

**RECENT POLLEN SPECTRA FROM THE DECIDUOUS
AND CONIFEROUS-DECIDUOUS FORESTS OF
NORTHEASTERN MINNESOTA: A STUDY IN
POLLEN DISPERSAL**

RECENT POLLEN SPECTRA FROM THE DECIDUOUS AND CONIFEROUS- DECIDUOUS FORESTS OF NORTHEASTEN MINNESOTA: A STUDY IN POLLEN DISPERSAL¹

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Abstract. Pollen samples were taken along nine transects across local vegetational belts bordering bogs or ponds in overall deciduous and coniferous-deciduous forest regions. Three types of pollen rain are distinguished: local, extralocal, and regional. Local pollen rain is derived from plants that grow at or very close to the sampling point. High local values are common in all sorts of vegetation types: lakes, bogs, marshes, and forests. Extralocal pollen rain is derived largely from trees that grow on the slopes and upland adjacent to the sampling site, but not extensively over larger areas. When excluded from the pollen sum along with the local types, its curves increase slightly, but noticeably, along the transect as the source of dispersal is approached. The regional pollen rain is derived from plants common far beyond the immediate basin slopes. When the extralocal and local types are excluded from the sum of upland pollen types, the regional pollen rain differs little from site to site. Its recognition permits comparison of modern and presettlement pollen rain with the composition of the recent regional vegetation.

INTRODUCTION

In the interpretation of pollen diagrams it has long been realized that pollen percentages do not accurately reflect the actual composition of the vegetation. This is because pollen production and pollen dispersal are widely different in the various plant species. In theory it would be possible to take into account only the pollen production and accordingly to neglect the factor of dispersal, if the vegetation surrounding the sampling point were homogeneous. However, this condition is rarely met. Usually we find in an area a mosaic of plant communities. This is not only true on a large scale, e.g. in such plant formations as prairie and deciduous forest, but also on a much smaller scale within the formation, largely as a result of topography and soil. Each of these communities contributes to the pollen rain at the sampling point in the way that is characteristic for that point under investigation. Each area has its own typical constellation and composition of plant communities, which will never be duplicated elsewhere. Site A, for instance, is located closer to a plant community "a" than site B. Pollen from commu-

nity "a" thus would show up better in the pollen spectrum of site A than that of site B. For this reason, at least in principle, the results at site A cannot be obtained at site B even if the two sites are close.

The dispersal of pollen grains from their source can be shown by a theoretical model (Fig. 1). The dispersal curves start at various levels on the ordinate, depending upon the pollen production. With increasing distance from the source the amount of pollen will decrease logarithmically. However, on theoretical grounds the pollen precipitation from an elevated point source first increases over a short distance and then decreases (Eisenhut 1961, Tauber 1965). In a few cases this initial rise of the dispersal curve has been found in dispersal experiments (Persson 1955, Federova 1956). The relative scarcity of the phenomenon in experiments might be explained by the fact that point sources do not exist in nature. Pollen sources in nature have a certain volume, and for that reason the initial rise of any point source within that area might be overshadowed by the local effect of other point sources in that area. At any rate this effect has been omitted from Fig. 1.

In principle the dispersal curve as shown in Fig. 1 may be divided into three parts. On the left the slope is steep, and the amount of pollen

¹ Contribution No. 30, Limnological Research Center. Mededelingen van het Botanisch Museum en Herbarium van de Rijksuniversiteit te Utrecht No. 272 (1966).

² Present address: Botanical Museum and Herbarium, Utrecht, The Netherlands.

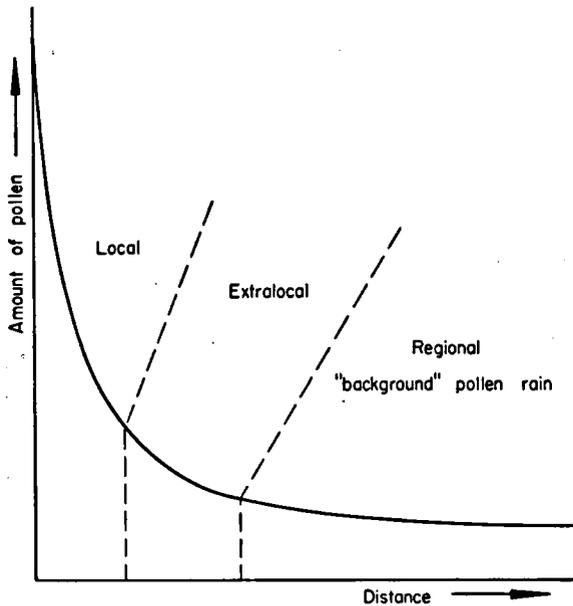


FIG. 1. Idealized relation between pollen rain and distance from the pollen source.

will vary much over short distances. Moreover, in this trajectory part of the pollen may be transported by some mechanism other than wind, e.g. anthers, catkins, rain, etc., often resulting in clusters of (immature) pollen in the samples. Consequently, not only large differences occur in amount of pollen over short distances but in addition many irregularities. The vegetation in the area around the source that shows these characteristics in its pollen rain will be called local vegetation, and accordingly the pollen rain in that area will be termed local pollen rain.

At great distances from the source the pollen-dispersal curve is practically parallel to the abscissa. In this area the amount of pollen will not vary even over larger distances. The pollen rain at these distances from the source will be called regional pollen rain, and the vegetation that produces it will be called regional vegetation. It is characterized by a composition of pollen types in the pollen rain independent of local situations. The work of McAndrews (1966) indicates that in our region the regional pollen rain reflects plant communities on the large scale of the plant formation.

In Fig. 1 we find between the regional and local trajectories a transitional trajectory. This pollen rain, here called extralocal, does not change over short distances to such an extent as is the case with the local trajectory. The amount of pollen, however, is here distinctly higher than the regional background pollen rain. The vegetation at distances sufficiently short to produce an extralocal

pollen rain accordingly is called extralocal vegetation.

Tauber (1965) divided the pollen deposition in a forested area into three components: a component through the trunk space, a component carried above the canopy, and a rainout component. Probably the extralocal effect is caused by the pollen transfer through the trunk space and his two other modes of transfer account for the regional pollen rain.

If a pollen diagram is used to infer climatic changes, then the diagram must register the regional pollen rain only, as the local and to some extent the extralocal pollen precipitation will distort the regional results. Faegri and Iversen (1964) state that diagrams with a strong local influence are almost impossible to evaluate in all detail. Such a strong local influence especially may be expected in peat bogs that produce their own pollen grains. The results of 50 years of pollen analysis indicate that pollen diagrams prepared from lake sediments in moderate-sized basins are highly comparable, a feature very desirable for the correlation of pollen diagrams. The local and extralocal pollen rain is here of minor importance. Yet this pollen rain might give us an impression of the vegetation in the immediate vicinity, because pollen seldom represented in the regional pollen rain may be present. Among these may be grains that are important indicators of vegetation types. The extralocal effect may be seen in pollen diagrams from small basins that contain higher pollen proportions from the upland vegetation growing in the immediate vicinity. Pffaffenberg (1952) found in small bogs in northwestern Germany higher percentages of *Quercus*, *Tilia*, and *Corylus* than in raised bogs in the same region. Iversen (1960, p. 28) in Denmark and Janssen (1960) in Holland found higher *Tilia* values on account of the short distance to the pollen source. Maher (1963) found in surface samples in small lakes within the altitudinal range of *Picea* in Colorado a higher ratio of *Picea/Pinus* pollen than in larger lakes.

In spite of the uniformity of pollen diagrams from larger lakes, the extralocal effect may be present to a certain degree, because a clear cut-off point between the local, extralocal, and regional vegetation cannot be established. The quantitative extent to which pollen from adjacent areas plays a role has remained relatively unknown. The precipitation of pollen dispersed only a short distance from the source can be studied, however, in recent pollen spectra that are obtained from surface materials collected along short transects. Such studies have been done in the northern lower peninsula of Michigan (Benninghoff 1960), in

Quebec (Potzger et al. 1957), and in Belgium (Heim 1962), and this approach has been used in the present study.

To study the contribution of local and extralocal vegetation to the pollen content of the sediment, surface samples were collected along short transects in the deciduous and coniferous-deciduous forest formations in northwestern Minnesota (Fig. 2). The sites were also selected to aid in the interpretation of the *Quercus-Ostrya* and *Pinus strobus* assemblage zones of the postglacial as defined by McAndrews (1966) for this part of the state. The vegetation analysis carried out to evaluate the ecological importance of pollen indicators and a pollen diagram from a small pond where some influence of extralocal vegetation might be expected will be published separately.

To study the effect of distance from the source upon the pollen rain, samples were collected along

nine transects in Minnesota—six in the coniferous-deciduous forest formation in Itasca State Park (Fig. 3) and three in the deciduous forest formation southwest of St. Cloud (Fig. 4). Each transect approaches various types of local forest that are quite different from the regional character of the forest formation. The pollen percentages have therefore been compared both with the composition of the forest types along the transects that might contribute to an extralocal effect and with the general tree composition of the regional vegetation. Accordingly the results of studies of tree pollen and shrub pollen from these two regions will be discussed separately. A more general discussion of the distribution of pollen from herbs and waterplants then follows.

To facilitate discussion of local, extralocal, and

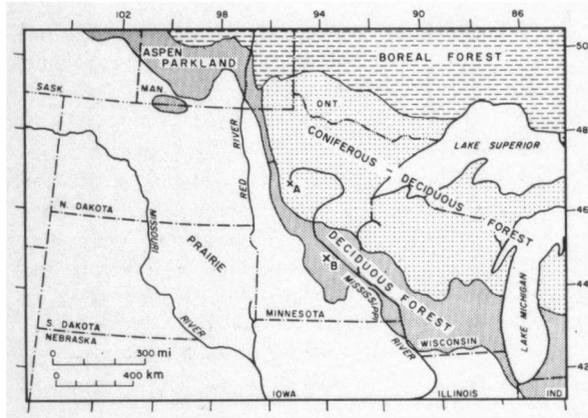
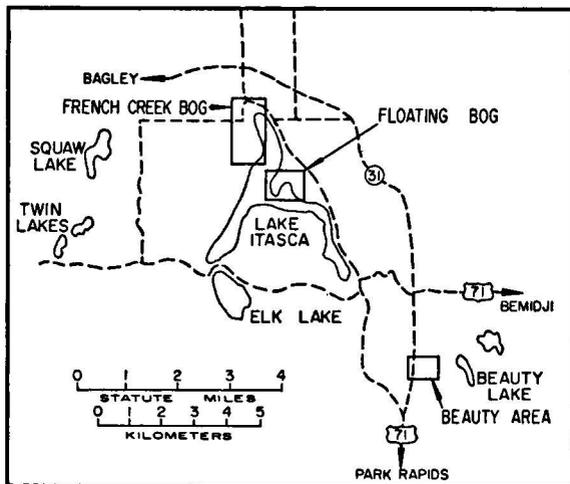
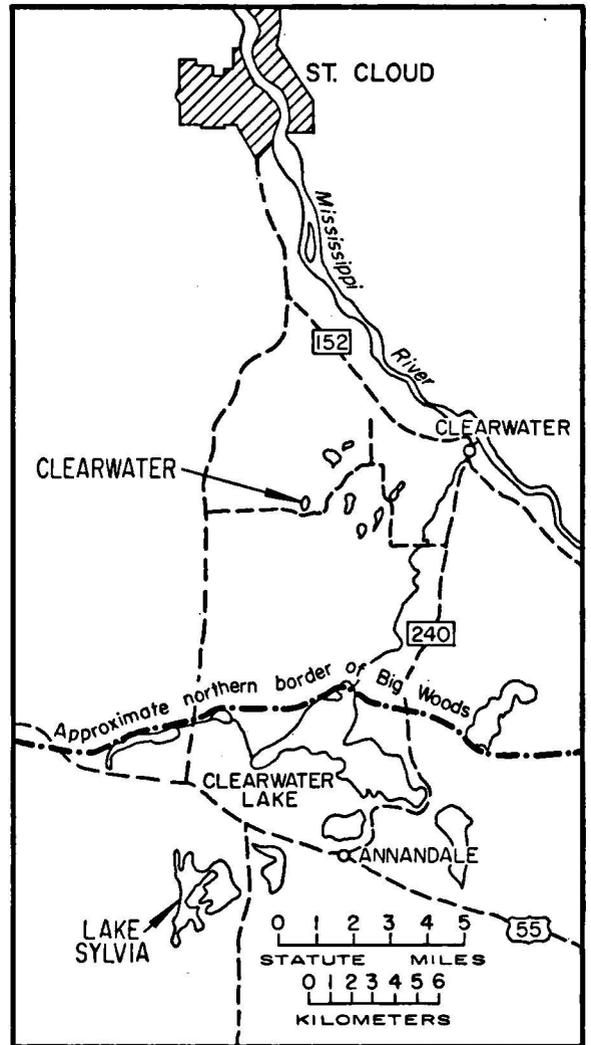


FIG. 2. Location of transects in the coniferous-deciduous (A) and deciduous (B) forest formations in Minnesota (after McAndrews 1966).



