulldozing. In my profiles the lower zone boundary can be readily located at the midpoint of the abrupt hemlock decline which, at Protection bog, has been dated at  $4390 \pm 110$  years B.P. (I-3550). However, the placement of the upper boundary is arbitrary because of the absence of any clear stratigraphic markers. I have chosen a point where

percentages of deciduous tree taxa are reduced over their C-2 maxima and where hemlock just begins to exceed 10 to 15 percent of the sum. Accepting this placement of the boundary, the culmination of the C-2 at Protection bog occurred  $1270 \pm 95$  years ago (I-3549). This is from 500 to 800 years younger than other age determinations of the C-2/C-3 transition from eastern North America (see Davis, 1965b).

Using the rate of sediment accumulation between the two highest C-14 dates at Protection bog (0.069 cm/year), hemlock percentages decreased from 23 to 8 percent in about 350 years. This is merely an estimation, however, because the sedimentation rate may have been less in the upper part of the gyttja than between the dated levels in the gyttja and peat. Furthermore, the 25 cm over which the reduction in hemlock percentages took place reflects the sampling interval I used in this part of the profile. Since the same change could have taken place in less than 25 cm, the time interval may actually have been shorter. The pollen stratigraphy across the transition should be determined in detail in future studies.

In the relative frequency diagrams the Tsuga reduction is compensated for by increases in a number of other arboreal pollen types, principally Fagus, Acer saccharum, Betula, Quercus and Carya. Lesser increases also occur in Pinus strobus, Fraxinus americana and/or F. pennsylvanica, F. nigra and at one site, Carpinus-Ostrya. In no case are

any of the increases as prominent as the Tsuga decline. Size-frequency measurements from the upper and lower halves of zone C-2 at Allenberg bog indicate that Betula lenta and/or B. lutea were the main birches contributing to the pollen rain, but possibly a third species was present during the deposition of the upper part of the zone.

These changes indicate modifications in the regional vegetation which simultaneously favored the expansion of dry site oak and hickory forests and mesic communities containing beech, sugar maple and birch. Traditionally zone C-2 in eastern North America has been interpreted as a xerothermic interval, a period of warm and dry climate during which oak and hickory forests expanded at the expense of more mesophytic associations (see Deevey, 1949). Although a decrease in the representation of hemlock, a strongly mesophytic species, and the corresponding increase in oak and hickory in western New York State is the expected pattern, if we accept the xerothermic interpretation, the coordinated increases in Acer saccharum, Betula lenta and/or B. lutea and Fagus grandifolia, all of which are mesophytes, are contradictory.

A drier, more continental climate during the C-2 would be better documented if an analogue for the vegetation could be found where such a climate prevails at the present time. The Beech-maple forest region of central Ohio and Indiana is a logical place to look for surface pollen assemblages

similar to C-2 spectra from southwestern New York, but unfortunately no systematic study of the recent or subrecent pollen rain in Ohio and Indiana has been made. Pollen profiles from this area provide some comparative data, however. The topmost spectra in the diagrams from north-central and northeastern Ohio presented by Sears (1942), which in most cases probably represent the subrecent pollen rain, do not match any of my C-2 assemblages, nor do spectra from just beneath the post-settlement Ambrosia peak at Silver Lake in western Ohio. In both areas Quercus and Carya values are larger and Fagus representation is much weaker than at any of my southwestern New York sites. However, the lack of correspondence is not conclusive proof of the absence of a relationship because the pollen rain has been determined at so few sites in this part of the Midwest. Until such information is forthcoming, it seems best to reserve judgment on the current existence of a probable analogue for the C-2 vegetation.

It has been postulated that a wedge of prairie vegetation extended through central Indiana and Ohio during the putative mid-postglacial xerothermic interval (see Benninghoff, 1964). This hypothesis was used by Shanks (1966) to explain the origin of prairie remnants in oak openings in the Erie-Ontario Lowland of western New York. There is, however, no C-2 increase in grass pollen at any of the sites I have studied in this area. All C-2 spectra are dominated by

arboreal pollen types and in only a few cases does nonarboreal pollen account for more than 3 percent of the sum. In these instances the NAP is clearly of local derivation. Of some interest in this regard, however, is the presence of Ephedra pollen in zone C-2 at Protection bog. If it could be established that Ephedra species were growing in the region during this time, the argument for an interval of xeric, continental climate would be improved. However, Maher's recent review (1964) has shown that Ephedra pollen, which has been found widely in the Great Lakes region, is not limited to any one constant stratigraphic interval, but rather it occurs sporadically in both late- and postglacial deposits. This fact and the presence of Ephedra pollen in a surface sample near Lake Simcoe, north of Lake Ontario (King and Kapp, 1963) and elsewhere implies that an extra-regional origin, through long-distance wind transport from the southwestern United States, is the most likely explanation for the presence of Ephedra pollen in western New York. The occurrence of Liquidambar pollen in both late- and postglacial sediments in this region can be explained in the same way. At the present time the northern limit of sweet gum is southern Ohio and central West Virginia about 300 mi south and southwest of the sites included in this study.

In eastern North America pollen profiles with two hemlock maxima separated by a single interval of low hemlock percentages are known from a broad area including northwestern

Pennsylvania (Walker and Hartman, 1960), New York State (Cox, 1959; McCulloch, 1939; Dunham, 1965; Durkee, 1960), northern Vermont (Davis, 1965b), southern Vermont (Whitehead and Bentley, 1963), southern New England (Davis, 1967b; Deevey, 1939, 1943) and Maine (Deevey, 1951). In Canada a hemlock decline is present in what appears to be a top-truncated profile obtained from a site west of Hamilton, Ontario (Terasmae in Karrow, 1963), a Tsuga minimum occurs in profiles from the Gatineau Valley region of Quebec, 30 to 60 mi north of Ottawa (Pötzger and Courtemanche, 1956) and a mid-postglacial decline in Tsuga percentages occurs farther east in Nova Scotia (Livingstone, 1968). South of the glacial boundary at Bear Meadows bog in central Pennsylvania (Kovar, 1964) a mid-postglacial Tsuga minimum also occurs. It remains to be established, however, whether the hemlock decline was strictly synchronous over the entire region just described. Radiocarbon dates are available from only scattered localities but they show a surprising degree of accord. The Protection bog date of  $4390 \pm 110$  years B.P. agrees favorably with the Tsuga minimum which started at Rogers Lake, Connecticut about 4100 years ago (Davis, 1967b) and with the abrupt Tsuga decline dated at  $4540 \pm 140$  years B.P. at Crystal Lake near Halifax, Nova Scotia (Livingstone, 1968).

Can the hemlock decline be explained in any other way than by postulating a xerothermic interval? Viewing the tripartite C zone as a unit, the decline seems to occur at a



time when soil development had progressed to a point where, by late C-1 time, the soil supported the same forest types that exist in the area today. Furthermore, the pollen evidence indicates that no new taxa entered the region following deposition of the lower third of the C-1, although data are not available on the immigration of such species as Liriodendron tulipifera, Magnolia acuminata, Prunus serotina and a few others that, while not important species regionally, are nonetheless significant members of certain forest communities. Whatever was responsible for the modifications in the mid-postglacial vegetation of southwestern New York would seem to have effected a fairly stable situation, as least in respect to entry of new species into the area and probably soil development as well.

In any event hemlock appears to be the key to the interpretation of zone C-2. The relative frequency diagrams clearly depict a reduction in Tsuga percentages and an enlargement of values for temperate deciduous tree pollen types. It is difficult, however, to determine which was cause and which effect because of the nature of expressing data in percentages, i.e. when the relative numbers of one category increase, a concomitant reduction in one or several others must occur. Therefore, the hemlock decline could represent an actual reduction in the number of Tsuga grains being deposited per year or an increase in the deposition rates of Fagus, Acer saccharum, Quercus and other pollen types, while

Tsuga pollen deposition remained constant. In the former case, increases in relative numbers of deciduous tree taxa would be artifacts of the percentage system providing their deposition rates remained constant; in the latter the converse would pertain.

Insofar as the absolute pollen frequency or the number of grains/unit volume of sediment represents actual deposition rates of the various pollen types, the absolute frequency diagram from Houghton bog shows that a significant reduction in the numbers of Tsuga pollen/ml took place across the C-1/C-2 boundary and that low absolute numbers persist throughout zone C-2. Of interest also is the fact that Fagus, Acer saccharum, Quercus and Betula, which showed the greatest relative frequency increases during the change from zone C-1 to zone C-2, are not any more strongly represented in the C-2 than in the upper part of the C-1. Although these features are meaningful only if the rate of sediment accumulation was constant across the interval (and unfortunately I was not able to obtain radiocarbon dates which would enable its determination in Houghton bog), at sites in eastern North America where sedimentation rates have been determined (Davis, 1967b; Ogden, 1967) it was more or less constant between late C-1 and late C-2 time. This may not be universally true in all small lake basins but, in the absence of differences in sediment lithology, it seems

reasonable to extend the assumption of a uniform sedimentation rate to Houghton bog.

