ON THE RELATION BETWEEN THE CONTEMPORARY POLLEN SPECTRA AND VEGETATION OF THE FOREST-GRASSLAND TRANSITION IN MANITOBA

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ABSTRACT

To provide a basis for the interpretation of late-Pleistocene fossil data, pollen spectra were tabulated from 72 sites in the forest-grassland transition of Manitoba. The area under study was divided into 8 landform-vegetation zones: I. Main Boreal Forest (with upland and lowland sub-groups); II. Southern Boreal Forest, primarily on uplands; III. Deciduous Forest on uplands; IV. Deciduous Forest on lowlands and alluvium; V. Aspen Parkland on till plains and lacustrine deposits; VI. Grasslands on till plains; VII. Pine Forest on upland sand plains; VIII. Spruce Parkland on a sandy glacial delta. Distinct differences in the preponderance of main pollen types were recorded across the forest-grassland transition, and between the main regions I-VIII. The 52 atmospheric spectra demonstrated that *Populus* is represented proportionally, while it is absent or rare in the 19 sediment samples. The results were applied to a specific problem of interpretation of Holocene pollen spectra from Manitoba, confirming the tentative reconstructions suggested earlier.

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INTRODUCTION

This investigation was conceived as an integral preliminary step in a general study of the Holocene paleoecology of west-central Canada. The larger enquiry is designed to elucidate the nature of environmental change in west-central Canada since deglaciation, primarily by the application of pollen analysis and macrofossil study of limnic sediments (Ritchie 1964).

While pollen and spores preserved in limnic and bog deposits have been studied and recorded since the latter part of the 19th century, von Post (1916) is generally accredited with first transforming this paleoecological tool into a systematic, quantitative discipline. Neishtadt (1952) claims however, parenthetically, that Dokturovsky (1918) introduced the quantitative method of analysis of sub-fossil pollen and spores, contemporaneously with but independently of von Post. The application of the method to studies of Quaternary vegetation history, glacial history and paleoclimatology, the development of bog vegetation and archaeology, has spread rapidly, and the frequent demonstrations of regional parallelism in pollen diagrams have established a general acceptance of the validity of the method.

Briefly, the application of pollen analysis to the problems of paleoecology involves three successive steps. First, the relative amounts of pollen types in close-interval samples of appropriate sediments are calculated as percentages of the total pollen in each sample. (Relative rather than absolute numbers of pollen are used, since the sum of pollen in a unit volume of sedimentary matrix is a function of the rate of sedimentation which is an unknown variable). The separate pollen spectra from each sample are arranged in stratigraphic sequence and depicted diagrammatically to yield the familiar pollen diagram. The difficulties and sources of error encountered at this initial stage are due largely to sampling and human errors (cf. Faegri and Iversen 1950).

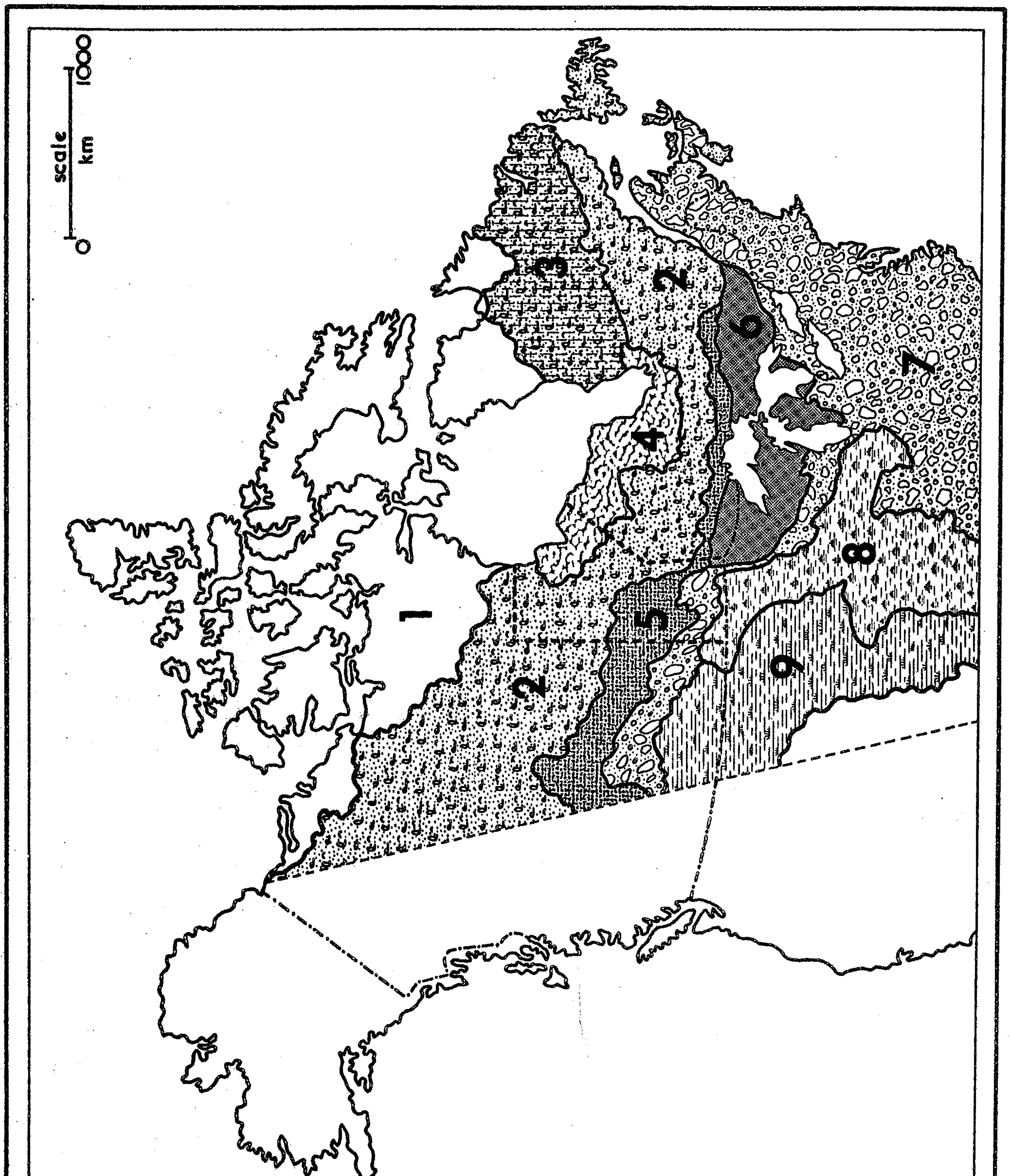
The second phase entails the interpretation of the diagram in terms of vegetation. That is, the pollen assemblages comprising the various spectrum types distinguished in a diagram are translated into putative patterns of plant community. Unfortunately, there is an intrinsic variability in pollen spectra which precludes a direct correlation between the relative amount of pollen of any particular type and its relative abundance in the vegetation.