ITASCA AREA

FIG. 3. Index map of Itasca State Park area, showing location of areas studied.



ST. CLOUD AREA

FIG. 4. Index map of St. Cloud area, showing location of Lake Sylvia and Clearwater areas.

regional pollen rain, pollen percentages have been calculated in three ways—as percentage of total pollen from upland plants, as percentage of total pollen from upland forest plants excluding certain herbs, and as percentage of pollen from upland plants not occurring along the transect. In the last case the pollen sum differs for each transect, and the data are shown on special diagrams termed transect diagrams. Percentages calculated in the first two ways are presented in the main diagrams, together with quantitative data on the vegetation.

The data are presented to allow comparison of the proportions of plants in the vegetation with the proportion of pollen in the surface samples. Throughout the discussion the terms over-, equal-, and under-representation will be used frequently. For various reasons a pollen type is never consistently represented in the sense that a fixed proportion exists between pollen percentage and the part that the plant plays in the vegetation. The various factors that determine this proportion have been discussed recently by Davis (1963). One factor must be stressed here, i.e., that the selection of the pollen sum influences the percentage of a pollen type and therefore its representation. In the present study a comparison between pollen percentages based upon an upland-forest pollen sum will be made.

Samples along the transects were taken during the summers of 1962, 1963, and 1964 during the tenure of National Science Foundation summer fellowships at the Lake Itasca Biological Station, arranged by Dr. W. H. Marshall, Director. Laboratory work has been carried out at the Limnological Research Center, University of Minnesota, Prof. H. E. Wright, Director, with the financial support of the Hill Family Foundation. The author wishes to express his gratitude to Dr. H. E. Wright, Dr. E. J. Cushing, and Dr. J. H. McAndrews for their helpful discussions and assistance in the field, and to these persons and to Dr. Margaret B. Davis for critical reading of the manuscript. Tabulations of the pollen counts are available at the Limnological Research Center, University of Minnesota. They are also on file with the American Documentation Institute as Document No. 9170 with the ADI Auxiliary Publications Project, Photoduplication Service, Library of Congress, Washington, D. C., from whom a copy may be secured by citing the document number and by remitting \$1.25 for photoprints or \$1.25 for 35-mm microfilm.

METHODS

Surface samples

Collection.—Surface samples comprise four kinds of materials: (1) *Sphagnum* polsters (S);

(2) other moss polsters (B); (3) top layer of soils (A_0); and (4) top layer of lake sediments (M). Each sample was composed of 5–10 subsamples from an area of about 1 m². Moss samples were obtained from dead wood and from the bases of trees as well as from moss covering the ground. Lake samples, all of them marl, were obtained by diving.

Preparation.—Samples were boiled for 10 min in 10% KOH, sieved through a fine screen, and washed thrice with water on the screen by squeezing the fluid out of the material. The material can be stored permanently in glacial acetic acid. Part of it was prepared for microscopic investigation by acetolysis for 10 min. The water was then replaced in turn by 95% ethanol, 100% ethanol, and benzene, and the preparation was then embedded in silicone oil (2,000 cs).

Vegetational analysis

Regional.—The composition of the regional vegetation has been obtained from the general land survey by the Federal Government in the last century, before or during settlement of white man in this part of the country. Since the vegetation before and after the arrival of the settlers is not the same, it is not appropriate to compare recent pollen spectra with subrecent vegetational data. A justification for doing so, however, is found in the work of McAndrews (1966), which, apart from the rise of *Ambrosia* in postsettlement time, reports the same proportions between the trees in the regional pollen analyses before and after settlement.

To calculate the composition of the regional vegetation an area of 65 km² around the transects was used. How large an area contributes to the pollen rain at the sampling point is not known, but data from Hyde and Williams (1945) seem to indicate that pollen transport over 10 km is of minor importance. Similarly, Tsukada (1958) reports that in a forested region most of the pollen precipitation comes from an area within a few kilometers.

From the land-survey data importance values (I.V.) of trees were calculated from basal area, relative density, and relative frequency (Curtis and McIntosh 1951). For comparison with the pollen percentages of the samples, the importance values have been expressed as percentages of the sum of all importance values (% I.V.) (Tables I, II). In Table I the seven regional % I.V.'s have been combined into three groups, because some of the transects are located so close to each other that they include the same witness trees and thus show identical importance values.

For the calculation of the regional importance

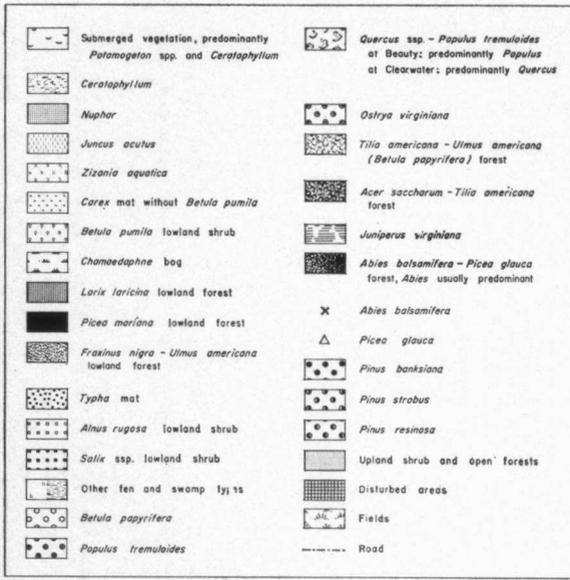


FIG. 5. Explanation for vegetation maps (Figs. 6-9).

value, only upland trees have been used. *Picea* and *Larix laricina*, though present in the land-survey data, have been excluded. These trees frequently occur along the transects and therefore

have been excluded from the percentage calculations of the pollen types. The same principle has been used in the calculation of the regional pollen percentages.

Local and extralocal.—The vegetational types along the transects may produce at any point a local or extralocal pollen rain and are therefore described as local or extralocal vegetation. The quantitative data on the composition of upland forest were obtained by analyzing the tree composition according to the quarter method (Cottam and Curtis 1956). Percentage I.V.'s (Tables I and II) were calculated according to the same procedure as from the regional data. In tables and diagrams this upland vegetation will be referred to as the extralocal vegetation *sensu stricto*.

A percentage evaluation of tree composition is of course impossible when the vegetation consists of one tree species only or no trees at all. Most commonly this applies for lowland vegetational types—*Fraxinus nigra*, *Picea mariana*, and *Larix laricina* forests and *Carex* mats. These types have been studied using methods of the Zürich-Montpellier school of phytosociology, where mass proportions of the various species are estimated. Since a quantitative comparison between pollen

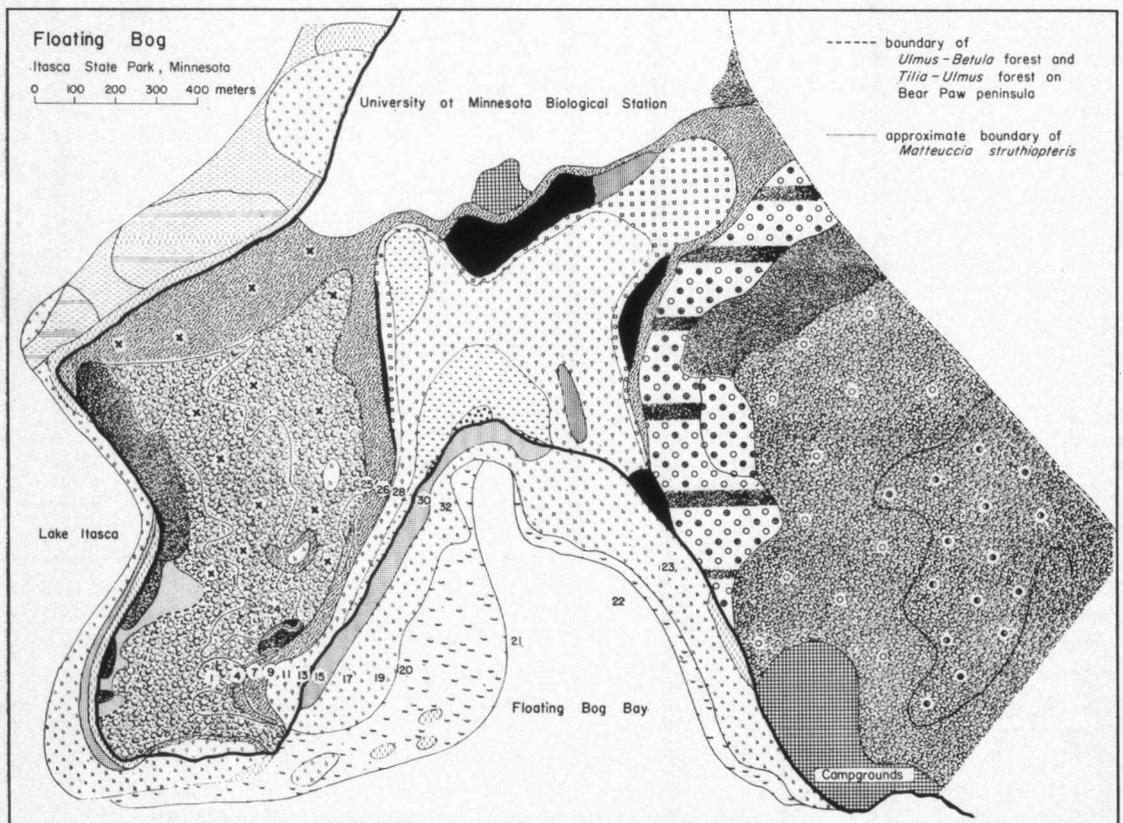


FIG. 6. Vegetation map of Floating Bog area, Itasca State Park, showing location of surface samples. For explanation of symbols, see Fig. 5.

percentages and composition of the vegetation by this method would be highly inaccurate, a full exposition of these vegetation types is not given.

Vegetational maps

General vegetation maps have been made of the various vegetational types in the transect areas by visual inspection and with the aid of aerial photographs (Figs. 5–9). The delimitation of the various vegetational units was based on the broad physiognomic character of the vegetation and the dominance of its components. In the Itasca State Park region these vegetational types are more or less equivalent to vegetational types established by analyses following methods of the Zürich-Montpellier school (Braun-Blanquet 1951, Janssen *unpublished*³). The vegetation around the Beauty and Bohall transects is rather homogeneous, so no maps were prepared for these areas.

Main pollen diagrams

Arrangement.—The data have been plotted on two main diagrams (envelope under rear cover). Diagram 1 (Fig. 10) contains all the pollen types included in the upland pollen sum (see below), and diagram 2 (Fig. 11) all the other types. At the top of the main diagrams are shown cross sections of the vegetation along the transects. The various vegetational belts along the transects, also shown in Fig. 5–9, have been characterized briefly by their dominants. Below this, distance scale and sample number have been mentioned. At the bottom of the diagram the sample material is indicated. At the right is the percentage scale; to have the low percentages stand out more clearly each pollen curve is accompanied by another curve showing the same percentages but 10 times exaggerated. In diagram 1 the pollen sum (total pollen of upland plants) is shown above the pollen curves. At the right side of each transect, bars are drawn to indicate the % I.V. of regional and extralocal vegetation. In diagram 1 the arrangement of pollen types is according to trees, shrubs, and herbs. In diagram 2 the number-letter combination at the left side of the diagram refers to groups of plants that belong ecologically together (Janssen, *unpublished data*).³ These groups frequently occur in definite vegetation belts along the transect.