The absolute pollen frequency data indicate that the C-2 modifications in the relative frequency diagrams were produced mainly by a decrease in the absolute numbers of hemlock, a species whose silvical characteristics are fairly well known (Fowells, 1965; Hough, 1960). Hemlock mortality can be caused by a variety of environmental factors, but drought is most important because of hemlock's shallow root system. Severe damage to hemlock stands over a broad area following the droughts of the early 1930's is well documented in the literature. For example, Secrest et al. (1941) estimate that 50 million board feet of hemlock died in the 230,000 acre Menominee Indian Reservation in Wisconsin during the three years between 1931 and 1933. These authorities demonstrated that under drought conditions root tips are rapidly killed and gradually the larger roots become weakened leaving the affected trees open to fungus and insect attack. To the east, hemlock mortality during the same drought period has been recorded at the Allegheny National Forest (Hough, 1936b) and near New Haven, Connecticut where in a 0.1 acre sample plot dead hemlock saplings and trees comprised 75 percent of the total (Stickel, 1933). In the latter region seedlings were killed outright and mortality in all size classes probably was enhanced by shallow soils developed directly over bedrock.

Data from a more detailed study on the effect of the 1930 drought on different forest types near State College in central Pennsylvania collected by McIntyre and Schnur (1936) supplies additional pertinent information. These authors examined 23 plots each 66 by 100 feet spread among chestnut oak, hemlock, scarlet oak-black oak and white pine-chestnut oak forest types. Eighty-four percent of the total basal area of hemlock was lost from the entire sample. By comparison, black oak lost 52 percent, chestnut oak 28 percent, red oak 26 percent and sugar maple 11 percent. Before the drought the four hemlock type plots contained abundant Tsuga canadensis, 60, 67, 78 and 60 percent expressed as a percentage of total basal area, while after the drought the relative dominance of hemlock was reduced to 2, 6, 66 and 24 percent in the same plots. The hemlock type changed from one dominated by this species to one of mixed composition, mainly chestnut and red oak with much smaller amounts of hemlock. In a general way this change parallels that observed in zone C-2 sediments from western New York with the exception of the importance of beech, sugar maple and yellow and/or sweet birch in the C-2 sediments from this region.

I suggest, therefore, that the hemlock decline can be viewed as a response to several severe drought years. The recorded devastation of hemlock during the 1930 drought from Wisconsin to southern Connecticut and the accordance of the dates of the hemlock decline between western New York,

New England and Nova Scotia might furnish the basis for postulating that widespread droughts might also have occurred about 4400 years ago. This new hypothesis, which can be partly tested by obtaining additional radiocarbon dates, to further check the synchronicity of the mid-postglacial hemlock decline, differs from the xerothermic interpretation in the nature and duration of the warm-dry climatic optimum. I feel that the modifications in the pollen record can be as well explained by postulating a series of severe droughts, perhaps distributed over several centuries or even over much less time, as by postulating an interval of xeric, continental climate lasting several millenia.

The return of Tsuga to a position of prominence in the pollen diagrams by zone C-3 time may represent the orderly and gradual succession of hemlock into communities to which it formerly belonged. Competition between hemlock and other mesophytes, particularly beech, would accompany this change and would affect the speed of hemlock reestablishment. Tsuga was never completely eliminated from the region because its pollen was continuously being deposited, even though in one instance, it reached as low as 4 percent of the sum. Tsuga likely survived in especially favorable edaphic situations, perhaps in the deeper gullies that were cooler and moister than the surrounding upland.

If the decline in hemlock alone produced the C-2 modifications in the pollen diagrams from southwestern New

York, biotic factors rather than climate must also be considered as possible causative agents. Certain insects including two species of hemlock loopers and the hemlock borer are known to cause local mortality, as are foraging deer, porcupines and rabbits (Fowells, 1965). Man may also have played a role. The Protection bog date for the C-1/C-2 boundary corresponds to a period during which central and western New York were occupied by Indians of the Lamoka culture (Ritchie, 1965). They subsisted by hunting, fishing and gathering; agriculture came somewhat later, about 1000 B.C. Little is known about the hunting techniques of these Indians, but apparently their main weapon was a javelin propelled by a throwing board which was used to secure large game, mostly the white-tailed deer. They probably used dogs during the hunt and it is not inconceivable that fire was used to drive game. Hemlock is known to be vulnerable to fire damage and, although old trees may survive light surface fires because of their thick bark, the roots are easily damaged by a burn that extends deeper than the loose surface litter.

I attempted to measure the influence and periodicity of past fires in southwestern New York by recording the number of charcoal fragments over 30 mu in size while counting to the basic pollen sum, but charcoal frequency does not seem to have been any greater in zone C-2 than in C-1. However, my counting technique needs refinement before fire

damage can be ruled out completely. For one thing, charcoal is brittle and larger pieces probably fragment during maceration, suggesting that a smaller minimum size should have been established before counting. Of more serious consequence is the sampling interval which in this part of the profile was 25 cm, definitely too great to regularly document an annual event such as a fire. While I cannot rule out direct or indirect biotic interaction as the cause of the hemlock decline with the existing data, it seems unlikely that a biological agent would have led to a reduction in hemlock percentages over the broad area in which they occur. Locally they may have been important but certainly not across many hundreds of miles.

One last topic remains to be discussed before leaving zone C-2. In certain regions two Fagus maxima occur in sediments which are approximately contemporaneous with the C-2 in western New York. For example at Silver Lake in western Ohio, Ogden (1966) considers the xerothermic interval to be represented by a minimum in beech pollen covering the interval between 3600 and 1300 years B.P. This is about the same time period during which a Fagus minimum has been found in southern New England deposits (Davis, 1967b; see also Deevey, 1943). The only diagram from New York State in which a similar change occurs is Cox's undated Consaulus bog profile (1959) from eastern New York near Albany. In this profile the Fagus and Tsuga minima are not coordinated, as they are

in southern New England, but rather the former occurs slightly above the latter. Although Fagus is characterized by erratic fluctuations in certain other of Cox's diagrams, a strong C-2 Fagus representation occurs in all. The significance of the bimodal Fagus curve in deposits to the east and west of southwestern New York is not known. Since the Fagus and Tsuga declines are not entirely synchronous, it seems likely that different factors were responsible in each case. The relationship between the two should be pursued in future research.

#### ZONE C-3

Two important changes in the pollen record characterize this zone, the most recent in origin. These are the return of Tsuga (subzone C-3a) and the occurrence of high percentages of NAP above the pre-/post-settlement boundary (subzone C-3b). Following the C-2 Tsuga minimum, hemlock values steadily increase higher in the profiles until near the end of the C-3a, the lower of the two subzones, where they are similar in magnitude to those of the C-1. Percentages of deciduous tree taxa are reduced over their C-2 maxima, but they still remain strongly represented upward to the C-3a/C-3b boundary. Across this interval at the three sites where zone C-3 sediments were sampled, Tsuga increases mainly at the expense of Fagus, indicating an increased role for the former in the regional vegetation. This may have been



enhanced by a trend toward a moister and a somewhat cooler climate which many feel has prevailed during the past several millenia (Sears, 1932) and may represent a continuation of succession begun during zone C-2 time.

This climatic trend seems affirmed at sites in northern New York (Durkee, 1960) and Canada (Pötzger and Courtemanche, 1956) by a Picea increase in sediments that appear equivalent to zone C-3 sediments in western New York where spruce, although very sparsely represented in the upper 25 cm in Houghton and Protection bogs, shows a distinct increase upward in zone C-3 at Allenberg bog. Spruce pollen encountered during the counts at the two former sites is mostly restricted to post-settlement spectra and, therefore, probably originated mainly from planted trees. At Allenberg bog, however, spruce occurs regularly throughout zones C-2 and C-3 but apparently was absent near the sampling point during the deposition of zone C-1. The small size of the spruce pollen (generally  $< 92 \mu$ ) in both the C-2 and C-3 indicates the presence of only Picea mariana which likely grew on the bog mat. Two grains larger than  $100 \mu$  found in zone C-3b at Allenberg probably were contributed by introduced cultivated species. The Allenberg bog spruce increase needs further documentation in western New York because, rather than indicating a climatic trend, changes in the hydrology of the peat deposit, induced by either physiographic modifications or biotic factors (e.g. beavers), may explain

what at the present time appears to be only a localized increase.