Two important sources of variability have been recognized in spectra from west-central Canada (Erdtman 1943, and Ritchie and Lichti-Federovich 1963) - the first is wide variation in the relative amounts of pollen produced by the various components of the vegetation, varying from the high producing anemophilous types (<u>Pinus</u>, <u>Betula</u>, <u>Artemisia</u>) through moderate and low producing anemophilous genera (<u>Quercus</u>, <u>Ulmus</u>, <u>Corylus</u>) to extremely low producers among amphiphilous and entomophilous types (<u>Tilia</u>, <u>Prunus</u>, <u>Rosa</u> and many herbs). Secondly, Erdtman (l. cit. p. 190-1) found strong evidence that one of the most important genera in the forest vegetation of Alberta, <u>Populus</u>, although it is anemophilous and apparently produces copious pollen, is absent or very rare in pollen spectra from present-day sites where it is abundant in the surrounding vegetation. It has been assumed that this is due to either "the difficulty of recognizing <u>Populus</u> pollen in the deposits" (Faegri and Iversen 1950, p. 85) or to the strong susceptibility of its exine to oxidation or decomposition by micro-organisms (Erdtman, 1943, p. 195). Faegri and Iversen (l. cit.) suggest that the difficulty can be overcome by "careful examination", but this is clearly erroneous. There is little difficulty in detecting poplar pollen when it is present in a sample, and recent studies of late-glacial and early post-glacial sites in mid-western North America have revealed relatively high values for poplar (e.g. McAndrews 1963, Ritchie 1964, Wright _et al_ 1963). But all top sediment or bog surface samples recorded so far show very small amounts or no poplar pollen, indicating that Erdtman's suggestion is correct that the erratic registration of this type is related to its poor preservation.

The third and final step is to make paleoecological inferences from the reconstructed vegetation sequence. Thus the basic merit of paleoecological studies using pollen analysis is dependent directly on the validity and accuracy of the interpretation of pollen spectra.

This thesis is concerned with the prerequisites for adequate interpretation of pollen spectra, with particular reference to the transition from grassland to forest in west-central Canada.

The primary prerequisite is a knowledge of the relation, if any, between the composition of present-day vegetation and the pollen spectra produced. This need was recognized at the very outset of the development of pollen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analysis, when von Post (1916) stated that it was necessary to assess the relation between present day vegetation and contemporary pollen spectra, to facilitate the interpretation of Quaternary pollen assemblages. However, very little attempt was made to pursue such investigations, largely because pollen analysis was developed in N. W. European countries where intensive industrialisation and farming had removed or drastically altered most of the regional natural vegetation. Thus, the widely accepted, almost classical sequences of late- and post-glacial vegetation in N. W. Europe have been elucidated in large part by the subjective interpretation of pollen diagrams. An essentially similar procedure was adopted in N. America, where the early findings (e.g. Sears 1932, Hansen 1938, Potzger 1946) were completed and incorporated into the scientific literature before any serious attempt was made to examine the criteria of interpretation. However, recently more systematic attempts are being made to relate contemporary pollen spectra to the quantitative composition of vegetation (Davis and Goodlett 1960, Potter and Rowley 1960, and Ogden 1962).

In rigorous critiques of the theory of pollen analysis, Fagerlind (1952) and more recently Davis (1963) have stressed the need to derive factors or constants for individual pollen types by which their relative values in fossil assemblages might be adjusted or calibrated before interpretation is attempted. These constants, R-values, are derived by dividing the relative proportion (%) of pollen of a type by the relative (%) amount of it in the surrounding vegetation. Then the R-values for all types recorded are expressed as ratios, with the least value as unity. In applying such factors to a New England post-glacial spectrum, Davis (l. cit.) has concluded that the original interpretation (Davis 1958) in terms of a Pine Period is entirely spurious, and the new interpretation assigns Pinus a maximum of 8% of the forest composition, with fir, maple and poplar as the dominants. However, there are several limitations to this correction method:

a) The available methods of sampling vegetation quantitatively seldom account for the totality of plant communities in an area, and it is doubtful if the labour involved in overcoming this difficulty would be worthwhile.

b) Perhaps the most serious weakness, overlooked by Davis, is that there is no method available at present to determine the areal extent of the vegetation contributing pollen to a particular sampling site. Thus, there is no way of deciding the size of area to be sampled for vegetation composition.

c) R-values can be applied to Holocene data with very limited confidence. As Davis (l. cit.) points out, it is not at all certain that R-values have remained constant in time. Furthermore, R-values are seldom available for actual species, but for genera which might include species of very diverse ecology (e.g. Pinus, Betula, Artemisia).

d) Present-day vegetation and pollen spectra include a mixture of natural, semi-natural and artificial communities, difficult to assess quantitatively, and almost certainly giving distorted R-values.

An alternative to this approach has been proposed (Ritchie and Lichti-Federovich 1963). It rests on the initial proposition that the level of present-day knowledge about vegetation which gives the most balanced and accurate picture of vegetation is geographical.

More specifically, this approach can be enunciated as follows:

1. West-central Canada, and for the particular purposes of this thesis, the southern half of Manitoba, can be divided

into certain discrete, essentially geographical areas, on the basis of the predominant vegetation type (defined in terms of structure and composition) and the prevalent land-form. This is an old notion, which is in fact the essence of the Russian approach to both the classification of vegetation and the study of contemporary pollen spectra in relation to vegetation (cf. Grichuk 1942, Mal'gina 1952, Neishtadt 1957 and Zaklinskaya 1951). It is an approach "from the top" rather than "from below", by separating landscape into major geographical units, further divided only to the level of knowledge where balance is maintained. This is the level of the landform-vegetation type or the landschaft-phytocenose. Further, this approach is closely related to the total site classification of land, such as Hills (1959, 1961) has proposed and implemented in Ontario.

2. If the theory of pollen analysis has even partial validity, it should be possible to characterize landform-vegetation regions in terms of pollen spectra.

3. If it proved possible in fact to establish correlations between pollen spectra and landform-vegetation types, a less subjective entry might be possible into the interpretation of sub-fossil spectra.

There is adequate information in the existing literature to classify southern Manitoba into landform-vegetation zones. In fact, the forest classification by Rowe (1959) distinguishes between the component sections of the main forest regions in terms of landforms. This work, together with those of Bird (1961), Ellis (1938), Ritchie (1962) and Weir (1960), was used to draw the landform-vegetation map shown in Figs. 3 and 4. (The Manitoba Forest Inventory Reports and the Manitoba Soil Survey Reports were also consulted, referred to specifically in the chapter on Results). While these zones certainly include small areas of atypical landforms and/or vegetation, the subdivision used here is probably adequate to explore the relation of pollen spectra to vegetation. If it were possible to characterize these zones in terms of pollen spectra, then it would be of interest to refine further the grouping and make more intensive studies of pollen spectra in smaller areas. The area under study spans the transition from grassland in the southwest to forest in the northeast, and provides a region suitably diverse and yet reasonably compact.

For the purposes of this study, atmospheric samples were collected for 1963 at meteorological stations in

Manitoba, and surficial limnic sediments were sampled from a number of suitable lakes in the forest-grassland transition area (Fig. 3). The main purpose of studying atmospheric samples is to assemble the evidence necessary to examine the proposition that differential decomposition of pollen takes place after it has settled out on lake bottoms. More specifically, the problem of Populus should be studied - "If Populus pollen is poorly represented in Holocene sediments . . . . then we should at least be aware of the probable extent of this gap in the fossil record" (Ritchie and Lichti-Federovich 1963 p. 96). By gaining knowledge of the assemblages of pollen types from both air and lake mud samples, particularly those involving substantial amounts of poplar pollen, it might prove possible to avoid too serious a misinterpretation of fossil spectra because of the erratic registration of poplar pollen.