Upland pollen sum.—For the establishment of the upland pollen sum the principle of anemophily/entomophily was abandoned. Instead a pollen sum was selected containing all the pollen types that could be identified morphologically as referable to upland plants. Excluded from the pollen sum

³ C. R. Janssen. Manuscript. A floristic study of forests and bog vegetation in the Itasca State Park area, Northwestern Minnesota.

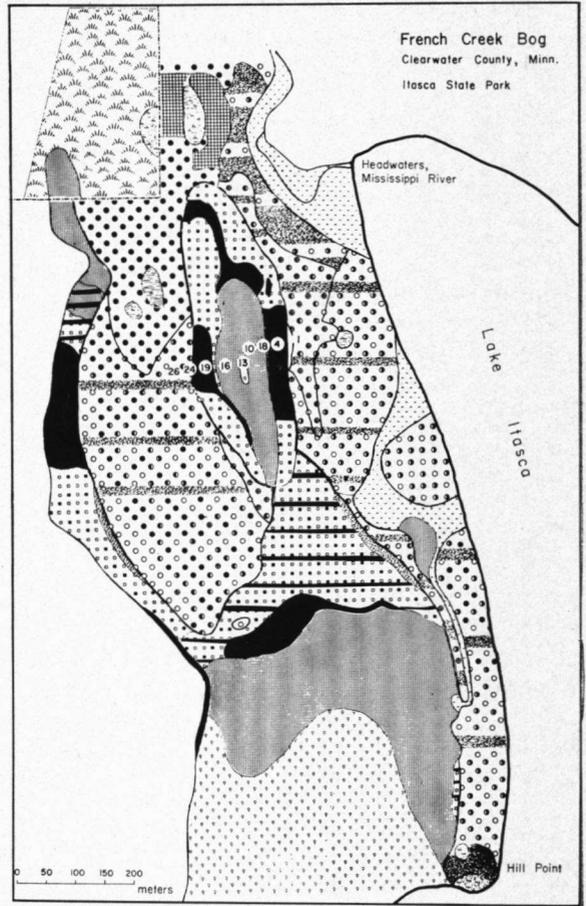


FIG. 7. Vegetation map of French Creek Bog area, Itasca State Park, showing location of surface samples. For explanation of symbols, see Fig. 5.

were all the lowland types as well as all those for which no pollen-morphological or ecological decision could be made as to upland or lowland source (e.g. Cyperaceae, Poaceae). Pollen types excluded because of lowland origin are *Salix*, *Alnus*, and *Larix*. Although *Picea* occurs both on upland (*P. glauca*) and lowland (*P. mariana*), pollen of the two species cannot be readily distinguished; *Picea* has been excluded because the lowland species is likely to be the more common in this region.

Lowland types include the marginal *Fraxinus nigra*-*Ulmus americana* communities, and accordingly pollen from plants belonging here were omitted from the pollen sum. An exception, however, has been made for *Ulmus* and *Betula*. The former occurs in lowland forest but can be found more frequently in upland communities. Two species of *Betula* are common in Minnesota, one on lowlands and the other on uplands. We thus have the same specific dual distribution as found for *Picea*. But unlike *Picea*, pollen of *Betula* is not almost exclusively from lowland origin.

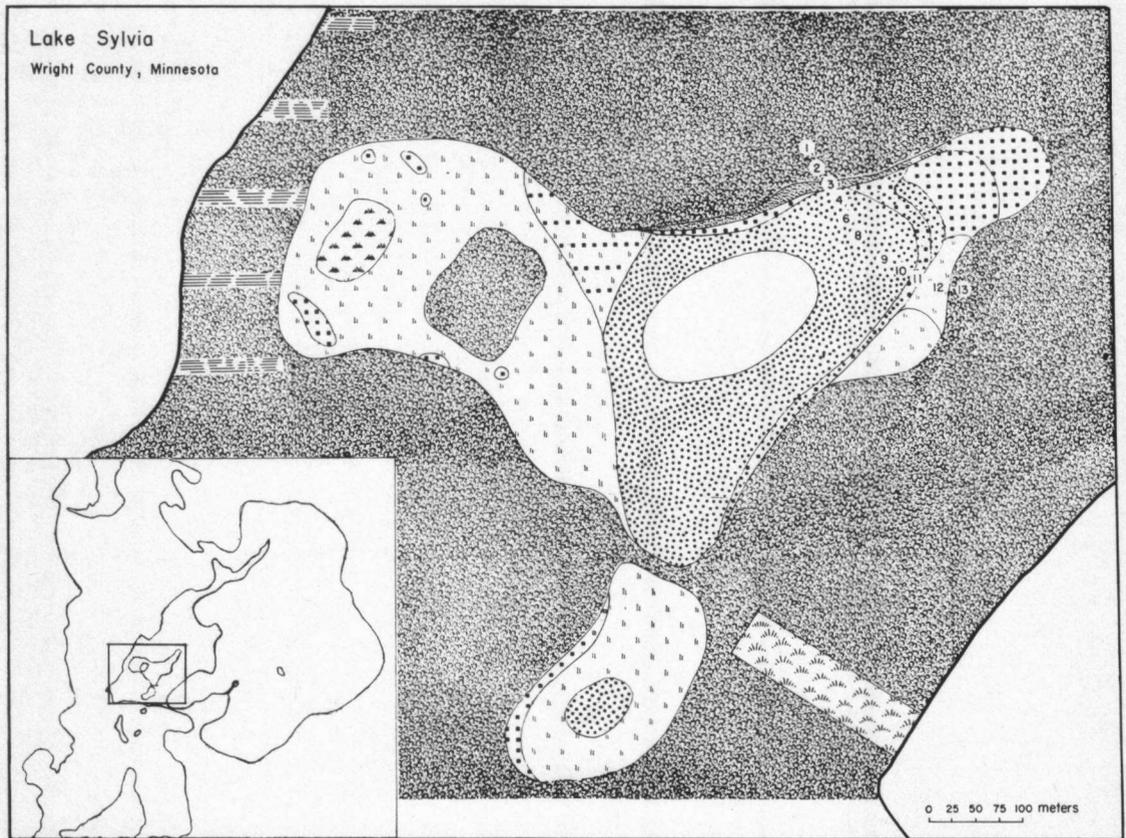


FIG. 8. Vegetation map of Lake Sylvia area, Wright County, showing location of surface samples. For explanation of symbols, see Fig. 5.

The exclusion from the pollen sum of the pollen types mentioned, which reach high values in many samples, makes a comparison with other Minnesota diagrams easier, because in most Minnesota diagrams these types show a low pollen percentage in postglacial sediments.

Upland-forest pollen sum.—The dashed curves in Fig. 10 represent percentages based upon the same pollen sum as in the normal curves of the diagram but without *Betula* and without pollen types that in Fig. 10 have been labeled prairie herbs (*Artemisia*, *Ambrosia*, *Chenopodiaceae/Amaranthaceae*), exotic prairie species, and miscellaneous weeds and herbs (mostly cultivated weeds and plants that are associated with fields, pastures, roadsides, etc.). These pollen types have been left in the pollen sum of the normal curves because they are upland types and belong to the regional pollen rain for all our transects. The reasons to exclude them from the upland-forest pollen sum are these:

1) The excluded types show in our samples irregular percentages. This is especially true for *Ambrosia*, less so for *Artemisia* and *Chenopodiaceae/Amaranthaceae*.

2) High *Ambrosia* values occur in Minnesota

diagrams only in postsettlement time, so comparison with presettlement pollen spectra is easier if *Ambrosia* is excluded.

3) The % I.V.'s have been based either upon my own tree counts or upon the surveyors' records, both of which deal with trees only.

4) A comparison with other studies (generally based upon a tree-pollen sum) remains possible.

For these reasons in the following discussion of each pollen type, the % I.V. of the components of the vegetation will be compared with pollen percentages based upon this upland-forest pollen sum.

Transect pollen diagrams

The study of pollen dispersal requires transects running through vegetational types that show breaks with neighboring ones. These breaks commonly occur where strong differences in topography can be found, e.g. lake shores, border between upland forest and bog mat, etc. The transects thus include upland communities, and the upland pollen types may therefore show a strong local overrepresentation, distorting the curves of the pollen types of the regional pollen rain. Therefore small diagrams for the transects have been prepared (Fig. 12–16) in which pollen percentages

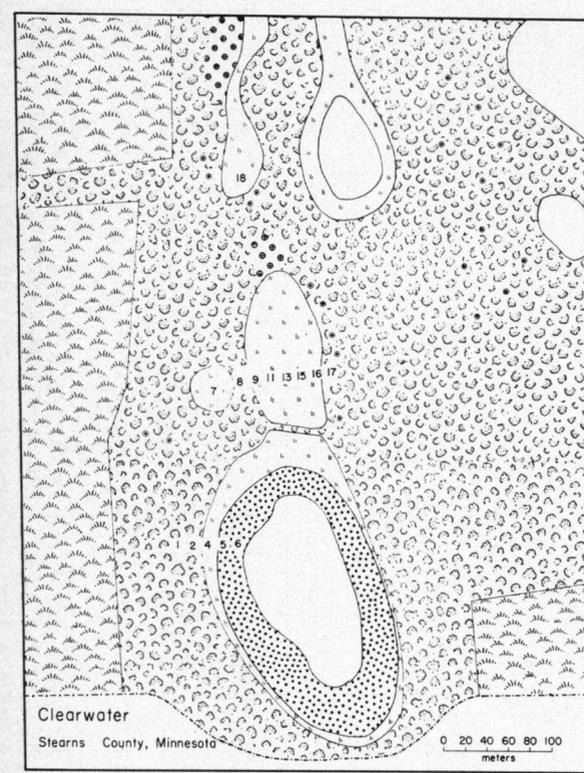


FIG. 9. Vegetation map of Clearwater area, Wright County, showing location of surface samples. For explanation of symbols, see Fig. 5.

for the most abundant pollen types have been calculated upon the upland pollen sum (see main diagram 1) but comprising only those upland pollen types that do not occur along the transects (group A). The pollen types from plants that occur along the transects are held outside the pollen sum of the transect diagrams (group B).

As a result of this principle, *Ambrosia*, *Artemisia*, the Chenopodiaceae/Amaranthaceae, and indicators of cultivation in all cases have been included in the pollen sum. The present study deals with forests only, and these herbs thus never occur along the transects. Included too are pollen from trees not native to northwestern Minnesota (e.g. *Carya*, *Juglans*). Separation thus has been made in the transect diagrams between types that would show a regional pollen percentage and those that would show a local or extralocal percentage. Some of the transects also show regional values of lowland pollen types, but because of their generally low regional values their exclusion from the pollen sum of the transect diagrams does not change the level of the other regional curves to a great extent.

It may be expected that the curves of the local pollen types will show definite maxima in the vegetational zones along the transect where these

pollen sources occur. It is in this group B of the transect diagrams that the effect of short distance from the pollen source may best be studied.

Regional pollen averages

To facilitate discussion of representation of pollen types, for each pollen type a regional average percentage based upon the upland-forest pollen sum has been calculated as well as the range of percentages (Tables I and III). For a calculation of the average percentage, only pollen spectra have been used that do not contain any local or extralocal value for the type under consideration or for any other type included in the pollen sum. Thus the spectra of the Bohall transect have been omitted altogether, because *Pinus* shows raised values here and would therefore depress the regional values of other pollen types.

The average percentage for the spectra used has been calculated by dividing the total grains of each pollen type by the total of the pollen sums for these spectra. For a discussion which spectra have been used for the calculation of the regional percentage, the reader is referred to the sections on the discussion of the individual pollen types.