In New England, Castanea pollen shows a decided increase in the C-2 (Davis, 1967b; Deevey, 1939) but this is not true in southwestern New York. Although regularly present upward from either zones C-1 or C-2 in the deposits I have studied, maximum Castanea values are reached near the end of the C-2 at Houghton bog (1.8 percent) and near the middle of this zone at Allenberg bog (4.2 percent). Less than 1 percent occurs at equivalent positions in the Protection bog profile. Castanea was recorded in the original lot survey data only around Allenberg bog, and according to Gordon (1940), the pre-settlement distribution of chestnut mainly included the southern part of Cattaraugus County where it grew with oak on dry upper plateau slopes and tops and in Mixed mesophytic forests. Since Allenberg bog is near the area of maximum chestnut occurrence, while the two Valley Heads sites are about 25 mi to the north, my profiles, taken at face value, indicate that chestnut was never very abundant north of central Cattaraugus County in the Allegheny Upland of western New York.

Increasing Tsuga percentages in sediments that appear to be stratigraphically equivalent to the C-3a in western New York occur across an area that approximately coincides with the Hemlock-white pine-northern hardwood Forest region. A clearly defined hemlock increase is not apparent

in profiles from Nova Scotia, however. As was the case in zone C-1, the maximum values attained by Tsuga vary from district to district. For example, hemlock does not exceed 10 percent in the C-3 just south of the Forest region at Rogers Lake, Connecticut, while in western New York it reaches over 25 percent. At Rogers Lake, the highest C-3 hemlock percentages occur between about 1500 B.P. and the Ambrosia peak which marks the advent of European settlement.

To the west but still within the Forest region, the hemlock increase is more pronounced and parallels my findings in western New York. The C-14 dated Maple River Township bog diagram prepared by Hushen and Benninghoff (unpublished ms) from Emmet County near the northern tip of the Lower Peninsula of Michigan shows that hemlock was weakly represented (10 percent or less of the sum) between 4000 and about 3200 years B.P. at which time the increase began. After several erratic fluctuations upward in the profile, hemlock accounts for 50 percent of the sum in two spectra just beneath the pre-/post-settlement boundary. This change was accomplished largely at the expense of Pinus. The weak character of hemlock representation during the C-1 and C-2 in profiles from Michigan and Wisconsin has already been mentioned, but nevertheless a few Tsuga stands probably existed at favorable sites in the region. The Tsuga increase can be viewed as an expansion of these colonies or, alternately, immigration from some source area may be represented.

In all, the pollen record for hemlock is worthy of continued study. As more C-14 dated profiles become available from southern Ontario, which appears to have been the principal westward migration route for hemlock, a more critical analysis of its postglacial history will be possible.

The settlement of western New York, which began about 1800, and the attendant forest clearance is sharply marked by increasing NAP percentages and by the presence of wind-blown silt and clay in the Allenberg, Houghton and Protection bog profiles. Arboreal pollen drops to 50 percent or less of the sum over a very narrow interval indicating the catastrophic effect of European settlement on the natural vegetation. Although there is no clear evidence of Indian agriculture in any of my diagrams, low but perhaps significant percentages of Ambrosia and Rumex pollen which expand upward from zone C-3a below the pre-/post-settlement boundary, may have originated from weeds occupying cleared areas where corn, squash and beans were being grown by the Indians. It might be claimed that these pollen types were intrusions from more recent sediments, but Plantago pollen which would be expected to show the same behavior does not occur below the boundary except for rare single grain occurrences. Rayback's map (1966) of known Indian settlements shows a concentration of villages just west of Allenberg bog in eastern Chautauqua and western Cattaraugus Counties. Other villages are known from near the head of Cattaraugus Creek fairly close to both

Houghton and Protection bogs. I do not know how many of these sites were inhabited by agricultural Indians or exactly at what times they were occupied, but the high incidence of Indian habitation in certain parts of southwestern New York indicates that any associated agricultural activities could be recorded in zone C-3 sediments.

Pollen from cultivated species was found from the beginning of the C-3b to the surface. Agriculture indicators, including Zea and pollen from other cereals (counted as Gramineae), occur at Protection, Houghton and Allenberg bogs, while Fagopyrum, the buckwheat, was found only at the two last named sites. Ambrosia pollen is the dominant NAP type in the zone and reflects the high incidence of disturbed nonforest habitats where the common A. artemisiifolia and A. trifida and the less frequent adventive, A. psilostachya, continue to flourish today. Maximum Plantago, Rumex, Chenop., and Cichorioideae values are further evidence of the abundance of surfaces occupied by weedy species. Peak high-spine Compositae percentages may be in part due to increased frequencies of weedy species, but they could also reflect a local change in bog surface conditions favoring an increase in on-site taxa, such as certain Bidens species.

## SUMMARY AND CONCLUSIONS

1. All of western New York, except the Salamanca reentrant, a semicircular area on the south approximately bounded by the present course of the Allegheny River, was apparently ice-covered sometime during the Wisconsin glaciation. The various drift sheets in the region lack definitive dates, but the following correlations have been used in a recent review of the Pleistocene geology of New York State (Muller, 1965):

Lake Escarpment-Valley Heads Moraine: assigned to the Port Huron (Mankato) Substage, ca. 13,000 years B.P.;

Kent (Binghamton) Moraine: assigned to Cary Substage, minimum date 14,000 years B.P.;

Olean Moraine: pre-Cary (may be Tazewell or earlier).

Other moraines associated with these are considered short recessional still-stands or minor readvances of the ice margin. Recently obtained C-14 age determinations, which indicate the Kent ice overrode the area around Cleveland, Ohio about 23,250 years ago (White, 1968), will necessitate some revision in the above chronology. Recession to a point north of the Niagara escarpment in northwestern New York State was complete

by 12,500 years B.P. and ice apparently never again re-advanced into western New York.

2. Pollen succession was studied in sediments from four basins located on drift sheets of different age: Houghton and Protection bogs associated with the Valley Heads moraine, Allenberg bog on Kent drift and the Genesee Valley Peat Works on Olean drift. Houghton and Protection bogs are 10 mi apart and Allenberg bog is 25 to 35 mi southwest of these. The Peat Works is 35 mi southeast of the former two sites and 50 mi east of Allenberg bog.
3. The Portage escarpment separates western New York into two physiographic divisions: the Allegheny Upland in the south and the Erie-Ontario Lowland in the north. At the time of arrival of European settlers, the entire region was forested except for limited areas of prairie-like openings in the lowland. Forests of the Hemlock-white pine-northern hardwood Formation covered the upland, while beech-sugar maple and oak-hickory communities belonging to the Deciduous forest Formation occurred in the lowland. The ecotone between the two was not sharp and large inclusions of hemlock-hardwoods have been identified in the lowland. Upland oak forests are mainly limited to dry plateau tops and S-facing slopes near the Pennsylvania border.

4. An analysis of the bearing-trees recorded in the original lot survey notes for areas around Houghton, Protection and Allenberg bogs shows Fagus grandifolia, followed by Acer saccharum, to have the largest Importance Values. Tsuga canadensis is third in importance in two of the three areas. When frequency of mention data were computed from the same survey notes, Fagus continues to head the list. Second and third in frequency are Acer saccharum and Tsuga canadensis around Allenberg bog, Acer saccharum and Tilia americana about Houghton bog and Tsuga canadensis and Acer saccharum around Protection bog. Point-quarter sampling of three existing forest stands shows dominance by the same three leading species but with a change in the order of decreasing Importance Values. At all three sites Acer saccharum heads the list followed by Fagus grandifolia and Tsuga canadensis.
5. The relative frequency of different pollen types in surface and pre-settlement spectra divided by a percentage estimate of the importance of species in a vegetation sample contributing a given pollen type provides a measure of the degree of representation of these pollen types in relation to the vegetation surrounding a depositional basin. These ratios or R values were calculated in several ways using surface pollen spectra compared with composition data collected by the U.S.



Forest Service in existing forests and pre-settlement spectra compared with importance percentages and frequency of mention values derived from the original lot survey data. The computations indicate that in Recent and sub-Recent sediment samples from western New York, pollen from Betula spp., Pinus spp., Quercus spp. and Tsuga canadensis are over-represented, Carpinus caroliniana and/or Ostrya virginiana, Fagus grandifolia and Juglans cinerea are proportionately represented and that Acer rubrum and/or A. saccharinum, A. saccharum, Castanea dentata, Carya spp., Fraxinus americana and/or F. pennsylvanica, F. nigra, Populus spp. and Tilia americana are under-represented.