II. METHODS AND PROCEDURES

A. Sampling Problems

Early sampling of atmospheric pollen and spores in North America was directed towards the detection and measurement of allergy types, and the unmodified Durham sampler (Wodehouse 1945, Durham 1946) had been adopted throughout the continent. However, this gravity sampler has shortcomings, which have been reviewed recently by Gregory (1961) in a general consideration of samplers and sampling problems. He offers data from wind tunnel studies to support his conclusion that an automatic, volumetric trap of the type designed by Hirst (1952) is the most efficient within the limits of practicability. A Hirst Spore Trap was used in a study related to the present investigation, to examine the spora of one season at Winnipeg (Ritchie and Lichti-Federovich 1963). However, the Hirst and Durham samplers are unsuitable for an extensive survey of the type proposed here, since they require daily attention. Furthermore, Hirst Traps could not be used concurrently at many stations because of the considerable capital expense involved and the need for a continuous source of electrical power.

The desideratum is a device which collects a cumulative sample for one season with minimum cost and operation. The open dish type, which has been used by Hesselman (1919), Lüdi and Vareschi (1936), and others, is considered to be a simple method of collecting efficiently samples of pollen through natural aerial sedimentation (cf. Faegri and Iversen 1950 p. 34). Its only limitation is that it must be covered during rain to avoid overflow and loss of spora. Unfortunately, this introduces another source of loss, as it excludes from the sample those spora removed from the atmosphere by rain. Leopold (1962) has suggested that the standard rain gauge can be used as a sampler to include the spora removed by rain, but her preliminary data indicate that its efficiency at other times is questionable.

As a compromise, an open dish type was used for this investigation, placed inside a standard weather screen (Fig. 2)

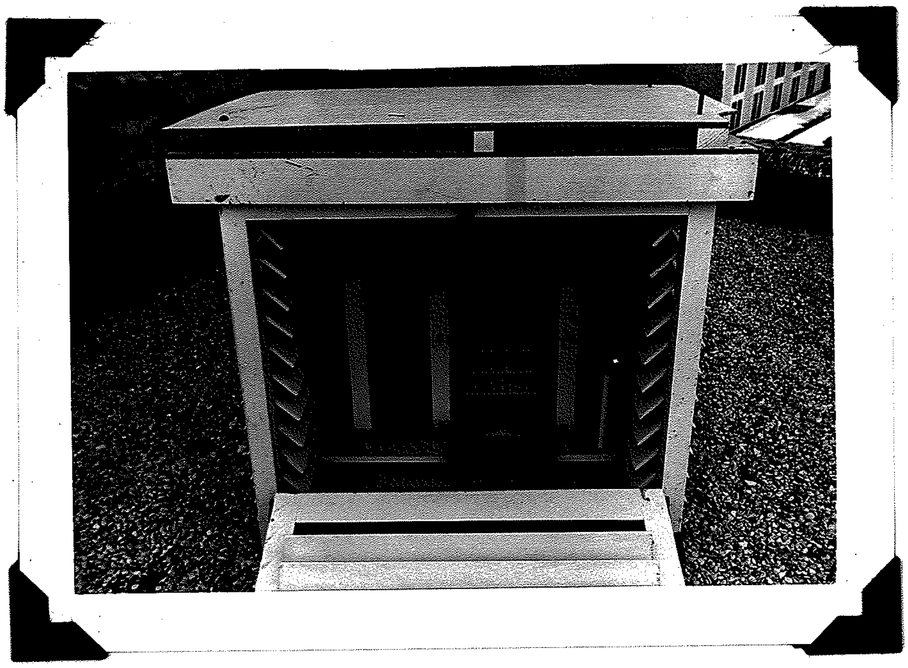


Fig. 2. A view of an open Stevenson Weather Screen, showing the position of the Petri dish sunk in a plywood board on the base.

To test its efficiency, such a sampler was set up alongside a Hirst Spore Trap on the roof of the Buller Biological Laboratories, during the season of 1962. The results are summarized in Table 1. They show reasonable consistency in the proportions of the main pollen types between the two samplers, and suggest that the open dish in a weather screen

TABLE 1

The main pollen types, expressed as percentages of the sum of all types recorded, in samples from a Hirst Spore Trap and a Weather Screen Petri dish, for the year 1962

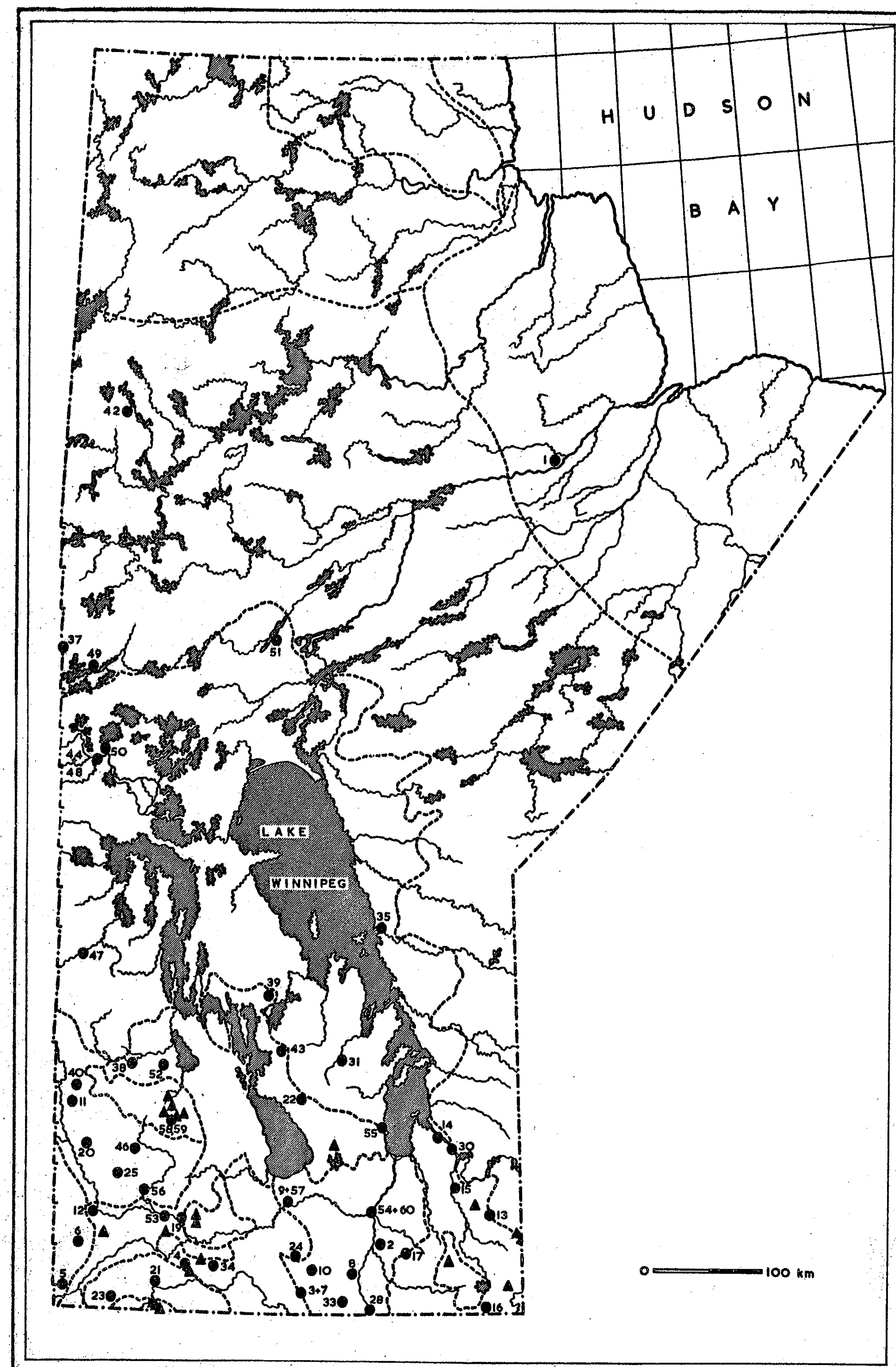
	Hirst	Petri dish		Hirst	Petri dish
Picea	1.7	2.4	Alnus	4.2	3.4
Pinus	13.6	15.7	Corylus	0.2	0.5
Betula	4.6	7.0	Salix	1.9	1.7
Populus	29.1	27.7	Shrub Total	6.4	5.6
Quercus	3.0	4.1	Gramineae	7.3	8.5
Ulmus	7.0	10.3	Cheno-Amar.	2.1	2.0
Fraxinus	1.5	2.0	Ambrosieae	7.7	4.7
Acer	4.7	4.9	Artemisia	3.2	2.8
Total AP	65.6	74.1	Total NAP	27.4	19.7