TREES AND SHRUBS IN THE CONIFEROUS-DECIDUOUS FOREST FORMATION

Description of the transects

The transects—Floating Bog 1 and 2, French Creek Bog, Bohall, Beauty 1, and Beauty 2—are located within the boundaries of Itasca State Park in Clearwater and Hubbard Counties, Minnesota, with the exception of Beauty 2, just outside the eastern limit of the park. All the transects are located in the area covered by sandy loam till deposited by the Wadena Lobe. In spite of the uniform upland soil types the upland forest types are strongly differentiated. The transects that have been selected approach a *Tilia americana-Ulmus americana-Betula papyrifera* forest, a mixed *Pinus-Populus tremuloides-Betula papyrifera* forest, a *Pinus resinosa* forest, and a *Populus tremuloides-Quercus macrocarpa* forest.

Floating Bog 1 and 2.—Located south of the University of Minnesota Biological Station at Itasca State Park, SW $\frac{1}{4}$ NE $\frac{1}{4}$ Sec 11, T143N, R36W (Fig. 6).

Floating Bog 1 transect starts in the southern part of Bear Paw Peninsula in a mesic *Tilia-Ulmus* forest with a dense undergrowth of *Mateuccia struthiopteris*. It runs east across narrow belts of *Fraxinus nigra-Ulmus americana* lowland forest (towards the upland side much *Acer spicatum*, towards the bay side much *Salix* shrub), *Betula pumila* shrub, *Nuphar*, *Zizania aquatica*,

TABLE I. Coniferous-deciduous forest formation. Percentage importance values for extralocal and regional vegetation, and average regional pollen percentages near the transects based on a variable pollen sum of upland-forest pollen (see Table II, and text). Taxa below the break were excluded from the percentage base in the calculations.

Taxon	Percentage importance value										Average regional pollen percentage
	Extralocal							Regional			
	Floating Bog 1	Floating Bog 2	Bohall	French Creek Bog east	French Creek Bog west	Beauty 1	Beauty 2	Floating Bog 1, 2	French Creek Bog Bohall	Beauty 1, 2	
<i>Tilia</i>	52.7	2.3	—	—	—	—	—	—	—	2.0	0.16
<i>Ulm</i> s.....	23.8	43.2	—	—	—	—	—	2.2	—	—	1.61
<i>Frazinus pennsylvanica</i>	15.5	6.3	—	—	—	—	—	—	—	—	—
<i>Betula papyrifera</i>	6.9	30.7	12.6	4.6	22.6	34.11	—	6.9	9.6	5.9	15.70
<i>Abies</i>	0-8	17.2	11.6	13.8	24.3	—	—	2.1	1.7	1.0	1.40
<i>Pinus resinosa/banksiana</i>	—	—	62.5	44.5	28.5	—	—	58.1	55.1	42.5	—
<i>Pinus strobus</i>	—	—	5.9	5.2	1.8	—	—	10.3	12.5	13.2	—
<i>Pinus</i> spp. (total).....	—	—	(68.4)	(49.7)	(30.3)	—	—	(68.4)	(67.6)	(55.7)	78.8
<i>Picea glauca</i>	—	—	7.2	4.9	10.0	—	—	—	—	—	—
<i>Populus tremuloides</i>	—	—	—	26.8	12.5	38.6	92.8	18.7	15.9	26.9	—
<i>Quercus</i>	—	—	—	—	—	19.2	4.0	1.5	3.5	4.4	8.30
<i>Populus grandidentata</i>	—	—	—	—	—	3.4	—	—	—	—	—
<i>Acer rubrum</i>	—	—	—	—	—	4.5	—	—	—	—	0.18
<i>Prunus serotina</i>	—	—	—	—	—	—	3.1	—	—	—	—
<i>Acer saccharum</i>	—	—	—	—	—	—	—	—	0.9	3.5	0.12
<i>Populus balsamifera</i>	—	—	—	—	—	—	—	—	0.9	1.1	—
Number of trees counted.....	73	70	72	76	78	69	77	86	110	112	—
<i>Larix laricina</i>	—	—	—	—	—	—	—	8.9	7.2	2.4	0.03
<i>Picea mariana</i>	—	—	—	—	—	—	—	6.0	6.2	1.0	2.73
<i>Ostrya</i>	—	—	—	—	—	—	—	—	—	—	0.39
<i>Frazinus nigra</i>	—	—	—	—	—	—	—	—	—	—	2.36
<i>Salix</i>	—	—	—	—	—	—	—	—	—	—	1.30
<i>Corylus</i>	—	—	—	—	—	—	—	—	—	—	0.75
<i>Alnus</i>	—	—	—	—	—	—	—	—	—	—	4.36
<i>Acer spicatum</i>	—	—	—	—	—	—	—	—	—	—	0.06

Potamogeton, open water, and again *Zizania aquatica*. Floating Bog 2 transect to the north starts in a mesic *Ulmus americana*-*Betula papyrifera* forest and passes essentially the same belts as in transect 1. However, no *Acer spicatum* zone is present here, and a *Carex* zone without *Betula pumila* is intercalated between the *Betula pumila* and *Nuphar* belts.

French Creek Bog.—Located southwest of the headwaters of the Mississippi in Itasca State Park, W ½ NW ¼ Sec 2, T143N, R36W (Fig. 7).

The transect starts in an old *Pinus*-*Populus*-*Betula* forest. Much windfall, especially on the west side of the transect, has facilitated the establishment of *Abies balsamea* and *Picea glauca*. Table I shows that because of the difference in windfall on the two ends of the transect the highest % I.V.'s of *Picea* and *Abies* are found on the west side of the transect. The vegetation in the middle part of the transect is a young *Larix laricina* bog forest flanked by *Picea mariana*. On the west side of the transect some scattered *Alnus rugosa* shrubs are present between the *Picea mariana* and *Larix laricina* bog forest.

Bohall.—Located north of Bohall Lake, SE ¼ NW ¼ Sec 9, T143N, R36W.

The transect runs across a small pond in a mature *Pinus resinosa* forest. In most respects this forest shows the same composition as the forest at French Creek Bog. It differs in the absence of *Populus tremuloides*, lower % I.V. of *Abies* and *Picea*, and higher values for *Pinus*.

Beauty 1.—Located near Highway 71 at the beginning of the trail to Beauty Lake, NE ¼ NW ¼ Sec 32, T143N, R35W.

The transect runs across a *Chamaedaphne calyculata* bog bordered by *Alnus rugosa* shrub. In the surrounding forest *Populus tremuloides* is dominant, and *Betula papyrifera* is common.

Beauty 2.—Located along the trail to Beauty Lake halfway between the lake and Highway 71. NE ¼ Sec 32, T143N, R35W.

The transect runs across a *Salix*-*Alnus rugosa* swamp. The surrounding forest is much like the forest at Beauty 1. *Betula papyrifera*, however, is absent here, and *Quercus macrocarpa* is less common.

Regional averages and discussion of individual pollen types

In the following discussion the effect of increasing distance from the pollen source may be studied

TABLE II. Spectra used for the calculation of the average regional pollen percentages in the coniferous-deciduous forest formation (the calculated values are used in Table I)

Pollen type	Spectra	Pollen sum
<i>Abies</i>	Floating Bog 16-23, 30-32 French Creek Bog 10-16 Beauty 1 1-10 Beauty 2 1-4	10,526
<i>Acer saccharum</i>		
<i>Acer spicatum</i>		
<i>Acer rubrum</i>		
<i>Ostrya</i>		
<i>Pinus</i>		
<i>Tilia</i>		
<i>Ulmus</i>		
<i>Fraxinus nigra</i>		
<i>Picea</i>		
<i>Larix laricina</i>		
<i>Corylus</i>	Floating Bog 16-23, 30-32 French Creek Bog 10-16	6,074
<i>Quercus</i>		
<i>Alnus</i>		
<i>Betula</i>	Floating Bog 16-23, 30-32	2,418
<i>Salix</i>		

in group B of the transect diagrams (Fig. 12-16). These diagrams, however, are not well suited to compare the pollen rain with the regional and extralocal vegetation nor with other pollen diagrams in Minnesota. For this purpose the reader is referred to Table I and the main diagrams.

From the transect diagrams it appears that the regional tree- and shrub-pollen percentages are approximately the same for all the transects in the coniferous-deciduous formation. This undoubtedly is a result of the fact that the transects are relatively close to each other—less than 5 miles apart—and that they are located in the same vegetational formation. Thus one regional average for all the transects in this formation could be calculated. Not all the spectra from the transect have been used. Spectra that contain local or extralocal values, if included in the pollen sum (here upland-forest pollen sum) have been excluded. Table II shows the spectra that have been used for these calculations.

Tilia.—Average regional percentage is 0.16%; curve is highly interrupted. *Tilia* is strongly underrepresented. Regional values are found on the bay side of Floating Bog 1. Closer to the *Tilia-Ulmus* forest, extralocal values culminate in a local percentage of 36% in such a forest. An extralocal rise in percentages can be found at Floating Bog 2. Local values, however, are absent because this transect ends in the *Betula papyrifera-Ulmus americana* forest, in which *Tilia* plays but a minor role. We thus find that approximately 200 m from a *Tilia* forest the percentage of *Tilia* has decreased to its normal background value. According to Pohl (1937), the pollen production of *Tilia cordata* is rather large. Its dispersal, however, seems to be poor on account of

its zoogamous nature (Hyde and Williams 1945). *Tilia* thus is usually strongly underrepresented, when compared with any parameter of the composition of the vegetation (percentage basal area, Davis and Goodlett 1960; cover, Mullenders 1962).

Ulmus.—Average regional percentage is 1.6% (range 0.5-4.0%); curve is continuous. At Floating Bog 1, especially in the transect diagram (Fig. 12), *Ulmus* percentages increase at the water edge of the floating mat. This might be considered as the extralocal effect. There is no local effect of *Ulmus* in the *Fraxinus nigra-Ulmus americana* forest, however, even not in the *Acer spicatum* zone that has partly an *Ulmus* overstory. *Ulmus* pollen culminates in the area between the *Tilia-Ulmus* forest and the *Acer spicatum* zone. Here indeed a number of large *Ulmus* trees were present. At Floating Bog 1, where the extralocal vegetation contains more *Tilia* than *Ulmus* (Table I), the local percentage of *Tilia* is accordingly higher than that of *Ulmus*. Both genera show an extralocal effect over approximately the same distance from the source of pollen dispersal. *Ulmus*, however, ends up with a higher regional percentage than *Tilia*, reversing the pollen proportions in the forest. These features may be explained by a better dispersal of *Ulmus*. Indeed in surface-sample studies *Ulmus* usually is underrepresented but to a much less extent than *Tilia* (Davis and Goodlett 1960).

Fraxinus nigra.—Average regional percentage is 2.3% (range 1.7-4.8%); curve is continuous. The black ash at the Floating Bog and Beauty transects shows the same features as *Ulmus*; about the same regional percentage and extralocal values over the same distance. This is in agreement with data from Davis and Goodlett (1960), who found ash and elm slightly underrepresented in approximately the same degree. Some authors, however, report differences in dispersal and production of the two genera. According to Dyakowska (1937), *Fraxinus excelsior* pollen settles in motionless air at a speed of 5.21 cm/sec, faster than *Ulmus glabra* (3.24 cm/sec). Wright (1952) found a much faster decline in percentage of the highest frequency with increasing distance for *Fraxinus pennsylvanica* than for *Ulmus americana*. Pohl (1937) reports a rather low pollen production of *Fraxinus excelsior*. The similarity between *Fraxinus nigra* and *Ulmus* at Floating Bog perhaps is a result of a wider regional distribution of *Fraxinus* than *Ulmus*. Unfortunately in the surveyors' records the calculated percentage importance value is too low to allow any conclusion.

Acer saccharum.—*Acer saccharum* is not present along any of the transects. It shows a highly

interrupted curve with a regional percentage up to 0.7% averaging 0.12%.

Acer rubrum.—Average regional percentage is 0.18% (range 0–0.4%); curve is highly interrupted. The presence of this tree in the extralocal vegetation of Beauty 1 (% I.V., 4.5) does not raise the background pollen rain to extralocal values.

Acer spicatum.—Pollen is almost absent in the regional pollen rain. At Floating Bog 1, local percentages are strongly raised at stations underneath the *Acer spicatum* shrubs.

Rhamnus.—Pollen is almost absent in the regional pollen rain. Local values at Floating Bog

1 are higher in samples from the *Fraxinus nigra-Ulmus americana* forest.