6. A clearly defined T zone characterized by 50 percent or more nonarbooreal pollen underlying a zone of spruce pollen domination was found in basal inorganic sediments only at Allenberg bog. T zone pollen assemblages contain 20 percent Picea, 10 percent Pinus, 3 to 8 percent Quercus, 3 to 5 percent Fraxinus nigra, 15 to 25 percent Cyperaceae, about 10 percent Gramineae and numerous other NAP types and closely match the pollen rain today in the boreal forest-tundra ecotone at Fort Churchill, Manitoba where discontinuous spruce stands occur interspersed with herbaceous communities in a park-tundra. This implies that the climate in southwestern New York during the deposition of zone T was probably similar to

that in this part of the subarctic today. No positive tundra indicator pollen types were found, although microspores of a subarctic species, Selaginella selaginoides, occur in several spectra.

7. Abundant herb pollen was present in basal sediments at the Genesee Valley Peat Works, but a zone in which spruce dominates is not present higher in the profile making the meaning of the basal herb-spruce-pine assemblage at this site somewhat obscure. If local overrepresentation and redeposition were not operative, then an open vegetation perhaps similar to the park-tundra of T zone time at Allenberg bog existed around the Genesee Valley site. However, there is some evidence to suggest that the pollen rain was heavily influenced by near- and on-site herbs and therefore that the regional vegetation was a denser spruce-pine forest. Since the peat works are on the oldest drift sheet in western New York, the basal sediments may antedate comparable deposits elsewhere in eastern North America. If subsequent C-14 dating bears out their antiquity and if the pollen assemblage is taken at face value, a park-tundra may have covered the Alleghany Upland in southern New York during the "classical" Wisconsin glaciations. More data are needed from additional sites in the region to further document this hypothesis.

8. Zone A at Allenberg bog is a long interval of domination by spruce and pine pollen. Changes in Fraxinus nigra, Quercus, Pinus and Picea percentages permit subdivision of the zone following the sequence recognized in certain profiles from southern New England where such changes have been interpreted as vegetation modifications in response to the Two Creeks--Valders climatic changes. However, absolute pollen frequency data from Allenberg bog indicate that an increase in the absolute numbers of spruce and pine pollen being deposited per unit volume of sediment--evidence of an increased abundance of spruce-pine forests on the landscape--was responsible for changes in the Quercus and Fraxinus nigra curves at this site. The absolute numbers of these pollen types remained more or less constant across the interval in which relative pollen frequency changes took place.
9. Zone A pollen assemblages from Allenberg, Houghton and Protection bogs contain both Picea glauca and P. mariana and are similar to existing surface pollen accumulations in the open boreal woodland of central Quebec. In contrast to the situation in Michigan, Wisconsin and Minnesota, Pinus banksiana and/or P. resinosa grew in southwestern New York during zone A time. Abies balsamea and Larix laricina were members of the A zone forests and deciduous trees, whose pollen consistently occurs in the zone, may have occupied favorable sites within



some tens of miles of the basins. This is particularly true of Quercus spp. and Fraxinus nigra and perhaps Carpinus-Ostrya also. The presence of Acer, Carya, Juglans, Tsuga and Ulmus pollen probably reflects wind transport from distant sources. The bottom of zone A at Houghton bog has been dated at  $11,880 \pm 730$  years B.P.

10. Mosses from an organic bed deposited  $12,100 \pm 400$  years ago along the southern edge of Lake Iroquois near Lockport, N.Y. and a pollen spectrum from associated lacustrine sediments indicate the existence of a mosaic of plant communities in northwestern New York at this time. Species characteristic of dry dune sand, rich fens and better drained fen edges probably occupied the area between the lake edge and a spruce-fir-larch forest occurring some distance inland. Exposed rocky habitats may have existed also. The occurrence of two typical arctic and subarctic mosses, Aulacomnium acuminatum and A. turgidum, indicates the possible presence of limited patches of tundra vegetation.
11. The spruce-pine woodland disappeared from 9500 to 10,500 years ago near the Valley Heads sites and was succeeded by zone B forests in which Pinus strobus held a dominant position. Abies balsamea flourished briefly during the transition. At some sites lower pine-birch and upper pine-oak subzones can be distinguished. A

Pinus strobus cone was recovered from sediments about 10,500 years old at Protection bog and clearly establishes the presence of this species in southwestern New York during the deterioration of the spruce-pine woodland. The B zone pine peak was dated at  $9030 \pm 150$  years B.P. at Protection bog.

12. Zone C-1 is characterized by high percentages of Tsuga canadensis and increasing values for Fagus grandifolia. Other species which grow on the Alleghany Upland at the present time are also represented in this zone. The similarity of the pollen assemblages near the end of zone C-1 and those found immediately beneath the pre-/post-settlement boundary indicate that the zone records the regional development of forests of the hemlock-northern hardwoods type. Forest composition likely was as complex as now occurs in the upland. No major changes took place in the vegetation of southwestern New York during the duration of the C-1, although the Fagus increase may indicate a trend toward increased mesophytism.
13. An abrupt hemlock decline at Allenberg, Houghton and Protection bogs which has been dated at  $4390 \pm 110$  years B.P. at the last named site, marks the beginning of zone C-2. The relative frequency of Acer saccharum, Betula, Carya, Fagus, Fraxinus, Pinus strobus and Quercus pollen all show small increases in this zone. However, absolute pollen frequency data imply that these changes were

induced by a decrease in the total number of hemlock grains being deposited per unit volume. Rather than a long interval of xeric, continental climate, the C-2 in southwestern New York seems to be a result of differences in hemlock abundance alone. A series of severe droughts, which are known to cause heavy hemlock mortality in existing stands, occurring over several years or tens of years is postulated as the cause of the hemlock decline. Biotic factors, including man, may or may not have played a secondary role. Hemlock was never completely eliminated from southwestern New York during the C-2.

14. Zone C-3a began  $1270 \pm 95$  years ago at Protection bog and records the return of hemlock to a position of prominence in the regional vegetation. This change may have been influenced by a climatic trend toward greater moisture during the past several millenia but the hemlock return following the low, early in C-2 time, may represent successional recovery. There is some evidence that Indian agriculture is recorded in the upper half of this subzone.
15. European settlement and forest clearance occurred during the deposition of the topmost pollen assemblages belonging to subzone C-3b. Pollen from agricultural indicators, including Fagopyrum, Zea and other cereals, was found in this subzone and the high frequencies of

Ambrosia, Cheno-Am, Plantago and Rumex pollen, species which grow in disturbed habitats, are characteristic. Zone C-3b sediments contain large quantities of silt and clay blown in from bare areas around the basins.



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## APPENDICES

- A. Pollen Spectra Above and Below Gyttja Samples Used  
C-14 Age Determinations at Protection Bog
- B-H. Percentages of Minor Pollen and Spore Types not  
Shown on Pollen Diagrams

### NOTE

The notation "comp." after certain pollen taxa indicates the degree of certainty in the identification of difficult pollen grains (Benninghoff and Kapp, 1962). It is used when a grain is provisionally assigned to a taxon and to convey that uncertainty exists about the conclusiveness of identification. If no notation follows a taxon, the identification is considered positive.