might be sufficiently accurate for an extensive survey of the kind proposed here.

Also, in 1962, Petri dishes were placed in weather screens at 54 Meteorological Stations in Manitoba. (This, and the 1963 study, were made possible by the co-operation of the Regional Meteorologist for Manitoba). The 1962 project served to explore the feasibility of such an investigation, and the results are not used in this thesis.

For the 1963 season, a 9 cm Petri dish containing 25 ml glycerine was placed in each Weather Screen at 58 Meteorological Stations in Manitoba, (Fig. 3; Table 2). Two drops of dilute mercuric chloride were added to the glycerine to inhibit fungal and bacterial activity. Each dish was placed in a circular hole, 9.4 cm in diameter, cut into a piece of 5-plywood 1.9 cm thick and 18 x 18 cm in size. This was attached to the base of the Weather Screen so that the Petri dish rested on the bottom piece (Fig. 2). The purpose of the plywood board was to reduce the edge effect of the dish, which has been shown to cause differential sedimentation at high wind speeds (Gregory 1961).

The limitations of this sampler are as follows: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16

TABLE 2

A list of the locations of atmospheric and top sediment* samples, grouped according to zonal type.

Zonal Type	Sample Stations	Reference Number	Long.	Lat.
Ia	Bird	1	94°13'	56°30'
	Lynn Lake	42	101°02'	56°51'
Ib	Flin Flon	37	101°45'	54°45'
	Cranberry Portage	49	101°23'	54°36'
	Wabowden	51	98°38'	54°52'
	Guy Hill	50	101°05'	53°58'
	The Pas	44	101°15'	53°50'
	The Pas	48	101°15'	53°50'
	Berens River	35	97°01'	52°21'
	Hodgson	31	97°34'	51°13'
	Clear Lake	58	99°57'	50°44'
	Pine Falls	14	96°15'	50°34'
II	Great Falls	30	96°01'	50°28'
	Seven Sisters	15	96°01'	50°07'
	Catherine Lake*	70	99°52'	50°41'
	Moon Lake*	71	100°03'	50°53'
	E Lake*	72	99°39'	50°43'
	F Lake*	73	99°57'	50°44'
	R Lake*	74	99°39'	50°43'
	Moose Lake*	75	95°19'	49°12'
	Julius Bog*	76	96°13'	50°00'
	Inglis	40	101°15'	50°57'
	Russell	11	101°17'	50°46'
	Birtle	20	101°02'	50°25'
	Strathclair	46	100°23'	50°24'
III	Hamiota	25	100°36'	50°11'
	Rivers	56	100°14'	50°02'
	Baldur	34	99°14'	49°23'
	Peace Lake*	77	100°03'	49°01'
	Bower Lake*	78	100°04'	49°04'
	Max Lake*	79	100°09'	49°04'
	Portage-la-Prairie	9	98°17'	49°58'
	Winnipeg	60	97°08'	49°49'
IVa	Winnipeg	54	97°13'	49°54'
	Roland	10	97°57'	49°27'
	Morris	8	97°27'	49°21'
	Emerson	28	97°12'	49°00'

TABLE 2 cont'd

Zonal Type	Sample Stations	Reference Number	Long.	Lat.
IVb	Portage-la-Prairie	57	98°17'	49°52'
	Niverville	2	97°04'	49°36'
	Steinbach	17	96°41'	49°32'
	Altona	33	97°33'	49°07'
V	Swan River	47	101°15'	52°06'
	Gilbert Plains	38	100°29'	51°09'
	Dauphin	52	100°03'	51°09'
	Gypsumville	39	98°37'	51°47'
	Moosehorn	43	98°25'	51°18'
	Brandon	53	99°57'	49°51'
	Virden	12	100°55'	49°52'
	North Shoal Lake*	80	97°38'	50°29'
	Oak Lake*	81	100°45'	49°40'
VI	Reston	6	101°05'	49°32'
	Pierson	5	101°15'	49°11'
	Boissevain	21	100°03'	49°14'
	Goodlands	23	100°36'	49°06'
VII	Marchand Lake*	82	96°23'	49°26'
VIII	Wet Lake*	83	99°35'	49°50'
Boundary Stations				
I-II	Rennie	13	95°34'	49°53'
	Falcon Lake*	84	95°15'	49°41'
II-V	Eriksdale	22	98°07'	50°52'
	Gimli	44	97°00'	50°38'
	McCreary	59	99°37'	50°42'
II-VII	Sprague	16	95°37'	49°05'
III-IV	Graysville	24	98°09'	49°30'
	Morden	3	98°06'	49°10'
	Morden	7	98°06'	49°10'
III-V	Lake Clementi*	85	99°56'	49°43'
	V Lake*	86	99°17'	49°24'
	W. Lake*	87	99°41'	49°31'
III-VI	Ninette	4	99°37'	49°24'
	Pelican Lake*	88	99°35'	49°20'
V-VIII	Camp Shilo	19	99°37'	49°49'

1) Pollen removed from the air by rain is not recorded, unless it happens to be re-floated.

2) The efficiency declines in calm or scarcely moving air. However, a survey of wind-speed data for several stations in Manitoba showed that the incidence of calm or almost calm periods is extremely low. Thus it appears to be a reasonable supposition that there is an adequate circulation of air inside the screen - this assumption is also shared by the meteorologists of course, whose temperature and relative humidity instruments are placed inside the Weather Screens.

3) The locations of meteorological stations are invariably associated with human settlements, and the influence of disturbed and planted elements in the flora is likely to be present in varying degrees. On the other hand, by regulation, the immediate precincts of the weather stations must be open, cleared of arboreal vegetation, so that direct local effects might be somewhat reduced in pollen spectra.

The dishes were placed in the screens several weeks before the earliest expected flowering of local plants and removed after the latest autumn flowering ceased. In practice, these studies, and the earlier work of Walton and Dudley

(1940, 1947), indicate that sampling need not be started before mid-March nor extended beyond mid-November. At the end of the season the glycerine and contents were washed with distilled water into plastic bottles and returned to the laboratory for analysis.

Top sediments from 19 lakes (locations shown on Fig. 3 and in Table 2) were sampled by one of the following two methods:

a) The upper meter of sediment was taken from a number of lakes, either through late winter ice or from a boat, using a piston sampler designed according to Livingstone (1955) with modifications suggested by Rowley and Dahl (1955). Only the top sample was used for the present investigation.

b) In other lakes, particularly those deeper than 10 m, a weighted cup sampler (designed after Welch 1948) was employed to draw up about 30 ml of sediment. Six samples were taken from approximately the center of each lake basin and mixed together thoroughly before processing.