Ostrya.—Average regional percentage is 0.39% (range 0–1.6%); curve is interrupted in places. At Floating Bog the *Tilia-Ulmus* and *Betula-Ulmus* forests have some *Ostrya* in the shrub layer, but a local rise in the percentage is absent.

Corylus.—Average regional percentage is 0.75% (range 0.2–1.9%). Two species of *Corylus* (*C. cornuta* and *C. americana*) occur abundantly in the understory of several forest types in the region. A cover of more than 80% in the shrub layer has been found in the forests surrounding the Bohall and Beauty transects. *Corylus* is less dense in

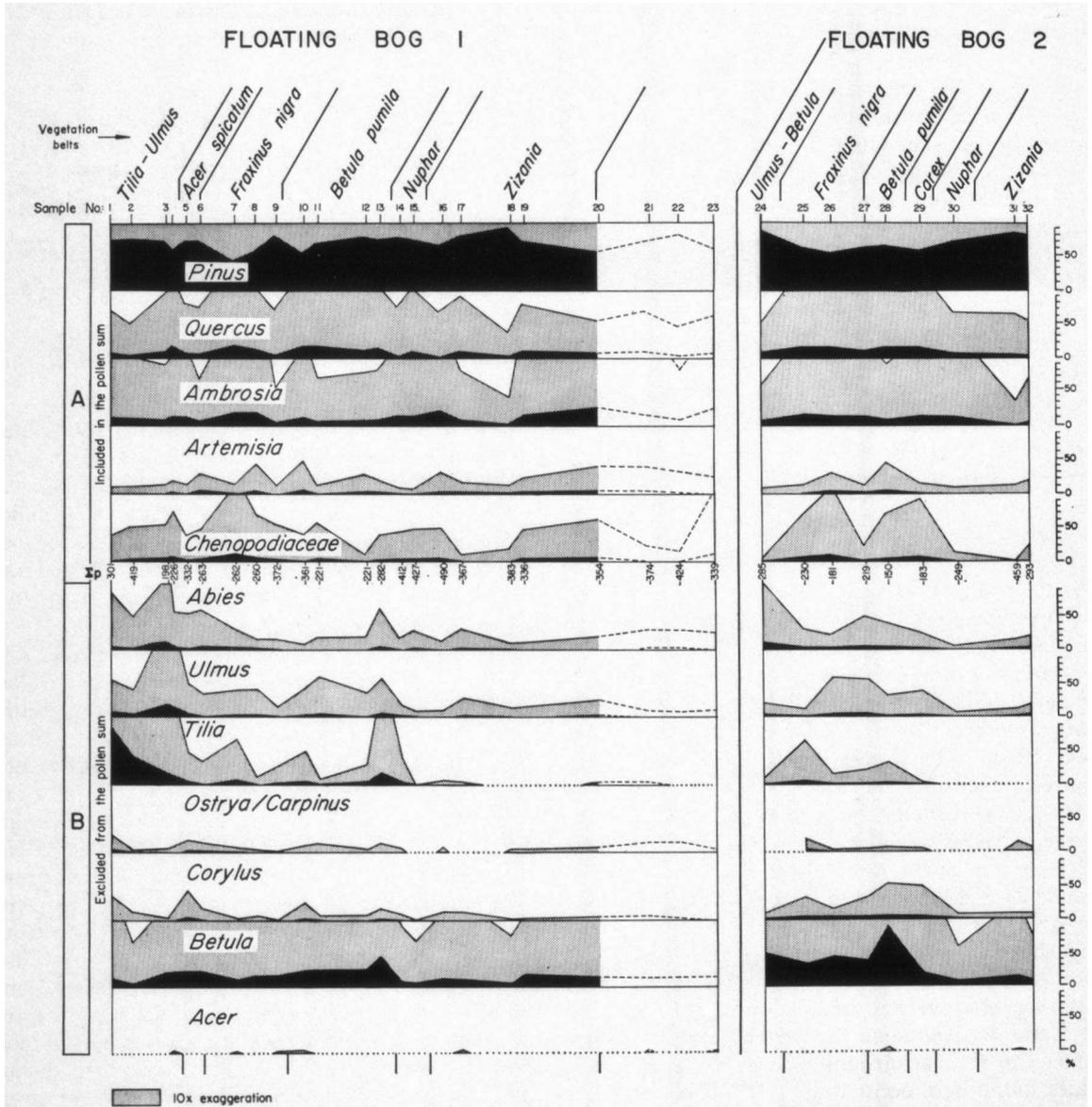


FIG. 12. Simplified pollen diagram for Floating Bog transects corrected by exclusion of local and extralocal pollen types. The headings refer to the same vegetation belts plotted across the top of main diagrams (Figs. 10–11).

the shrub layer at French Creek Bog because of the shade of the invading *Abies balsamea* and *Picea glauca*. At Floating Bog it occurs in varying quantities in the upland forest and in the *Fraxinus-Ulmus* lowland forest.

Corylus avellana shows a high pollen production (Pohl 1937) and belongs to a group of pollen grains with a low settling velocity (Dyakowska 1937).

Pollen of *Corylus* is noted for its poor dispersal. Erdtman (1935) reported a common occurrence of *Corylus* in forests in Canada but a representation in surface samples less than 1%. Firbas (1934) and Bertsch (1935) report only higher percentages (5–13%) close to *Corylus avellana* shrubs.

In closed forests high percentages of *Corylus* were found by Jonassen (1950) only underneath *Corylus avellana* shrubs. Potzger et al. (1957) found the same in Quebec; of five forest samples only one shows a *Corylus* percentage of 8%, and in the other four samples it is absent. The low regional value in our samples is in agreement with these data.

Corylus pollen is most abundant at Beauty and Bohall, where we find an almost closed cover of *Corylus* in the understory of the surrounding forest. At Bohall *Corylus* shrub occurs at the border of the forest and the pond, where it flowers abundantly in the sunlight and produces a distinct local rise of the *Corylus* curve of the corrected diagrams. Samples in the middle part of both the Bohall and Beauty 2 transects show lower percentages but higher than the regional values (extralocal effect?). In contrast, at French Creek Bog the transect does not leave the forest, so *Corylus* does not flower there and thus cannot produce any local increase in pollen percentage.

Abies.—Average regional percentage is 1.4% (range 0.3–3.6%). Along all the transects where *Abies* is present we find a distinct local or extralocal effect. This may be studied best in the transect diagrams. Floating Bog 1 shows an extralocal percentage in samples 3–6, because the transect passes here a patch of *Abies balsamea* forest to the north. The same feature shows in sample 24 at Floating Bog 2, which is situated just north of the small *Abies* stand. French Creek Bog shows high local values in the upland forest only. In both the western and eastern belts of *Picea mariana* we find high extralocal values. In the *Larix laricina* zone the percentages have been reduced to the background value. The extralocal values found here occur thus over a short distance (30 m only). At Bohall, samples 1–3 have been taken in *Pinus resinosa* forest with a few *Abies* trees in the lower forest layer. Therefore the

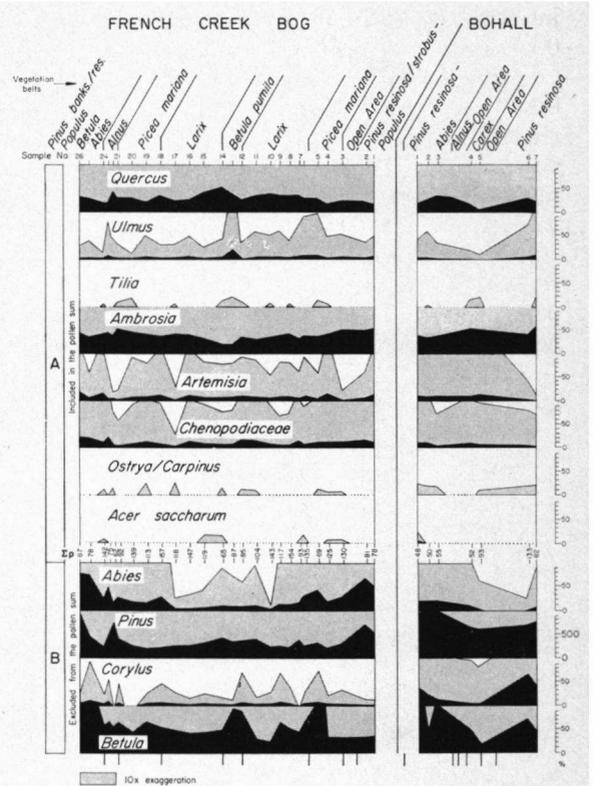


FIG. 13. Simplified pollen diagram for French Creek Bog and Bohall transects, as in Fig. 12.

Abies local percentages are here the highest found along this transect and are at the same level as the extralocal percentages at French Creek Bog. At Bohall, accordingly, we do not find any extralocal percentage. The highest (extralocal) pollen percentage ever found in surface samples in the Itasca region was 12%, for a small pond surrounded by a dense *Abies* stand.

According to Dyakowska and Zurzycki (1959) *Abies alba* pollen is very heavy (three to four times that of *Picea excelsa*) and therefore settles rapidly (Dyakowska 1937). These features are responsible for the often reported underrepresentation of *Abies* species (*Abies balsamea*, Davis and Goodlett 1960; *Abies lasiocarpa*, Bent and Wright 1963). Carroll (1943), however, found for *Abies fraseri* a lesser underrepresentation. McAndrews (1966), comparing presettlement vegetation with presettlement pollen percentages, found an equal representation for *Abies balsamea*. In our studies presettlement vegetation data have been compared with postsettlement regional pollen rain. Because *Abies* is the tree that has profited most from the protection of Itasca State Park during the past 50 years, we expected to find an overrepresentation for *Abies*. This is not the case, for *Abies* is still equally represented. Perhaps the *Abies* are young and do not reach the upper canopy

of the forest. This would prevent them from contributing more pollen to the present pollen rain than 50 years ago.

Larix.—Average regional percentage is 0.03%. Pollen is only occasionally present. Comparison with the regional percentage reveals a strong underrepresentation. *Larix* especially is noted for this. Erdtman (1935) reports the absence of pollen of this tree in the boreal forests of Canada. Davis and Goodlett (1960) place *Larix* at the end of the series of pollen types arranged according to their representation. The same is seen in the work of Potzger et al. (1957). Benninghoff (1960) found the highest percentages of *Larix* (2.6%) in a *Chamaedaphne* bog adjacent to a *Picea-Larix* forest. The strong underrepresentation is without doubt a result of the physical properties of the grain. According to Dyakowska (1937) *Larix polonica* settles twice as rapidly as *Picea*. Knoll (1932) reports an equal settling velocity.

In our samples we find even in the *Larix laricina* stand at French Creek Bog only a slightly raised percentage. Higher local values (up to 18%) have been found in isolated samples in a *Larix* stand in the deciduous forest formation near St. Cloud. This stand was much older than that of French Creek Bog which might have been too young to produce *Larix* pollen.

Picea.—Average regional percentage is 2.73%; curve is continuous. *Picea* is underrepresented in the regional pollen rain, but less so than *Larix* (Table I). A majority of authors report an underrepresentation of *Picea*. In a list of pollen types arranged according to their representation Davis and Goodlett (1960) place *Picea* as the first pollen type that is clearly underrepresented (ratio of basal area to pollen percentage is 11:4). An approximately equal representation is given by Potzger et al. (1957). According to Aario (1940) *Picea* is underrepresented in Finland in forests containing that tree. King and Kapp (1963) found *Picea* underrepresented in the regional pollen rain in eastern Ontario, though it is as abundant as *Pinus* in the forest.

At French Creek Bog in the *Picea mariana* belt local *Picea* values reach 29%. In the adjacent *Larix laricina* zone even close to the *Picea* belt the *Picea* percentages are scarcely higher than are the background values. This seems to indicate that the underrepresentation of *Picea* is more the result of its poor dispersal than insufficient pollen production. Indeed Pohl (1937) places *Picea excelsa* among notably high pollen producers, e.g. *Corylus*. Jonassen (1950) favors for *Picea excelsa* a poor production but agrees with the poor dispersal. In his work *Picea* decreased from 59%

to 7% at 200 m from a *Picea excelsa* forest. Maher (1963) found in the San Juan Mountains, Colorado, that *Picea* disperses over shorter distances than *Pinus*. The short dispersal is consistent with the relatively high speed of free fall (Dyakowska 1937). In the Itasca transects a distinct extralocal trajectory is absent. The results of Heim (1962) in the Haut-Fagnes, however, indicate that in the case of large *Picea* stands a short extralocal trajectory is present sometimes.