## APPENDIX A

## POLLEN SPECTRA ABOVE AND BELOW GYTTJA SAMPLES USED FOR

## C-14 AGE DETERMINATION AT PROTECTION BOG

Taxa	Depths (m)			
	3.56	3.66	5.35	5.45
<b>Arboreal Pollen (AP)<sup>1</sup></b>				
<u>Picea</u>	---	---	0.7	---
<u>Abies</u>	---	---	0.6	0.4
<u>Larix</u>	---	---	0.3	---
<u>Pinus</u> undifferentiated	0.9	0.5	20.9	21.2
<u>P. Haploxyton</u>	1.4	1.4	22.6	23.6
<u>P. Diploxyton</u>	0.2	0.2	3.2	2.9
<u>Juniperus</u>	---	---	---	0.1
<u>Tsuga</u>	16.7	23.2	2.1	1.5
<u>Fagus</u>	35.4	38.2	0.7	0.3
<u>Acer saccharum</u>	8.6	7.7	1.5	1.3
<u>Tilia</u>	0.9	0.6	0.3	---
<u>Fraxinus</u> 4-colpate	3.9	1.8	0.6	0.6
<u>Juglans cinerea</u>	1.3	0.3	0.1	0.3
<u>Carya</u>	1.4	1.1	1.0	0.6
<u>Quercus</u>	6.8	7.5	22.3	19.5
<u>Ulmus</u>	5.0	6.4	6.0	6.0
<u>Betula</u>	11.0	5.4	6.2	8.8
<u>Fraxinus</u> 3-colpate	2.0	1.9	1.2	2.3
<u>Acer rubrum/saccharinum</u>	---	0.3	---	---
<u>Carpinus-Ostrya</u>	0.8	0.6	6.0	7.2
<u>Corylus</u>	---	---	0.4	0.7
<u>Platanus</u>	0.9	1.4	0.4	0.4
% AP	97.3	98.7	97.3	97.8
<b>Nonarboreal Pollen (NAP)<sup>1</sup></b>				
<u>Alnus</u>	0.6	0.3	0.7	0.5
<u>Salix</u>	0.3	---	0.7	0.1
<u>Viburnum</u>	0.3	---	---	---
Rosaceae	0.2	---	---	---
Cyperaceae	0.3	0.2	0.3	0.7
Gramineae	---	---	0.1	0.4
<u>Ambrosia</u>	0.3	0.2	0.1	---
<u>Artemisia</u>	0.2	0.2	0.3	0.1
<u>Xanthium</u>	0.3	---	---	0.1
High-spine Compositae	---	0.2	0.3	---
Cheno-Am.	0.2	---	---	---
<u>Ranunculus</u>	---	0.2	---	---
<u>Thalictrum</u>	---	0.2	---	---
% NAP	2.7	1.3	2.7	2.2
<b>Misc. Pollen (MP)<sup>2</sup></b>				
Ericaceae	0.5	0.2	---	---
<u>Nuphar</u>	---	---	0.4	---
<u>Sarracenia</u>	0.2	0.2	---	---
Polypodiaceae	---	0.2	3.0	3.3
Osmundaceae	0.5	0.5	---	---
broken Abietineae	---	---	1.1	0.4
unfamiliar	---	---	0.1	---
unknown	2.7	4.0	3.4	1.7

<sup>1</sup> Percentage base: sum AP + NAP.<sup>2</sup> Percentage base: sum AP + NAP + MP.

Depths (m)		Taxa																							
		Ephedra	Juniperus	Liquidambar	Myrica	Rosaceae	Viburnum	Caryophyllaceae	Coptis	Gentiana comp.	Labiatae	Leguminosae	Polygonum	Potentilla palustris	Ranunculus	Umbelliferae	Urticaceae	Vitis	Xanthium	Myriophyllum	Sagittaria	Sarracenia	Sparganium	Utricularia	Ophtologlossaceae
0.000	0.1	0.1	0.1	0.1	0.1	0.1	0.3	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.2	0.1	0.1	0.1	0.1	0.1	0.1
0.025	0.1	0.1	0.1	0.1	0.1	0.1	0.7	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.3	0.1	0.1	0.1	0.1
0.075	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1
0.125	0.1	0.1	0.1	0.1	0.1	0.1	0.4	0.1	0.1	0.1	0.1	0.6	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1
0.175	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.1	0.1	0.1
0.225	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
0.275	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
0.325	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
0.425	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
0.575	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
0.725	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
0.925	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
1.225	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
1.475	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
1.725	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
1.975	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
2.225	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
2.475	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
2.725	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
2.975	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
3.225	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
3.475	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
3.725	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
3.975	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
4.225	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
4.475	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
4.725	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
4.975	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
5.225	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
5.475	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
5.725	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
5.975	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
6.225	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
6.475	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
6.725	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
7.025	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1
7.325	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1

## APPENDIX C

## PERCENTAGES OF MINOR POLLEN AND SPORE TYPES NOT SHOWN ON POLLEN DIAGRAM:

## HOUGHTON BOG - SECTION A

Depths (m)	Taxa	Cephalanthus	Rhamnus comp.	Rhus	Rosaceae	Sambucus	Viburnum	Caryophyllaceae	Coptis	Labiatae	Leguminosae	Ranunculus	Rubiaceae	Thalictrum	Umbelliferae	Sagittaria	Sparganium	Typha	Utricularia	Ophioglossaceae
0.000		---	---	---	0.6	---	0.5	---	---	---	0.2	---	---	---	0.2	0.1	---	---	---	---
0.025		0.2	0.1	0.1	0.3	0.2	---	0.1	---	---	---	---	---	0.1	0.3	---	---	---	---	0.2
0.075		0.1	---	---	---	---	---	0.1	---	0.1	0.2	0.1	0.1	---	---	0.3	0.1	0.1	---	0.1
0.125		---	---	---	0.3	---	---	---	---	---	---	0.1	---	---	---	---	---	---	---	0.1
0.175		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
0.225		0.2	---	---	0.2	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
0.375		---	---	---	---	---	---	---	---	---	---	---	---	0.2	---	---	---	---	---	---
0.725		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	0.2	---
0.925		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	0.2	---	---
1.225		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
1.425		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
1.725		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	0.2
1.925		---	---	---	---	---	---	---	0.2	---	---	---	0.2	---	---	---	---	---	---	---
2.225		---	---	---	---	---	---	---	0.2	---	---	---	---	---	---	---	---	---	---	---
2.475		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
2.725		---	---	---	---	---	---	---	0.2	---	---	---	---	---	---	---	---	---	---	---
2.975		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
3.225		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
3.425		---	---	---	---	---	---	---	---	---	---	---	---	0.2	---	---	---	---	---	---
3.725		---	---	---	---	---	0.2	0.2	---	---	---	---	---	---	---	---	---	---	---	---
3.925		---	---	---	---	---	---	---	---	---	---	---	---	---	0.2	---	0.2	---	---	---





APPENDIX E  
PERCENTAGES OF MINOR POLLEN AND SPORE TYPES NOT SHOWN ON POLLEN DIAGRAM:  
ALLENBERG BOG - SECTION A

Depths (m)	Taxa	Juglans nigra	Liquidambar	Magnolia acuminata	Cephalanthus	Myrica	Rosaceae	Viburnum	Caryophyllaceae	Coptis	Labiatae	Leguminosae	Ranunculus	Thalictrum	Umbelliferae	Urticaceae	Vitis	Xanthium	Sagittaria	Sarracenia	Sparganum	Utricularia	Equisetum	Ophioglossaceae
0.000	0.2	0.1	---	---	---	---	2.6	0.1	---	---	---	---	---	---	---	0.1	---	0.1	---	---	---	---	---	---
0.025	---	---	---	0.1	---	---	1.1	0.3	---	---	0.3	0.2	---	---	0.5	---	0.2	0.1	0.3	---	---	0.1	---	0.1
0.075	0.2	0.1	---	---	---	---	0.7	0.3	---	---	---	0.2	---	---	0.2	0.2	---	0.1	---	---	0.1	---	0.1	---
0.125	0.2	0.1	---	0.1	0.1	---	1.1	2.3	---	---	0.1	0.1	0.4	---	---	---	---	---	0.1	0.1	---	---	---	---
0.175	0.3	0.2	---	---	---	---	0.3	1.2	---	---	---	---	---	---	---	0.2	---	---	---	0.1	0.1	---	---	---
0.225	0.2	---	0.3	---	---	---	0.2	---	---	---	---	---	---	---	---	---	---	---	---	---	0.4	---	---	---
0.275	---	0.2	---	---	---	---	0.2	---	---	---	---	---	---	---	---	---	---	---	---	---	1.6	---	---	---
0.325	---	0.2	---	---	---	---	---	---	---	---	---	---	0.2	0.2	---	---	---	---	---	---	0.7	---	---	---
0.375	0.3	---	0.2	---	---	---	0.2	---	---	---	---	---	---	---	---	---	---	---	---	---	0.5	---	---	---
0.425	0.2	---	---	---	---	---	0.2	0.2	---	---	---	---	---	0.3	---	---	---	---	---	---	0.4	---	---	---
0.475	0.2	---	---	---	---	0.2	---	0.5	---	---	---	---	---	0.2	---	---	---	---	---	---	---	---	---	---
0.675	---	---	---	---	---	---	0.2	---	---	---	---	---	0.2	---	---	---	---	---	---	---	---	---	---	---
0.925	---	---	---	---	---	---	---	0.9	---	0.3	---	---	---	---	---	---	---	---	---	---	---	---	---	---
1.117	---	---	---	---	---	---	0.3	0.2	---	0.3	---	---	---	0.2	---	---	---	---	---	---	0.7	---	---	---
1.425	---	---	0.2	---	---	---	---	0.2	---	---	---	---	---	0.2	---	---	---	---	---	---	0.3	---	---	---
1.675	0.2	---	---	---	---	---	1.1	0.5	---	0.2	---	---	---	0.2	---	---	---	---	---	---	0.4	---	---	---
1.925	---	0.2	---	---	---	---	---	---	0.2	---	---	---	---	---	---	0.3	---	---	---	---	0.2	0.2	---	---
2.175	0.2	---	---	---	---	---	0.3	0.5	---	---	---	---	---	0.5	---	---	---	---	---	---	0.3	0.1	0.1	---
2.425	---	---	---	---	---	---	0.5	0.3	---	---	---	---	---	0.2	---	---	---	---	---	---	0.1	0.1	---	---
2.675	---	---	---	---	---	0.2	0.5	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
2.925	0.2	---	---	---	---	---	0.2	---	---	---	---	---	---	---	---	---	---	---	---	---	0.3	---	---	---