The choice of lakes was governed by their accessibility and by the time available for this study. Several large areas in southern Manitoba lack entirely permanent water bodies.

B. Laboratory Methods

Atmospheric samples. Each suspension of pollen in glycerine with water was brought to a fixed volume (100 ml) by the addition of 95% ethyl alcohol. This was used for dilution to overcome the tendency of vesiculate coniferous pollen to float on the surface even after prolonged centrifugation at high speed. After thorough mixing, 10 ml aliquots were taken from each sample and processed in the following way:

1. Centrifuge (in all cases, 3000 rpm for 5 minutes) and decant; suspend the residue in 10 ml of cold hydrofluoric acid (50%) for 24 hours. This removes siliceous material.

2. Centrifuge and decant. Add 10 ml of glacial acetic acid and mix thoroughly.

3. Centrifuge and decant. Add 10 ml of acetolysis mixture (9 parts acetic anhydride to 1 part concentrated sulphuric acid) and place in a water bath at 100° C for 5 minutes. This removes cellulose, and while it is not entirely necessary for atmospheric samples, it was included so that the pollen could be compared with reference material which is prepared by acetolysis.

4. Centrifuge and decant. Wash in distilled water. Centrifuge and decant completely. Add 0.025 ml glycerine with safranin, mix thoroughly, place on a microscope slide and apply a coverslip.

This procedure is used for all contemporary and sub-fossil samples in the Paleoecology Laboratory of the University of Manitoba, and it is based on the recommendations of Faegri and Iversen (1950) and Brown (1960).

Top sediment samples. The above procedure was used for limnic sediment samples, after they had been boiled for 10 minutes in 5% potassium hydroxide to deflocculate the colloids.

C. Recording of Data

Identification and counting of pollen was accomplished with a compound light microscope at 600 magnifications, with a X 1425 oil immersion objective for critical examination. All pollen and spores of Tracheophyta were recorded. For each sample, counting was stopped when the pollen sum (total pollen and spores minus pollen types of primarily aquatic plants) reached 1000. A total of 71 samples was recorded.

The absolute numbers of pollen grains in sediment samples are a function of the rate of sedimentation, and of course statistical methods can not be used to analyse the variation of the data. However, the atmospheric samples yield absolute numbers of pollen types, since they are derived from the pollen rain of a single season collected in a standard volume of glycerine and processed in standard volumes of liquid. To provide a more objective assessment of the degree of similarity between the spectra from individual stations than is possible by direct inspection of the data, correlation coefficients were calculated for the 52 atmospheric stations, considering only the 16 main pollen types. The correlation coefficient of each station with all of the others was calculated from the following formula:

$$r = \frac{S\ (x - \bar{x})\ (y - \bar{y})}{S\sqrt{(x - x)^2\ (y - y)^2}}$$

correlation coefficient

The data were punched on to cards for a Fortran programme, and computed by an IBM 1620 digital computer. The results are presented in the Appendix and will be referred to at the appropriate point in the text.

III. RESULTS

A. Zonal Types

As intimated in the Introduction, the study area has been divided into general landform-vegetation regions, distinguished by the physiography and dominant vegetation type. These broad, geographical zones form the schematic outline for the arrangement and presentation of the results. For each zone, an account will be given of the pollen spectra recorded, after a brief statement of the characteristic landforms and vegetation.

Zone Ia. Main Boreal Forest - Lowlands type

The only station here, at Bird, is in the Gillam Section of the Lowlands, as designated by Ritchie (1962), and the following description pertains only to that section. The area lacks almost entirely relief, characterized by extensive, flat marine and glacial clays capped by peat mantles of varying depths. Deeper peats (approximately 1 m) bear an open *Picea mariana*-*Sphagnum* bog; shallower peats have continuous fen communities characterized by *Larix laricina* and *Betula glandulosa* with prominent sedge and hypnoid moss ground vegetation. Fragmentary alluvial deposits are occupied by seral communities of shrubs (chiefly *Salix* and *Alnus*) and trees (*Populus tremuloides*, *P. balsamifera* and *Picea glauca*).

The atmospheric pollen spectrum for Bird (Appendix, Table 1) is quite distinctive (cf. correlation coefficients in Appendix, Table 21) showing considerable representation of those types characteristic of the lowlands vegetation - *Betula*, *Larix*, *Alnus*, Cyperaceae and *Sphagnum*.

Zone Ib. Main Boreal Forest - Uplands type

This is an upland region, dominated by patternless glacial drift plains to the north and east and bedrock controlled relief in the southwest and extreme southeast (Ritchie 1962 and Weir, 1960). The characteristic vegetation of undisturbed sites is a closed spruce forest, dominated by *Picea mariana*. Bottomlands and alluvium have mixed forest types with *Picea glauca*, *Abies balsamea* (rare in the northern part), *Populus tremuloides* and *P. balsamifera*. The majority of upland sites bear secondary communities as the result of fire and felling, with *Salix*, *Alnus*, *Betula papyrifera*, *Populus tremuloides* and *Pinus banksiana* being the chief seral dominants. Pine also dominates open communities on bedrock ridges and sand plains; this is especially common in the Lynn Lake and Flin Flon regions.

The pollen spectra reflect this disturbed, northern boreal character of the zone, with the high values for conifer pollen showing a preponderance of *Pinus*. Alder, birch and lesser amounts of poplar comprise the remainder of the woody types. The proportion of non-arboreal types is small. With the exception of a few boundary stations (Rennie and McCreary in particular) and the Pine Falls Stations, the correlation coefficients between these Ib stations and all others are low or negative.

Zone II. Southern (Mixed) Boreal Forest

The greater part of this region - the modified Pre-Cambrian plains to the east and north of Lake Winnipeg and the modified till plain of the Interlake area - is a lowland plain with slight relief. Both areas have extensive lacustrine deposits from Glacial Lake Agassiz. Included in this region, although they are topographically somewhat different, are the Riding Mountain, Duck Mountain and Porcupine Mountain uplands. Data are available from only the Riding Mountain and as its vegetation is very similar to that of the area as a whole, they are included here.

The typical vegetation of mesic sites lacking recent disturbance is a closed mixed forest, dominated by Picea glauca, P. mariana, Populus balsamifera, with lesser amounts of Abies balsamea and Betula papyrifera (Rowe 1956, Manitoba Forest Resources Inventory Reports 1-6, 1956). Pinus banksiana, Populus tremuloides and Betula papyrifera are the main secondary dominants. Local peat bogs, particularly common on the lacustrine clays between bedrock ridges along the east side of Lake Winnipeg, bear a black spruce muskeg vegetation.

The summary tables in the Manitoba Forest Resources Inventory Reports indicate that the most abundant tree species of this area, in order of total relative volume, are Populus tremuloides, Picea glauca, P. mariana and Pinus banksiana. The atmospheric pollen spectra (Appendix, Table 2) show a general conformity with this gross forest composition, being dominated by poplar, pine and spruce. Birch is probably under-represented in the atmospheric spectra because of its low pollen production in 1963. The sediment spectra show low poplar values and are characterized by pine, birch, spruce and alder. Referring to the table of correlation coefficients (Appendix, Table 21), stations 5-14 show reasonably high positive correlations within the group. However, they also show high correlations with stations from the Deciduous Forest on Uplands region. The probable explanation is that conifers, particularly spruce, have been planted throughout the settled part of Manitoba and their contribution to the pollen spectra of deciduous forest regions is responsible for the partial resemblance between these spectra and those from mixed boreal forest areas.