Pinus.—Average regional percentage is 78.8%; curve is continuous. Comparison of the regional percentage with the regional % I.V. shows only a slight overrepresentation, in contrast to what is generally accepted. The work of McAndrews shows the same. The classical example for the overrepresentation of *Pinus* is the study of Aario (1940), who found in the tundra of Lapland a percentage of *Pinus* as high as that in the *Pinus* forest. Most of the many other reports of *Pinus* overrepresentation deal with regions where pine does not play an important part in the vegetation (e.g. Tsukada 1958, Davis and Goodlett 1960, Bent and Wright 1963) or is absent (e.g. Rudolph and Firbas 1926). Where pine is present to a large extent, *Pinus* is equally represented (Bent and Wright 1963, McAndrews 1966).

Potter and Rowley (1960) report from a *Juniperus Pinus-Quercus* vegetation in New Mexico even a strong underrepresentation of *Pinus*, resulting from locally overrepresented *Juniperus*.

Pinus sylvestris is one of the largest producers of pollen (Pohl 1937) which disperses very easily (Dyakowska 1937). Its ability to be transported over large distances explains why a considerable amount of *Pinus* pollen is still found in regions where pine is absent. Davis and Goodlett (1960) found but little difference in *Pinus* percentages between two sites 25 km apart that have distinctly different amounts of *Pinus* in the recent vegetation. According to these authors *Pinus* pollen is readily dispersed and falls as an even rain over a wide area.

In spite of this good dispersal, locally high percentages can be found. The corrected diagram of French Creek Bog shows higher percentages of *Pinus* on the two ends of the transect in the *Pinus* forest, a feature overshadowed by *Abies* and *Betula* in the normal diagram. This local effect has been shown too in dispersion studies of Buell (1947), Schmitt (1955), and Persson (1955). Buell found for *Pinus echinata* a decrease of 8-28% of the local amount at 150 m from the source. Persson reports for *Pinus sylvestris* a decrease to 10% at 700 m from the source.

The transect diagram of French Creek Bog does not show extralocal values, but at Bohall, where

Pinus plays a much larger part in the forest, the *Pinus* values in the middle part of the transect are definitely higher. This reflects the extralocal effect. The experiments of Wright (1952) show for *Pinus cembroides* how steep the dispersal curve is. At a distance of 3 m, 8,480 pollen grains were collected, but at 25 m only 5% as many (438 grains).

These data suggest that the extralocal trajectory for pine is very short. At French Creek Bog, where we find quite a large amount of *Populus tremuloides* in the forest, the short extralocal trajectory of pine would result in a possible extralocal pollen rain in the *Pinus*-*Populus* forest itself instead of in the bog. It is perhaps not without

significance that the "local" values on the east side of the French Creek Bog transect, where we find much *Populus*, are the same as the extralocal percentages at Bohall.

The Beauty transects show a much lower regional percentage of pine; at Beauty 1 this largely reflects the high *Betula* values. If *Betula* is removed from the pollen sum, as shown in the transect diagrams (Fig. 14), the regional percentage of *Pinus* is in line again. The lower regional percentages of *Pinus* at Beauty 2 are mainly the result of the unexplained raised values of *Ambrosia*.

Quercus.—Average regional percentage is 8.3% (range 3.8–11.4%). *Quercus* is overrepresented when compared with the regional % I.V. Overrepresentation of *Quercus* has been reported both in America (Hansen 1949, Davis and Goodlett 1960) and Japan (Tsukada 1958). In northwestern Minnesota McAndrews (1966) found overrepresentation also. European species are not big pollen producers (Pohl 1937). Indeed, *Quercus* in surface studies in Europe is usually not much overrepresented. Bastin (1964) found in Belgium but slight overrepresentation in forests where *Quercus* is abundantly present. Equal representations in Belgium have been reported by Heim (1962) and Mullenders (1962). Davis and Goodlett explain the difference in representation by assuming a heavy pollen production for *Quercus rubra*. It should be realized, however, that the representation of a pollen type is not only the result of its production and dispersal but also of the other pollen-producing species in the region. A heavy pollen production of *Pinus ponderosa* apparently is the reason for the underrepresentation of *Quercus* in *Quercus gambelli* groves in the Chuska Mountains (Bent and Wright 1963); elsewhere in New Mexico (Potter and Rowley 1960) *Quercus* is underrepresented on account of the overrepresentation of *Juniperus*.

In most of the regions reporting an overrepresentation of *Quercus*, *Pinus* plays but a little role in the surrounding vegetation. In the Itasca region, unlike the areas studied by Davis and Goodlett and by Tsukada, *Pinus* is an important part of the vegetation, and accordingly the observed *Quercus* overrepresentation must result either from an excellent pollen production or dispersal or both.

In all the transects, *Quercus* is found in the extralocal vegetation only at Beauty, where it occurs occasionally in the *Populus tremuloides* forest. Indeed the *Quercus* percentages are slightly higher here, but they fail to show a local or extralocal effect. Lower *Quercus* pollen percentages occur in the Bohall transect and the upland forest samples at French Creek Bog. This is clearly the

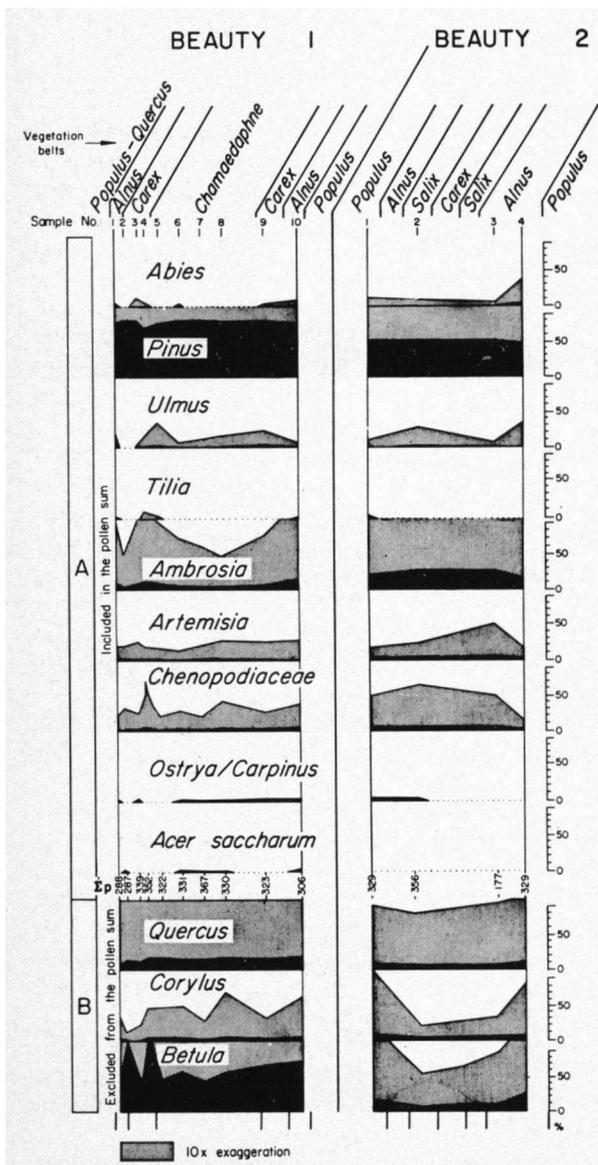


FIG. 14. Simplified pollen diagram for Beauty transects, as in Fig. 12.

result of the high local pine values, as in the Chuska Mountains (Bent and Wright 1963). The transect diagrams (*Pinus* excluded) show *Quercus* both at Bohall and French Creek Bog at the same level (Fig. 13).

Populus tremuloides.—A regional percentage for this species is difficult to indicate. The curve is commonly irregular. At Floating Bog, where nowhere along the transect does *Populus* occur, we find percentages between 0.5 and 5. It is not at all clear why *Populus* is higher in the *Fraxinus nigra* forest than out in the bay. At any rate the highest values of *Populus* along the Floating Bog transect are lower than the % I.V. calculated from the records of the surveyors. The underrepresentation of *Populus* is even more striking if we realize that *Populus* benefited most from the logging operations half a century ago. The Beauty transect, situated in a young forest of this type, does not show a higher *Populus* percentage than elsewhere, even right under the *Populus* trees. There are two exceptions, however. Sample 5 of French Creek Bog and sample 4 of Beauty 1 show 9.2% and 13.8% *Populus* respectively.

Ritchie and Lichti-Federovich (1963) found in atmospheric samples in the aspen parkland of Manitoba an average percentage for 3 years of 22.4%, in contrast to low percentages in surface samples. The statement of Erdtman (1935) that no *Populus tremuloides* pollen is present in surface samples from Alberta, Canada, in spite of the abundance of the tree seems to be valid for *Populus tremula* too (Mullenders 1962). It has often been assumed that the poor representation of *Populus* in surface samples results from poor preservation. Sangster and Dale (1961) found in a farm pond, a lake, and a swamp a faster decomposition of *Populus* than in a bog. The dispersal seems to be good (*Populus deltoides*, Wright 1952). The data of Pohl (1937) suggest a high pollen production for *Populus canadensis*.

It might be of significance that the observed high percentages of *Populus* in the two samples from French Creek Bog and Beauty 1 have been found in *Sphagnum* samples, which generally show the best-preserved pollen grains. It is not understood, however, why all the other *Sphagnum* samples do not show a consistently higher percentage than samples of soil, moss, or lake mud.

Betula.—The *Betula* curve is composed of pollen grains from two species: the lowland shrub *B. pumila* var. *glandulifera* and the upland tree *B. papyrifera*. *Betula lutea* occurs on Floating Bog, but it is rare in this region (Christ 1959). It must contribute few grains to the total pollen rain. Because of this dual distribution and because it occurs along the transects, *Betula* has been kept

outside the pollen sum in the transect diagrams.

The curve of *Betula* reflects precisely the local presence of either shrubs or trees. At Floating Bog 1 and 2 the zones of *Betula pumila* shrub are represented by maxima in the *Betula* curve (Fig. 11). Forest samples of Floating Bog 2 show higher percentages than forest samples at Floating Bog 1 because of the presence of *Betula papyrifera* in the northern part of the Bear Paw Peninsula. An equal rise of the *Betula* curve because of local occurrence of *Betula papyrifera* is present in samples on the west side of French Creek Bog, at Bohall, and at Beauty 1.

Because of the presence of two species along most of the transects, it is difficult to determine a regional percentage. The values of the lake samples of Floating Bog 1 indicate overrepresentation (8–24%, average 15.7%), but less than found by McAndrews (1966). The overrepresentation might be the result of the participation of *Betula pumila* in the pollen rain. At Beauty, however, *Betula pumila* is absent from the extralocal vegetation but still *Betula* is overrepresented. *Betula papyrifera* occurs along the transect at Beauty 1 only, which therefore shows locally high values at the end of the transect. In the middle part of this transect, however, the *Betula* percentages still are higher than at Beauty 2, which shows the same regional values as at Floating Bog. The percentages in the middle part of Beauty 1 must reflect the extralocal effect.

Alnus.—Average regional percentage is 4.36% (2–11%); curve is continuous. Because of the shrub habit of *Alnus rugosa*, no exact data about its part in the recent vegetation are available. We find at Floating Bog in the northeast corner of the mat a rather extensive area in which *Alnus* is the dominant shrub. This area, however, fails to show any effect upon the regional pollen rain in the Floating Bog transects. A large overrepresentation of *Alnus* because of its local occurrence often has been reported for *Alnus glutinosa* (Jonassen 1950, Janssen 1959). The same feature is present in the Beauty transects. At Beauty 1 the *Alnus* zone is narrow, and accordingly the local rise is modest when compared to the local effect at Beauty 2, where a much larger area is covered by this shrub. At Beauty 2, where a much larger area is covered by this shrub. At Beauty 1 an extralocal effect is absent. At Beauty 2 the samples outside the *Alnus* shrub area show a percentage higher than the regional value (extralocal values?).