APPENDIX F  
 PERCENTAGES OF MINOR POLLEN AND SPORE TYPES NOT SHOWN ON POLLEN DIAGRAM:  
 ALLENBERG BOG - SECTION B

Depths (m)	Taxa	Juglans nigra	Liquidambar	Magnolia acuminata	Nyssa sylvatica	Cephalanthus	Myrica	Rhus	Rosaceae	Viburnum	Caryophyllaceae	Coptis	Epilobium	Cichorioideae	Umbelliferae	Urticaceae	Xanthium	Myriophyllum	Potamogeton	Sarracenia	Utricularia	Equisetum	Ophioglossaceae
4.525		0.2	---	0.2	---	---	0.2	---	---	---	---	---	---	---	---	---	0.2	---	---	---	---	---	---
4.675		0.2	---	---	---	---	---	---	0.2	---	---	---	---	---	---	---	---	---	---	0.6	---	---	---
4.925		---	0.2	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	0.3	---	---	---
5.175		---	0.2	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	0.4	---	---	---
5.425		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	0.2	---	---	---
5.675		---	0.2	---	---	0.2	---	---	---	---	---	---	---	---	---	---	---	---	---	---	0.1	---	---
5.925		---	---	---	---	---	---	---	0.2	---	---	---	---	---	---	---	---	---	---	---	---	---	---
6.175		---	---	---	---	---	---	---	---	---	---	---	0.2	---	---	0.2	---	---	---	---	---	---	---
6.425		---	---	---	---	0.2	---	---	---	---	---	---	---	0.2	---	---	---	---	---	---	---	---	---
6.675		0.3	---	0.2	---	---	---	---	---	---	---	---	---	---	---	---	0.2	---	---	---	0.1	0.1	---
6.925		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
7.175		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	0.1	0.2	---
7.425		---	---	0.2	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	0.1	---	---	---
7.675		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
7.925		0.2	0.2	---	---	---	---	---	0.2	---	---	---	---	---	---	---	---	---	---	4.1	0.2	---	---
8.175		---	---	---	---	---	---	---	0.1	---	---	0.1	---	---	---	---	0.1	---	---	0.1	---	---	---
8.425		---	0.3	---	---	---	---	---	0.3	---	---	---	---	---	---	---	---	---	---	---	---	---	---
8.675		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
8.925		0.2	---	---	---	---	---	---	---	0.2	---	0.3	---	---	---	---	---	---	---	---	---	---	---
9.175		0.2	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
9.425		0.3	---	---	---	---	---	0.2	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
9.675		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
9.925		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
10.175		---	---	---	---	---	---	---	---	---	---	---	---	---	---	0.2	---	---	---	---	---	---	---
10.425		---	---	---	0.2	---	---	---	---	0.2	---	---	---	---	---	---	---	---	---	---	---	---	---
10.675		---	---	---	---	---	0.2	---	---	0.3	---	---	---	---	---	---	---	---	---	---	---	---	---
10.925		---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---	---
11.175		---	---	---	---	---	---	---	---	0.2	---	---	---	---	---	---	0.2	---	---	---	---	---	---
11.425		---	0.2	---	---	---	---	---	---	0.2	---	---	---	---	---	0.2	0.2	---	---	---	---	---	0.2
11.675		---	---	---	---	---	---	---	---	0.2	---	---	---	---	---	0.2	0.2	---	---	---	---	---	---
11.925		---	---	---	---	---	0.2	---	---	---	---	---	0.2	---	0.2	0.2	---	---	---	---	---	---	---
12.175		---	---	---	---	---	0.2	---	---	---	---	---	---	---	---	---	---	0.1	---	---	---	---	---
12.425		---	---	---	---	---	---	---	---	---	0.2	0.2	---	---	---	---	---	---	0.2	---	---	---	---

APPENDIX G  
PERCENTAGES OF MINOR POLLEN AND SPORE TYPES NOT SHOWN ON POLLEN DIAGRAM:

ALLENBERG BOG - SECTION C

Depths (m)	Taxa	Nyssa	Rhus comp.	Rosaceae	Viburnum	Caryophyllaceae	Coptis	Epiobium	Galium comp.	Gentiana comp.	Labiatae	Polygonum	Ranunculus	Umbelliferae	Urticaceae	Xanthium	Eriocaulon	Menyanthes	Sagittaria	Sparagium	Isaetes	Ophioglossaceae	Selaginella
11.525															0.3								
11.675																							
11.875					0.2																		
12.025					0.3										0.2								
12.175															0.4								
12.325				0.4																			
12.425				0.2																			
12.625		0.2																					
12.775																		0.1	0.3	0.3			
12.925																			0.3	0.1		0.1	
13.075							0.2												0.3	0.1			
13.225															0.1			0.1	0.1	0.3		0.1	
13.375				0.1																0.7			
13.525				0.3											0.1	0.1				0.3		0.1	
13.675				0.1									0.3							0.5			
13.825				0.2				0.2															
13.925				0.1					0.1		0.1											0.1	
14.125				0.2											0.2					0.5			
14.275			0.1						0.1									0.1				0.1	
14.425				0.1									0.3		0.1	0.1		0.1	0.1	0.4		0.1	
14.540	0.1			0.3							0.3		0.1							0.4		0.1	
14.660													0.3		0.3				0.1	0.1			
14.750													0.2		0.3				0.1	0.1			
14.870											0.1		0.1		0.3								
14.985				0.3		0.1				0.3			0.4	0.3								0.3	0.1
15.085				0.2		0.4					0.1		0.1										0.1
15.165						0.1					0.1	0.1	0.2				0.1						

## APPENDIX H

PERCENTAGES OF MINOR POLLEN AND SPORE TYPES NOT SHOWN ON POLLEN DIAGRAM: GENESEE VALLEY PEAT WORKS

[illegible]

## POLLEN DIAGRAMS

Only major pollen types are included in the following diagrams. See Appendices B to H for a listing of minor types.

When a given pollen type occurs with regularity across some interval but elsewhere is represented by only one or two grains which may be stratigraphically isolated from other occurrences immediately above and below, a + symbol is used in the diagram.

DIAGRAM 1. PROTECTION BOG: RELATIVE POLLEN FREQUENCY

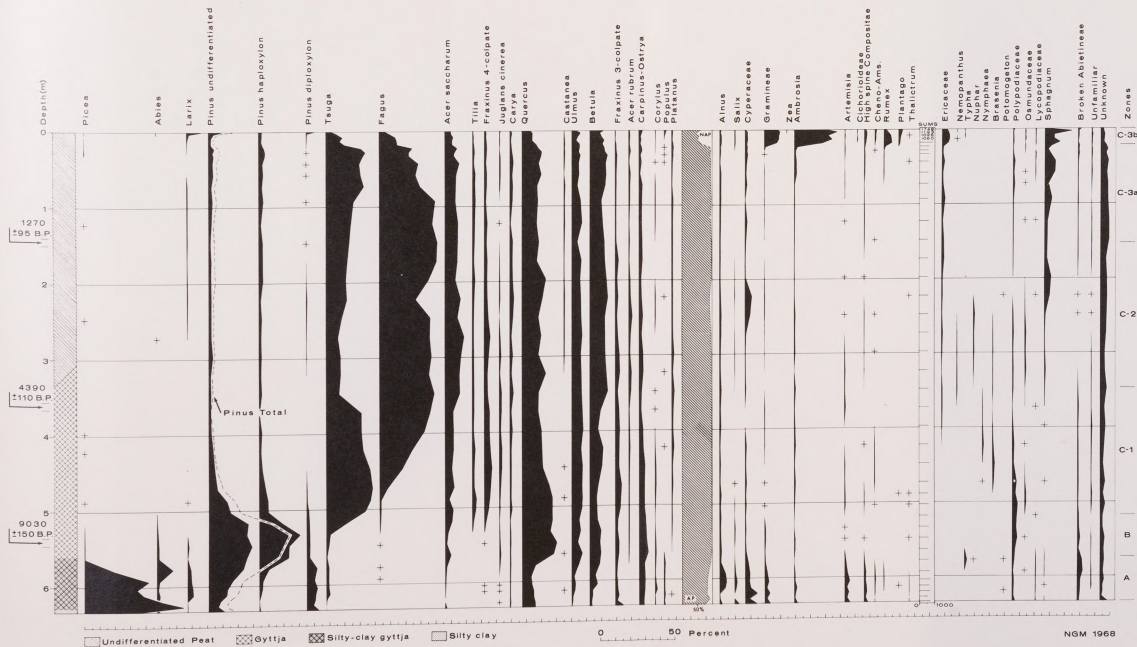
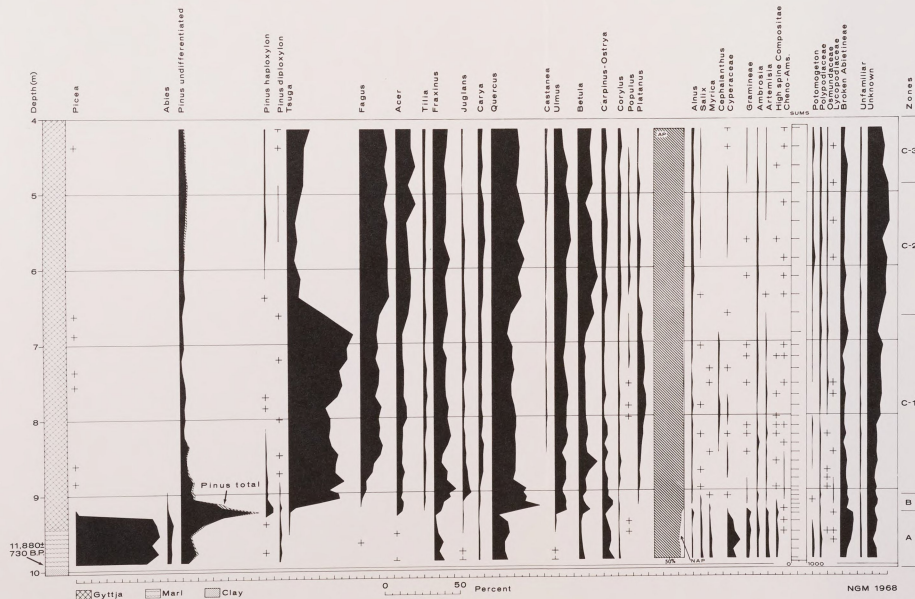