Zone III. Deciduous Forest on Uplands

This zone is discontinuous, consisting of several discrete upland areas (Fig. 3). Of these, the Turtle Mountain and Pembina Hills are Cretaceous uplands with glacial drift and undulating topography. The Tiger Hills and the Newdale Till Plain are regions of terminal and recessional moraine with knob and kettle topography prevalent in the former and undulating boulder till plains in the latter. (The Lower Assiniboine Delta has not been mapped separately in Fig. 3, because there were no pollen data available from this area).

Upland sites are covered by closed deciduous forests, dominated by *Populus tremuloides*, *Betula papyrifera* and *Quercus macrocarpa* (Moir and Potter, 1961, Lowe in Ellis and Shafer 1940). *Ulmus americana*, *Fraxinus pennsylvanica* and *Acer negundo* form local stands on bottomland soils and alluvium.

The atmospheric pollen spectra for Zone III (Appendix, Table 4) show two notable discrepancies from what might be expected and from the sediment sample spectra. The first is the low relative amount of birch and oak, due to poor pollen production and dispersal caused by cold and wet weather at the time of anthesis. The second is the relatively high proportion of herb pollen, originating in all probability from the cultivated lands which often surround these forested uplands. The correlation coefficients (Appendix, Table 21) indicate a high correlation between all Zone III stations except No. 15, at Baldur. This station is located in a region where there is a greater proportion of cultivated and disturbed land than elsewhere in Zone III. Stations 15-21 show high positive correlations with stations 35-37 of the Aspen Parkland region, and this illustrates the predictable point that the effects of clearing and agriculture reduce the distinguishing features of the pollen spectra of certain areas. Considering both the atmospheric and sediment samples in Zone III, the dominant pollen types are Populus (absent or grossly under-represented in sediments), Quercus and Betula. This conclusion is corroborated by the results of the pilot study of atmospheric pollen for 1962, at which time the weather was favourable at anthesis of the deciduous trees, giving considerably higher relative values for birch and oak.

Zone IV. Deciduous Forest on Alluvial and Lacustrine Deposits

Zone IV is represented by a single area, the Red River valley, a flat lowland plain of Glacial Lake Agassiz sediments with very local uplands. The 10 stations within this region have been separated into two groups: IVa, which includes the stations on or very near river systems, where alluvium is the prevalent substratum; and IVb, which groups together those located on the interfluvial plains of lacustrine clay.

The alluvial deposits of IVa are occupied by mixed deciduous forest communities, related floristically to the Deciduous Forest Region of adjacent Minnesota, dominated by

Ulmus americana, _Populus tremuloides_, _P. deltoides_, _Fraxinus pennsylvanica_, _Quercus macrocarpa_, _Acer negundo_ and locally _Tilia americana_. The pollen spectra from IVa (Appendix, Table 6) are characterized by deciduous trees, particularly poplar, oak, elm, ash and maple, a distinctive pollen assemblage found in no other zone. The local high relative values of non-arboreal pollen types register the proximity of agricultural land. Low positive or negative correlations are shown between these spectra and all others recorded, with the exception of a few stations in the Aspen Parkland. Such a finding is not incompatible with the pattern of regional vegetation, since there are areas to be found of predominantly aspen parkland vegetation with local stands of riparian forest, typical of Zone IVa.

The interfluvial plains (Zone IVb) are less readily defined in terms of natural vegetation. The influence of fire and grazing in pre-settlement times and that of post-settlement clearing, drainage and cultivation, has produced an array of highly artificial communities (Bird 1961). Residual poorly drained areas are occupied by marsh vegetation, related to the tall grass prairie of central Minnesota (cf. Bird 1961). Better drained sites in relatively undisturbed areas, particularly in the northern part of the plain, bear secondary stands of aspen poplar with oak on coarser soils. The pollen spectra accord reasonably well with this vegetation of semi-natural and artificial communities; the chief element is non-arboreal, with high relative values for cereal grasses, native grasses and adventives (particularly Chenopodiaceae-Amaranthaceae and Ambrosiae). This region has the greatest amount of weedy members of Ambrosiae and the representation of these types in the spectra is higher here than in any other zone. The four spectra from this zone are only moderately correlated with each other (Appendix, Table 21), but they are poorly correlated (low positive or negative values) with the spectra from other zones with the exception of the Aspen Parkland zone, as might be expected.

Zone V. Aspen Parkland on Modified Till Plains and Lacustrine Deposits

The zone consists of the southern interlake region of high lime tills variably modified by Glacial Lake Agassiz; the modified till plain between Lake Manitoba and the northwest escarpment; and the Glacial Lake Souris Plain with lacustrine deposits, gently rolling till plains and local dune systems. The typical vegetation consists of aspen dominated forests on moderately drained clay soils; oak-aspen forest on coarser soils, particularly beach ridges; mixed prairie communities on treeless mesic and xeric sites; and marsh, dominated by rushes, grasses and sedges in swales and depressions. A large portion of the land in this zone is under cultivation.

The atmospheric pollen spectra show about 40% of arboreal types, dominated by *Populus*. The Oak Lake spectrum is reasonably concordant with this, resembling closely the mean values from atmospheric samples calculated after excluding poplar from the pollen sum. The high pine proportion in the N. Shoal Lake sample is presumed to be due to the proximity of the site to the boreal forest region and to a relatively low total pollen rain for this station. Poplar, the main anemophilous plant of the southern interlake region, is under-represented because of poor preservation. The correlation coefficients within this zone are all positive and moderately high, but, as pointed out above, several of the Zone V spectra are correlated closely with spectra from Zones III and IV.

Zone VI. Grasslands on Till Plains

This zone consists of two discrete areas, the Waskada Till plain and the Oxbow Till plain (cf. Ellis and Shafer 1940 p. 17). These are gently undulating plains of till and ground moraine with local depressions harbouring saline soils and pothole lakes. According to Ellis and Shafer (l. cit.) and Bird (1961), the natural vegetation is grassland, related to the mixed prairie association of adjacent Saskatchewan and Alberta (cf. Coupland 1950 and 1961). Because of the widespread influences of pre-settlement and post-settlement disturbance, it is scarcely possible to delimit precisely the grassland area from contiguous Aspen Parkland. The mesic sites which bear vegetation types used to characterize zone groupings are invariably cultivated, while lake margin and alluvial sites are often relatively undisturbed but might bear vegetation markedly different from the potential communities of well drained situations. For example, local stands of poplar are found in Zone VI around small kettle lakes (so-called potholes) of till plains; oak occurs occasionally with poplar in stands on coarse, generally gravelly soils; and *Ulmus*, *Fraxinus* and *Acer* are present discontinuously on alluvium. Thus, this zone is distinguishable in Manitoba from Zone V by the shift in the relative amount of grassland as compared with forest vegetation.

The pollen spectra reflect this change, from a primarily arboreal assemblage in V to a herb-dominated type in VI. The exclusion of poplar from the pollen sum (Table 3) yields an average spectrum for these grassland stations with about 75% non-arboreal pollen types. The grassland stations show high positive correlation coefficients with each other, and low or negative correlation with stations from boreal regions. The occasionally high positive correlations with stations outside the grassland region, in the aspen parkland or deciduous forest on upland zones, are explicable in terms of the relatively extensive areas of treeless (under crops) land in the vicinity of some of these stations.