Salix.—Average regional percentage is 1.56%, curve is continuous. High local values are found along the transect where *Salix* is present. At Floating Bog 1, percentages are high in the *Salix*

TABLE III. Deciduous forest formation. Percentage importance values for extralocal and regional vegetation, and average regional pollen percentages near the transects based on a separate upland-forest pollen sum for each type (see text). Taxa below the break were excluded from the percentage base on the calculations.

Taxon	Percentage importance value				Average regional pollen percentage	
	Extralocal		Regional		Lake Sylvania	Clearwater
	Lake Sylvania	Clearwater	Lake Sylvania	Clearwater		
<i>Carya</i>	0.6		0.6		0.94	0.34
<i>Acer saccharum</i>	43.8		22.9	0.7	3.5	0.17
<i>Tilia</i>	14.3	1.1	9.5		2.80	0.94
<i>Ulmus</i>	13.0	2.2	25.3	9.1	38.0	8.04
<i>Ostrya</i>	15.4	10.3	18.8		3.25	1.28
<i>Populus tremuloïdes</i>	2.9	2.3	2.0	20.2		
<i>P. grandidentata</i>	2.0	2.1				
<i>Betula</i>	2.0	7.9	2.5	0.7	5.90	7.2
<i>Quercus</i>	2.4	56.6	14.8	68.2	32.9	85.3
<i>Acer rubrum</i>		6.0			0.17	0.21
<i>Prunus serotina</i>		8.7	0.5		0.14	0.3
Number of trees counted.....	170	153	178	177		
<i>Corylus</i>					0.37	0.25
<i>Abies</i>					0.27	
<i>Pinus</i>					13.3	11.0
<i>Alnus</i>					0.27	0.25
<i>Picea</i>					0.14	0.17
<i>Larix</i>					0.04	0.17

belt, which occurs in that part of the *Fraxinus nigra* forest that contains *Betula pumila*. In the rest of the *Betula pumila* zone other *Salix* species occur, but both their abundance and height are lower. As a result the local *Salix* percentages are lower. Both in the *Fraxinus nigra* forest and in the *Nuphar* belt, a short trajectory may be found, with extralocal percentages slightly higher than the regional values. At French Creek Bog *Salix* species, with low frequencies, are constituents of the bog forest, and as a result the local values are higher. Beauty 1 shows for unknown reasons all over the transect slightly higher percentages than the regional values. The steep drop from local to regional values, with a short extralocal trajectory only, is in agreement with the zoogamous nature of *Salix*, which accordingly is usually underrepresented.

The high local percentages indicate that the underrepresentation of *Salix* is a result of the poor dispersal of the pollen grains rather than a low pollen production.

Values larger than 3-4% for *Salix* in the diagrams means that *Salix* shrubs were actually present at the sampling site. This seems to be true even for treeless regions, where because of the absence of trees the total pollen precipitation is much lower, and accordingly *Salix* should be better represented.

Welten (1950) found in the alpine zone of the Alps that a percentage larger than 5% means well-developed shrubs. In Lapland *Salix* is low except

in areas of *Salix* shrub, where it may dominate in the pollen rain (Firbas 1934).

Carya, *Juglans*, *Celtis*.—These trees do not occur in the Itasca State Park region. Their pollen grains occur in the surface samples, however, as a result of long-distance transport.

TREES AND SHRUBS IN THE DECIDUOUS FOREST FORMATION

Description of the transects

The transects are located south of St. Cloud, Minnesota (Fig. 4). Table III shows that in contrast to the transects in the coniferous-deciduous forest formation the differences in the regional vegetation are much larger. Lake Sylvania is situated on the northern edge of the Big Woods (Daubenmire 1936) on grey glacial drift of the Des Moines Lobe. The Clearwater transects, approximately 12 miles to the north, are located in an area covered by brown drift from the Rainy Lobe.

Lake Sylvania.—Located in Wright County, Sec 33, T121N, R28W (Fig. 8).

The transect runs across a *Typha latifolia* mat, which covers a large part of an earlier pond. At the time the samples were taken, open water was still present. The surrounding forest is of the Big Woods type. The northern end of the transect runs through a forest with much *Acer saccharum*, *Tilia americana*, and *Ulmus americana*. On the southern end the forest is less tall, a larger amount

of *Ostrya virginiana* occurs, and *Acer*, *Tilia*, and *Ulmus* are reduced in number. In the northeastern part of the swamp is much *Salix*. On this side of the swamp on the upland are a few specimens of *Betula papyrifera*, the only ones in the area. Between the west side of the swamp and the lake a concentration of *Juniperus virginiana* is present.

Clearwater.—Located in Stearns County, S ½ SW ¼ Sec 1, T122N, R28W (Fig. 9).

Two transects cross swamps in *Quercus-Ostrya* woods. Four species of *Quercus* (*Q. macrocarpa*, *Q. alba*, *Q. rubra*, and *Q. ellipsoidalis*) are present. The forest is mixed with *Ostrya virginiana*, *Acer rubrum*, and *Prunus serotina*. Along Clearwater 1 the only *Tilia americana* tree found in the area occurs near sample 2. *Zea mays* plantations are near at hand.

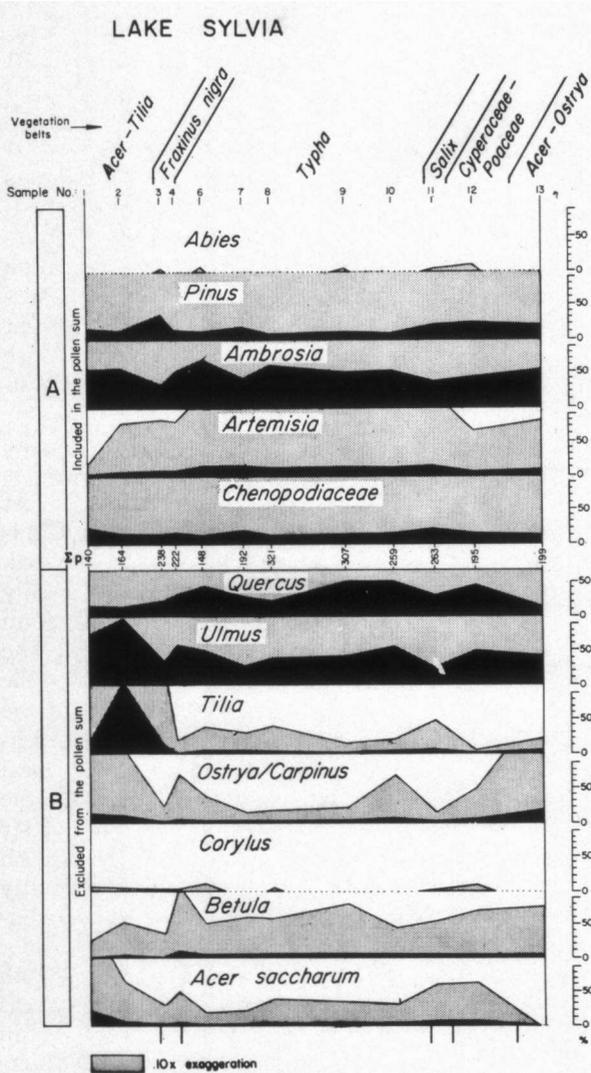


FIG. 15. Simplified pollen diagram for Lake Sylvia transect, as in Fig. 12.

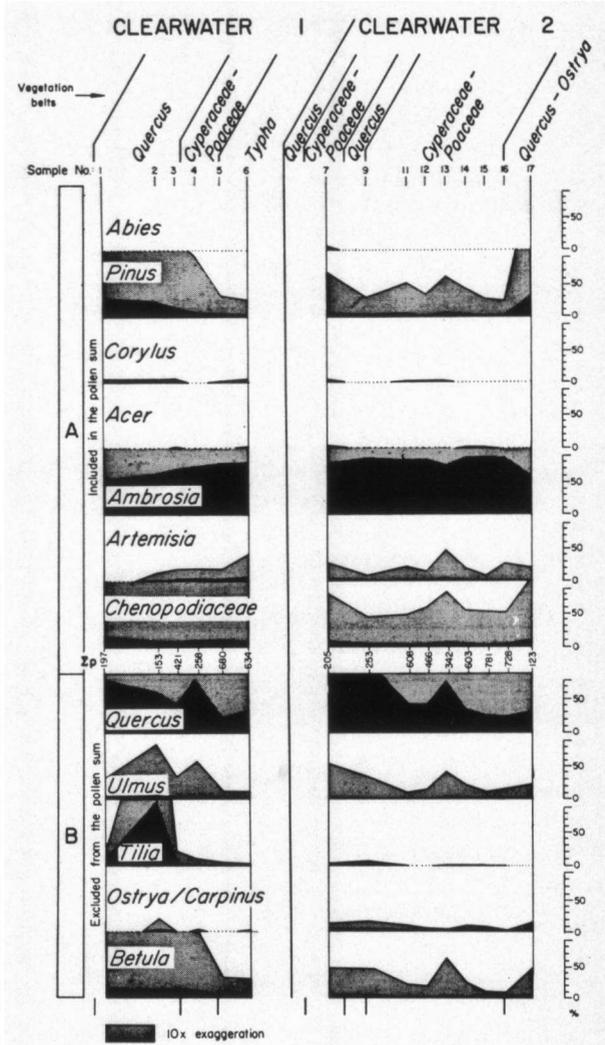


FIG. 16. Simplified pollen diagram for Clearwater transects, as in Fig. 12.

Regional averages and discussion of individual pollen types

Again the effect of increasing distance may be studied in the transect diagrams (Fig. 12-16) and the comparison with recent vegetation in Table II and Fig. 10 and 11.

For all the transects in the coniferous-deciduous forest formations of the Itasca Park area, one regional pollen percentage could be established because they all were situated in the same formation relatively close to each other. This is not the case with the Lake Sylvia and Clearwater transects in the deciduous forest formation. Because of their location in such widely different plant formations, a difference in regional pollen rain exists (Fig. 15 and 16).

For each transect the regional and extralocal composition of the tree vegetation are approxi-

mately the same (Table II). As a result it is difficult to determine a regional pollen percentage for many pollen types, for it is not possible to check any situations in which these types do not occur in the extralocal vegetation (e.g. transects covering larger distance outside the forest). Only for those types that do not occur in the deciduous forest at all (*Pinus*, *Abies*, *Ambrosia*, *Artemisia*) may the regional pollen percentage be determined.

On the other hand, many of the pollen curves show a steep slope at increasing distance from the source of dispersal. They remain horizontal outside the forest. Therefore the level of this horizontal trajectory will probably not differ too much from the regional values, and there is little evidence for extralocal values. In the following discussion an average regional percentage is based upon the horizontal trajectory along the transects. There is a possibility, however, that this part of the transects represents extralocal values rather than regional ones.

Pinus and Abies.—Average regional percentage for *Pinus* is 12% (range 6–30%), with continuous curve; for *Abies* 0.27% (range 0–0.4%), with highly interrupted curve. *Pinus* and *Abies* are lacking in the deciduous forest, and all the grains found in the samples must have traveled by long-distance transport. The regional values are lower than those found by McAndrews (1966) in the deciduous forest west of Lake Itasca. This might be explained by the greater width of the deciduous forest belt here compared to the Itasca region. In the latter region, *Pinus* and *Abies* trees are present only a few miles from the transects.

Tilia.—At Lake Sylvania the forest on one side of the transect has high local values of pollen. As along the Floating Bog transect, a steep drop in percentage occurs at the edge of the forest. A regional percentage of 2.80% (range 0.4–5.2%) remains. On the opposite side of the transect a local rise of *Tilia* (and of *Acer* and *Ulmus*) is lacking because of the much lower frequencies of these trees in this part of the forest. At Clearwater we find high local values close to the isolated *Tilia* tree in the *Quercus* forest. The regional percentage of 0.94% (range 0.3–2.4%) is much lower than that at Lake Sylvania.