DIAGRAM 3. HOUGHTON BOG-SECTION B: RELATIVE POLLEN FREQUENCY





**Figure 7. Houghton Bog - Section B: Number of  
Terrestrial Pollen and Spores  
Per Ml. of Wet Sediment**

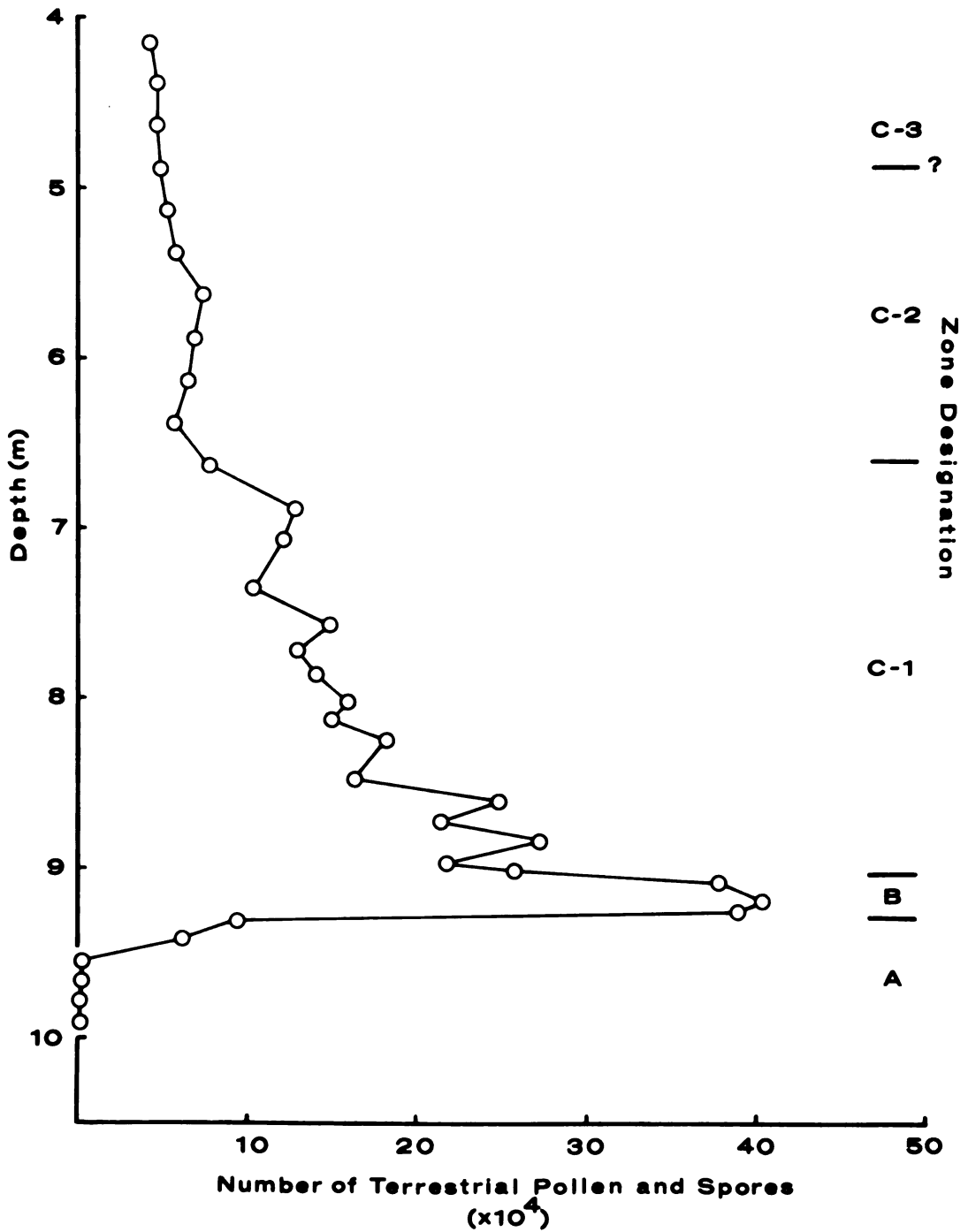
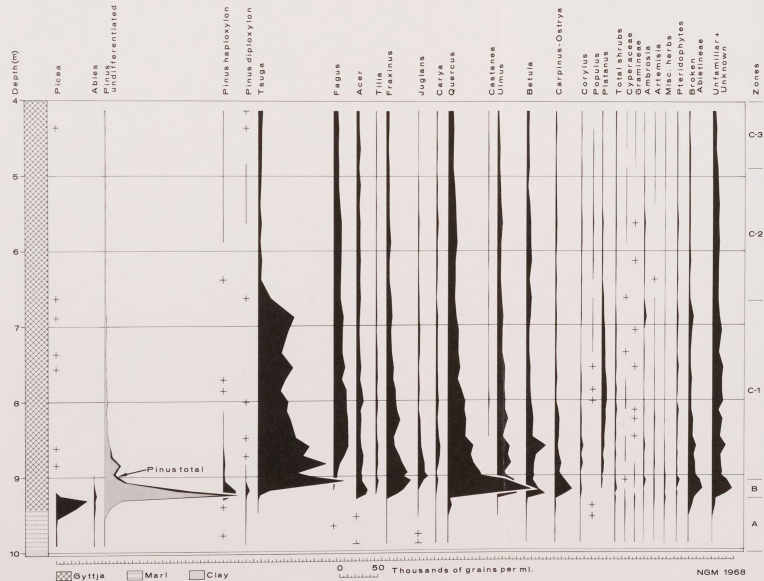