Zone VII. Sand Upland with Pine Forests

This isolated highland is a glacio-fluvial deposit of siliceous sands and gravels, locally overlying calcareous tills. The dominant forest tree is *Pinus banksiana*, forming mainly secondary stands in a region with a history of frequent forest fires.

Only one station was available - the top sediment sample from a small pond near the Marchand Forest Ranger Station. The pollen spectrum is overwhelmingly dominated by *Pinus* (Appendix, Table 10).

Zone VIII. Spruce Parkland on the Upper Assiniboine Delta

This area of outwash and lacustrine material, formed as a delta of the Assiniboine River in Glacial Lake Agassiz, constitutes an isolated region of distinctive landform and vegetation. The substratum is composed of coarse, medium and fine textured materials, locally modified by wind into dunes.

The level topography with medium sands in the western part is occupied by mixed prairie. The rolling dune areas have a spruce parkland vegetation, with clumps of *Picea glauca* surrounded by a lichen-prostrate shrub herb community (dominated by *Juniperus horizontalis* and *Arctostaphylos uva-ursi*); in hollows and more frequently towards the escarpment, groves of poplar and oak prevail.

The only sample available comes from a small lake on the north side of the area, where the coarse soils are replaced by heavier clays of the adjacent till plain. Here *Betula* is associated with *Picea*, *Populus* and *Quercus*. Also, in the vicinity are large plantations of *Pinus*.

The pollen spectrum shows a *Picea*-*Pinus*-*Betula*-*Quercus* arboreal assemblage, with high values of native grasses and *Artemisia*. A spectrum from a mosspolster, collected in this area, near Melbourne, and reported by West (1961), shows higher values for spruce. The fact that the polster sample was collected from a spruce community accounts for this difference in spruce values.

B. General Zonal Summary

For purposes of summing up the above data, the mean values for each of the sixteen main pollen types have been calculated for each zone. In addition, the values for the atmospheric samples have been recalculated as percentages of the pollen sum after subtraction of the poplar total. This facilitates a direct comparison of the atmospheric and sediment spectra, since it is apparent that the gross under-representation of poplar in sediments is related to poor preservation.

Inspection of Table 3 shows a fair agreement within zones between the mean spectra for sediment and atmospheric-without-poplar samples. A closer similarity would be unlikely for the following reasons:

a) The weather stations and lakes are located within a zone independently of each other, and seldom occur in close proximity.

b) As mentioned earlier, the data for atmospheric samples are for only one season and express variation related to particular weather conditions, whereas in sediment samples the seasonal effects are diminished, as they contain pollen of several years. In particular, it was observed that the flowering period of oak and birch at low latitudes coincided with periods of cool and wet weather. It is likely that this accounts for the low relative values of these types in Zones III and IV.

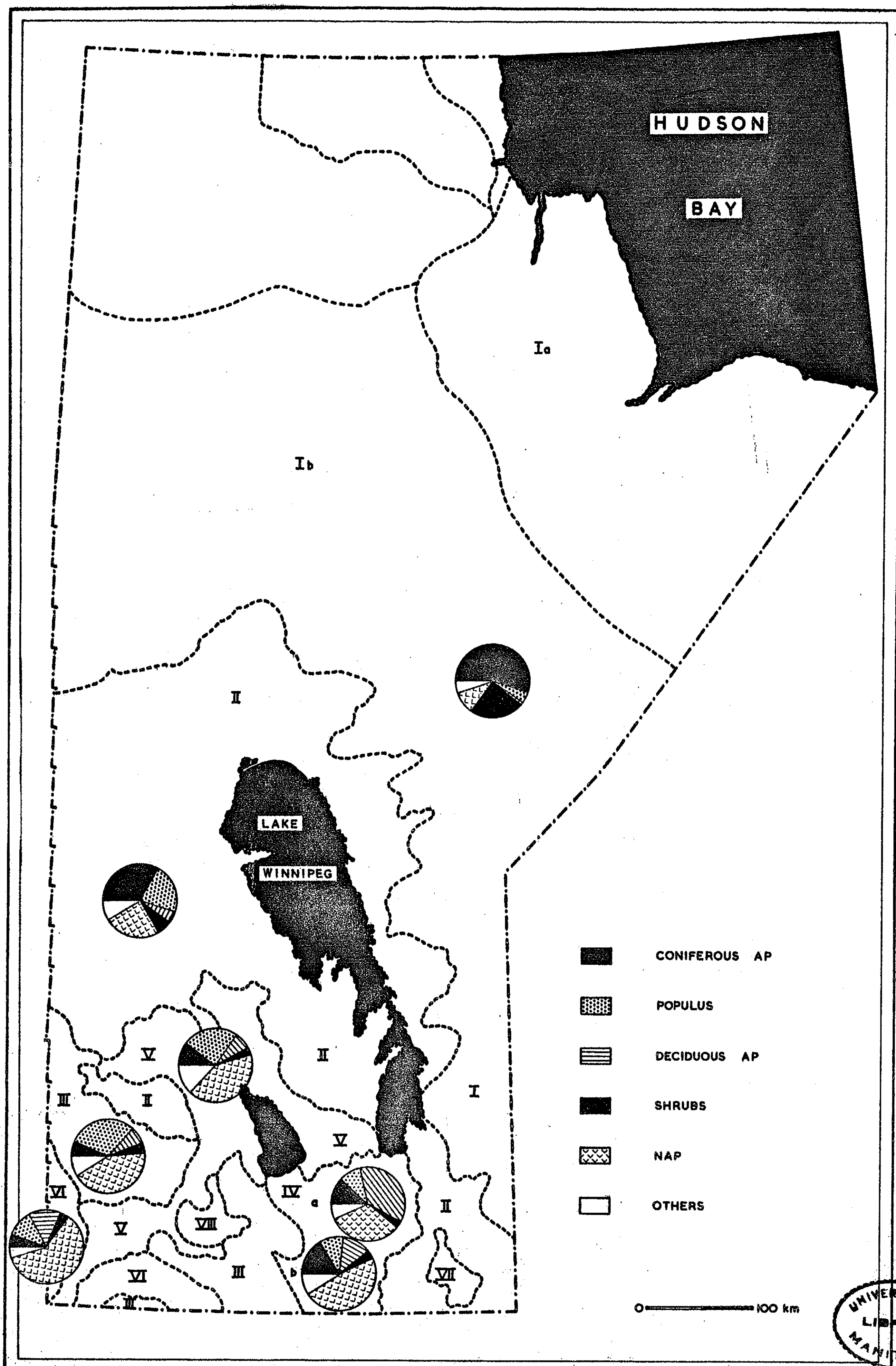
The zonal means for atmospheric spectra have also been summarized diagrammatically, showing their relative spatial position in Manitoba (Fig. 4).