Ulmus.—The *Ulmus* curve at Lake Sylvania bears the same relation to *Tilia* as at Floating Bog in the coniferous-deciduous forest region. The corrected diagram of Lake Sylvania (Fig. 15) shows high local values in the forest but not such a sharp decrease in the *Typha*-mat samples. Still an average regional percentage of 38% remains. Thus here too the data suggest a better dispersal for *Ulmus* than for *Tilia*. At Clearwater a much-reduced regional percentage of only 1–3% occurs,

because of the much lower % I.V. of *Ulmus* in the *Quercus* forest. There is a slight local effect in the forest where *Ulmus americana* trees are scattered.

Acer saccharum.—Average regional percentage at Lake Sylvania is 3.57% (range 1.6–6.3%). Raised local values occur in the forest. In spite of the fact that *Acer* is the dominant tree in the forest, it is strongly underrepresented in the pollen samples even in the forest. From this it follows that its pollen production must be low. This and the poor dispersal results in the underrepresentation so often reported (Tsukada 1958, and others). At Clearwater, *Acer* pollen grains are only occasionally present.

Ostrya.—Average regional percentage at Lake Sylvania is 3.25% (range 1.7–5.6%); curve is continuous. *Ostrya* is clearly underrepresented when compared with the regional and extralocal % I.V. of 15–20%. On both ends of the transect the local values are raised, with a possible extralocal trajectory at the margins of the *Typha* mat. At Clearwater we find even lower percentages in spite of an extralocal % I.V. of 10%.

The underrepresentation is in strong contrast to the observations of other authors. *Ostrya* is equally represented in Vermont (Davis and Goodlett 1960). McAndrews (1966) reports an overrepresentation in the deciduous forest formation west of Lake Itasca when compared with the surveyor's records. In his region the surveyor might not have included *Ostrya* in his records because of its small size. As a result of this the calculated % I.V. might be too low.

Quercus.—Average regional percentage at Lake Sylvania is 32.9% (range 25–40%). *Quercus* is overrepresented as in the Lake Itasca area. At Lake Sylvania the curves calculated from the upland-forest pollen sum show high percentages for oak relative to those in the maple forest. The locally raised percentages of several trees might explain the lower *Quercus* percentages in the forest. The transect diagram (Fig. 15), however, shows the same feature. *Quercus* has a low % I.V. in the forest (Table III), but it is absent along the transect. This explains the absence of a "positive local effect." This "negative local effect" might be the result of filtration inside the forest. At Clearwater the average regional percentage is 85.3%, much higher than at Lake Sylvania because of the greatly depressed *Ulmus* percentages. The transect diagram (Fig. 16) shows the local effect.

Corylus.—Average regional percentage at both Lake Sylvania and Clearwater is 0.25%; curve is interrupted. At Lake Sylvania *Corylus* occurs in the forest, but it fails to show higher pollen percentages than at Clearwater, where it does not

occur at all. We thus find essentially the same relations as in the Lake Itasca State Park area. That the regional pollen percentages are lower than in the Itasca State Park area is in agreement with the smaller regional importance of the shrub.

Betula.—Average regional percentage at both Lake Sylvia and Clearwater is 7–8%. In the regional vegetation of the two transects only *Betula papyrifera* occurs. *Betula pumila* is absent. In spite of this we still find a strong overrepresentation. The transect diagram of Clearwater 1 (Fig. 16), where *Betula* occurs along the transect, shows slightly raised local percentages in the *Quercus* forest.

Acer rubrum.—In spite of the fact that *Acer rubrum* trees are present in the *Quercus* forest around the Clearwater transects, we do not find locally raised values. The average regional percentage is even about the same as at Lake Sylvia, where only a few shrubs of *Acer rubrum* may be found in the *Acer saccharum* forest. This result is the same as found at Beauty.

Rhus glabra.—Pollen grains of *Rhus glabra* have been found occasionally at Clearwater. There are only a few shrubs present in the *Quercus* forest at Clearwater, but it is here very common along roadsides and margins of the forests. The low *Rhus* percentage apparently is a regional feature.

Carya, *Juglans*, and *Celtis*.—These trees are absent from the region around the Clearwater transects, so the regional values are as low as those in the Itasca State Park region. Though not reported in the notes of the 65-km² area used for calculations from the surveyors' records, *Carya*, *Juglans*, and *Celtis* are essentially components of the Big Woods. As a result the regional values at Lake Sylvia are slightly higher than at Clearwater (e.g., average regional percentage of *Carya* is 0.9% against 0.34% at Clearwater).

Alnus, *Picea*, and *Larix*.—These trees are not present in the local or extralocal vegetation. *Alnus* and *Picea* do not occur in the regional vegetation, and accordingly they show very low regional pollen percentages. *Larix* is a component of the regional vegetation but shows the same low regional pollen values.

HERBS AND HERB POLLEN IN BOTH REGIONS

Herbs not occurring along the transects

Ambrosia.—Apart from the irregularities in the *Ambrosia* curve, which will be discussed later, *Ambrosia* percentages are higher in the St. Cloud region than at Itasca State Park, no doubt a result of the greater degree of cultivation. Especially at Clearwater we find exceptionally high regional percentages (up to 295% in the calculation based upon the upland-forest pollen sum). The differ-

ence with Lake Sylvia, situated in a cultivated area as well, may be explained by its location. The Clearwater forest stand is small, with nearby *Zea mays* fields (where *Ambrosia* sp. grows as a weed) whereas the Lake Sylvia stand is located on a peninsula that is completely forested.

The same high *Ambrosia* values (265%) have been found in the cultivated deciduous forest belt of southern Ontario (Bassett and Terasmae 1962).

Exotics.—In all the transects are scattered occurrences of *Iva*, *Xanthium*, and *Sarcobatus* pollen. As these plants do not occur in any of the investigated areas, pollen grains in the samples must have traveled by long-distance transport. This is especially true for the single grain of *Ephedra* found in Floating Bog, for the closest area where *Ephedra* occurs is the southwestern United States. Long-distance transport of *Ephedra* pollen grains has been reported from Iowa and Manitoba (Maher 1964).

Weeds accompanying cultivation.—Pollen grains of these herbs occur in samples along all the transects. At Lake Sylvia and Clearwater, *Zea*, *Melilotus*, and *Trifolium repens* reach slightly higher values than along the other transects, probably a result of the higher degree of cultivation in these areas.

Herbs occurring along the transects

Upland herbs.—Herbs typically occurring in the understory of the forest have been found in local pollen samples only. This is especially striking at Floating Bog 1. *Matteuccia struthiopteris* covers approximately 80% of the floor of the *Tilia-Ulmus* forest, but in pollen samples outside its local occurrence it is absent. Likewise other typical plants of the mesic forest, e.g. *Celastrus*, *Asarum*, *Athyrium filix-femina*, and *Dryopteris spinulosa*, show up in local pollen samples only. The same applies for *Cornus canadensis* type at French Creek Bog. Thus most of the upland herbs do not leave any trace in the regional pollen rain in these forested regions. There are, however, some exceptions: *Pteridium*, *Prunus* type, *Amelanchier* type, *Humulus*, and *Thalictrum*.

Lowland herbs.—Most of the lowland herbs behave like the upland ones: pollen grains are present only when the plant occurs locally. In many cases pollen assemblages in lowland samples indicate clearly the type of local vegetation.

At French Creek Bog several of the herbs typical for the *Larix laricina* bog are found in the surface samples, e.g. *Sarracenia purpurea*, *Ledum groenlandicum*, *Sphagnum* sp., *Potentilla palustris*, *Menyanthes trifoliata*, and *Caltha* type. At Lake Sylvia, pollen grains of the *Typha*-mat types, i.e., *Bidens*, *Impatiens*, and *Sagittaria*, have been found

in the surface samples of the mat. The same holds for the various vegetation belts at Floating Bog. Abundant occurrence in the local vegetation does not necessarily mean that pollen percentages will be high. *Nuphar* flowered abundantly at the time of the sampling of the Floating Bog 1 transect and covered about 30% of the water surface, but only a few pollen grains have been found in this zone. The same is true for the Ericaceae at French Creek Bog and Beauty 1. *Ledum groenlandicum* occurs abundantly in the bog forest of French Creek Bog, but only a few grains of the *Ledum* type have been found in surface samples. Jonassen (1950) also found that Ericaceae do not assert themselves strongly in small bogs in a forest.

Thus most of the lowland herbs do not show up in the regional or extralocal pollen rain. Pollen types that have a regional percentage include *Typha latifolia*, *Sagittaria*, and *Sparganium*. The same types have been mentioned in this respect by Benninghoff (1960).

Poaceae, *Cyperaceae*.—*Poaceae* and *Cyperaceae* show low pollen values in forest samples. High local percentages of *Poaceae* have been found in the *Zizania aquatica* belt at Floating Bog. *Carex* mats and *Larix* bog forests show lower local values than the *Zizania* vegetation.

Cyperaceae pollen reaches its highest local values in the *Carex* mat. Representatives of both families are found almost in every vegetation type, and therefore it is difficult to separate extralocal and regional percentages from local values. Only the eastern side of the Floating Bog transect can be used for this. Indeed grass pollen of the *Zizania* type still can be found in large amounts in the open-water samples there. This is not necessarily an extralocal effect, however. It might be the result of *Zizania* pollen floating over the surface of the water.

Striking is the absence of an extralocal trajectory for *Cyperaceae* close to the *Carex* mat at Floating Bog 1 in the adjacent *Nuphar* and *Zizania* belts.

DISCUSSION AND CONCLUSIONS

The course of the curves of the regional pollen types may be studied best in group A of the transect diagrams. In these diagrams local and extralocal pollen types have been removed from the pollen sum, so the regional curves are unmasked. If the regional pollen rain is (by definition) the pollen rain that does not vary over larger distances, then even our short transect should show parallel regional curves. Such parallelism may be found, for instance, in the work of Müller (1937), who took surface samples in a *Fagus* forest and a *Pinus* forest. Reducing the values

of the overrepresented *Fagus* and *Pinus* to their original regional percentage, as found in larger bogs, resulted in "normal" values of the other pollen types. However, it is quite possible that the deposition of regional pollen varies in different vegetational types that may filter pollen differentially. Dengler (1955) found such a filtering effect in young stands. In his experiments the precipitation of pine pollen inside various stands was smaller than outside these stands. This influenced the proportions of the regional types even in diagrams based on a pollen sum comprising only regional types. Tauber (1965) pointed out that filtering of pollen is most likely in species that are densely branched and have sticky or hairy parts. A strong negative correlation between *Salix* and *Fagus* in a historical pollen diagram is explained by Tauber by filtration of *Fagus* pollen by *Salix* shrubs. In our diagrams, however, we find in a general way parallel curves over the entire transects—there is not a consistently different proportion in and outside the forest. This would indicate that, if filtration occurs in the forest, it must be at the same rate for all regional pollen types. A possible exception perhaps is *Quercus* at Lake Sylvia, where we find a "negative local effect" with higher values outside the forest than inside. Also, at French Creek Bog *Quercus* shows its highest values in a rather open young *Larix laricina* stand.

In spite of the fact that there is no consistent difference between the pollen percentages of the regional pollen types in the various vegetational zones, fluctuations do occur. These fluctuations are slight in the Beauty and Lake Sylvia transects. Stronger fluctuations can be found in the French Creek Bog, Bohall, and Clearwater transects and even more in the Floating Bog transects. At Floating Bog 1, for instance, the minimum and maximum percentage for pine is 40% and 90%, for *Chenopodiaceae*/*Amaranthaceae* 1% and 11%. Many of these irregularities are a result of the fluctuations of the *Ambrosia* curve, which mirrors one or more other dominant pollen types, usually *Pinus* (at Floating Bog, Lake Sylvia, Clearwater) or *Quercus* (at French Creek Bog). It is difficult to explain this. *Ambrosia* shows a large expansion in Minnesota in postsettlement time, and there may be a possibility, at least for the lake samples at Floating Bog, that some of the samples represent mixtures of pre- and postsettlement material. This possibility, however, fails to explain the variations in the pollen curves that also occur in moss samples.

Artemisia and the *Chenopodiaceae*/*Amaranthaceae* show more consistent percentages than does *Ambrosia*, but in some cases larger fluctuations

exist. French Creek Bog, for instance, shows abrupt minima in the curve for *Artemisia* in a row of normal values.

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