DIAGRAM 4. HOUGHTON BOG-SECTION B: ABSOLUTE POLLEN FREQUENCY



NGM 1968

DIAGRAM 5. ALLENBERG BOG-SECTION A: RELATIVE POLLEN FREQUENCY

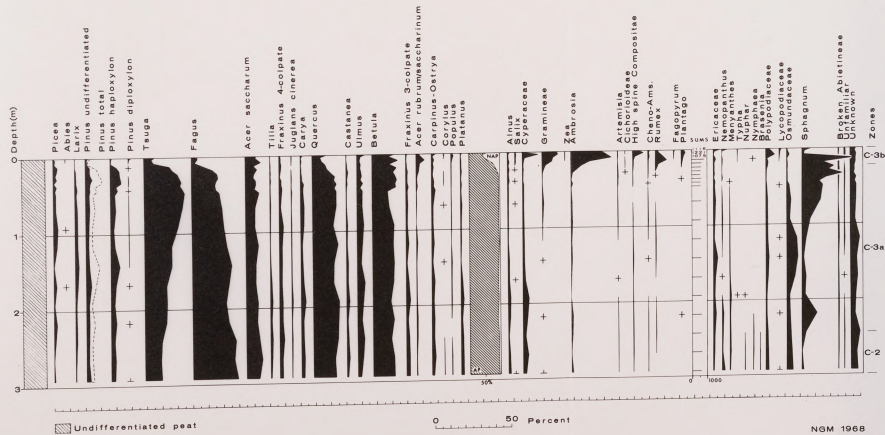


DIAGRAM 6. ALLENBERG BOG-SECTION B: RELATIVE POLLEN FREQUENCY

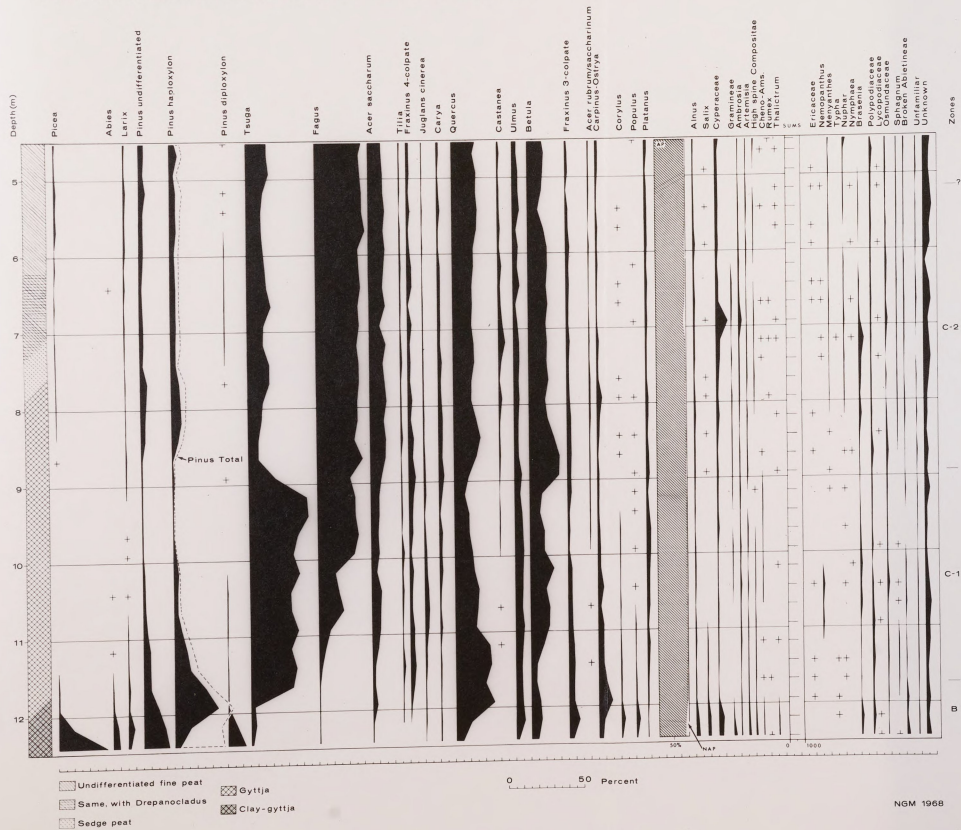
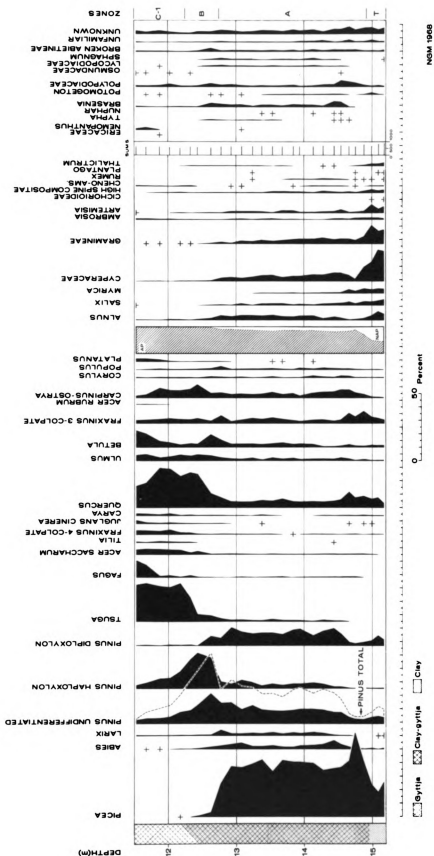


DIAGRAM 7. ALLENBERG BOG-SECTION C: RELATIVE POLLEN FREQUENCY



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**Figure 8. Allenberg Bog- Section C: Number of  
Terrestrial Pollen and Spores  
Per Ml. of Wet Sediment**

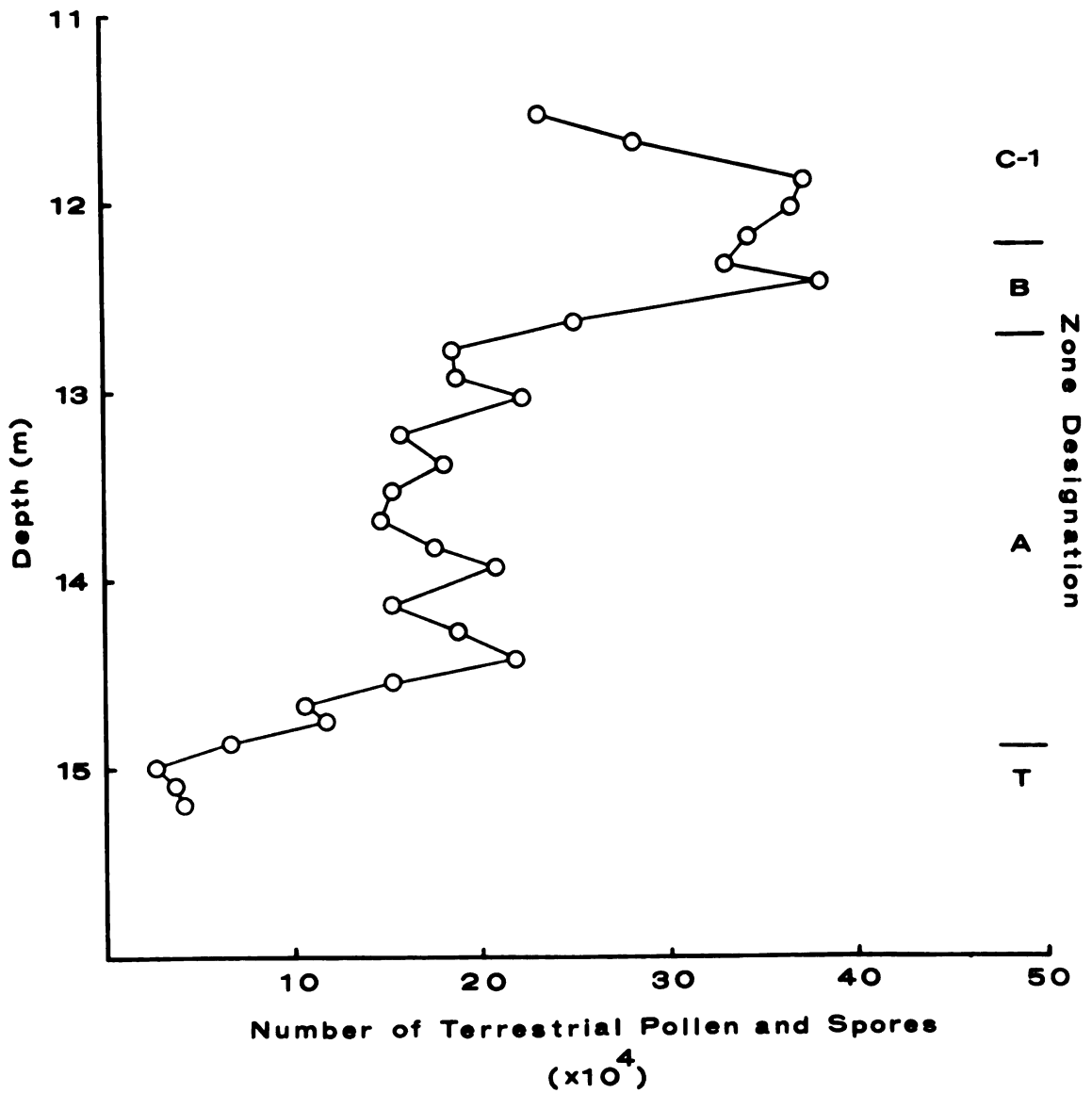


DIAGRAM 8. ALLENBERG BOG-SECTION C: ABSOLUTE POLLEN FREQUENCY