TABLE 3

Mean percentage of main pollen types

	Ia,Ib Main Boreal Forest			II Southern Boreal Forest			III Deciduous Forest on Uplands			IVa,IVb Deciduous Forest on Lowlands				V Aspen Parkland			VI Grassland	
	Atmospheric	Atmospheric	Atmospheric -Populus	Atmospheric	Atmospheric - Populus	Top sediment	Atmospheric	Atmospheric - Populus	Top sediment	Atmospheric	Atmospheric - Populus	Atmospheric	Atmospheric - Populus	Atmospheric	Atmospheric - Populus	Top sediment	Atmospheric	Atmospheric - Populus
Picea	3.8	7.9	8.4	6.2	8.0	16.9	0.6	1.0	2.1	1.3	1.5	1.0	1.1	1.1	1.4	6.4	0.5	0.5
Pinus	8.4	45.4	48.4	19.6	25.0	22.2	4.9	8.2	7.8	9.0	9.9	14.15	15.71	7.6	10.0	29.1	3.0	3.4
Betula	13.4	11.3	12.1	7.2	9.2	22.9	0.7	1.2	21.0	1.6	1.8	1.1	1.2	1.6	2.2	2.5	2.1	2.3
Populus	0.9	6.7	-	21.7	-	1.1	30.0	-	1.1	9.1	-	10.0	-	23.9	-	0.7	11.5	-
Quercus	0	0	0	0.6	0.7	0.9	1.2	2.0	14.3	11.0	12.1	3.1	3.4	1.6	2.0	1.5	1.5	1.7
Ulmus	0	0.1	0.1	1.7	2.1	0.5	1.1	1.9	1.3	8.2	9.0	1.4	1.5	0.6	0.8	0.4	2.1	2.3
Fraxinus	0	0.6	0.7	1.4	1.8	0.5	1.2	2.0	1.9	6.3	6.9	3.9	4.3	0.8	1.1	0	4.6	5.2
Acer	0	0	0	1.5	1.9	.01	3.6	6.0	0.5	11.3	12.4	4.2	4.6	4.6	6.0	0.2	6.1	6.9
Alnus	35.7	15.9	16.9	2.0	2.5	12.3	0.4	0.6	2.4	0.3	0.3	0.4	0.4	0.3	0.4	2.7	0.2	0.2
Corylus	0.1	0.6	0.6	0.5	0.6	1.6	0.4	0.7	3.1	0.5	0.6	0.8	0.9	0.3	0.4	0.5	0.2	0.3
Salix	5.0	2.6	2.8	4.0	5.0	2.1	4.3	7.2	3.2	2.0	2.1	2.7	3.0	2.8	3.7	1.7	3.6	4.0
Gramineae	18.1	4.0	4.3	20.2	25.8	3.7	26.6	44.0	11.1	13.5	14.8	25.5	28.3	28.0	36.7	20.6	31.7	35.8
Cheno-Amar.	1.2	0.7	0.8	2.0	2.6	1.8	7.5	12.5	4.2	9.1	10.0	10.5	11.7	6.4	8.4	12.5	12.6	14.2
Ambrosieae	0.2	0.2	0.3	0.9	1.2	1.5	2.4	4.0	3.8	8.2	9.0	8.8	9.8	2.1	2.8	3.7	6.2	7.0
Artemisia	1.6	1.0	1.1	1.9	2.4	7.7	5.7	9.6	16.1	2.2	2.4	3.5	3.9	5.5	7.2	11.1	9.8	11.1
Tree Total	29.9	72.3	77.2	60.2	49.2	66.3	43.6	19.4	50.3	57.9	53.7	38.7	31.9	41.8	23.4	40.8	31.2	22.3
Shrub Total	43.1	19.3	2.1	7.0	9.0	15.9	5.7	8.1	8.8	3.3	3.6	4.3	3.7	3.5	4.6	4.9	3.3	3.7
Herb Total	27.0	8.4	9.0	32.7	41.7	18.0	50.8	72.6	40.9	38.8	42.6	57.1	63.4	54.7	72.0	54.3	67.2	75.9

Fig. 4. A map of Manitoba showing the approximate boundaries of the landform-vegetation zones: Ia - Main Boreal Forest on Lowlands; Ib - Main Boreal Forest on Uplands; II - Southern Boreal Forest on Uplands; III - Deciduous Forest on Uplands; IV - Deciduous Forest on Lowlands and Alluvium; V - Aspen Parkland on Till Plains and Lacustrine Deposits; VI - Grasslands on Till Plains; VII - Pine Forest on Sandy Uplands; VIII - Spruce Parkland on Upper Assiniboine Delta. The circular diagrams show the average proportions of the pollen types designated in the legend.


HUDSON
BAY
Ia
Ib
II
LAKE
WINNIPEG
V
III
VI
IV
VIII
VII
CONIFEROUS AP
POPULUS
DECIDUOUS AP
SHRUBS
NAP
OTHERS
0 100 km

C. Boundary Cases

The data from a further 14 stations have been excluded from the above regions because they are located at or near the transition between two or more adjacent zones. They are referred to as Boundary Cases.

If the original proposition is valid, that land-form-vegetation zones can be characterized in terms of pollen spectra, then it is likely that these boundary cases will yield pollen spectra intermediate between the zonal types.

Between Zones I and II

While the two stations included here, at Rennie and Falcon Lake (Appendix, Table 12, 13), lie on the boundary between Zones Ib and II, their spectra are closer to the mean values of I. The atmospheric spectrum from Rennie shows a high positive correlation coefficient with the Lynn Lake and Cranberry Portage spectra of Zone I, and the Pine Falls spectrum of Zone II (Appendix, Table 21). These stations, like Rennie, are situated in areas of

Pre-Cambrian outcropping bedrock dominated by pine forests. The sediment sample from Falcon Lake shows relatively more *Betula* than the Rennie spectrum, but, as suggested above and later in the thesis, the contribution of birch to the 1963 pollen rain was impaired by unfavourable weather.

Between Zones II and V

The three stations in this category, at Gimli, Eriksdale and McCreary, lie near the boundary between the Southern Mixed Boreal Forest and the Aspen Parkland.

The Gimli and McCreary spectra (Appendix, Table 14) fit conformably an intermediate position, with high pine values confering a stronger resemblance to the Zone II than Zone V mean spectrum. Both stations have high positive correlation coefficients with stations in Zone II and V, and generally low or negative correlations with other stations (Appendix, Table 21). The Eriksdale spectrum shows moderately high positive correlations (0.30 to 0.90) with Zone II stations, as well as several from Zone III, and from Zone V. Due to the local preponderance of *Populus* groves at Eriksdale, this spectrum is entirely dominated by poplar.

Between Zones II and VII

A single spectrum, from Sprague (Appendix, Table 15), falls more or less between the mean values for Zone II atmospheric stations and the single sediment spectrum from Zone VII, although, of course, a direct comparison of atmospheric and sediment spectra has certain limitations, as discussed elsewhere in the thesis.

Between Zones III and IV

The atmospheric spectra for these stations (Appendix, Table 16) are not entirely intermediate between the mean spectrum types for Zones III and IV, but there is a strong resemblance between the Graysville station and Morden No. 7 and the mean spectrum for Zone IVb. Morden No. 13 is located at the experimental farm, which probably accounts for the relatively higher values for cereal grasses and Chenopodiineae. The correlation coefficients show generally negative values between these stations and boreal spectra (Zones I and II), and no clear grouping of coefficients with stations from Zones III to VI can be established.

Between Zones III and V

These three spectra (Appendix, Table 17) from lake sediments in the Tiger and Brandon Hills, fit conformably into the Zone III group of sediment spectra, except that they have relatively higher values for non-arboreal types. In general, it is difficult to establish a characteristic Aspen Parkland spectrum from sediment samples alone.

Between Zones III and VI

These stations, Ninette and Pelican Lake, are in close proximity. The sediment sample from Pelican Lake (Appendix, Table 18) is very similar to the mean spectrum type for Zone III sediments. The Ninette spectrum correlates poorly with those of Zones I, II, III, IVb, V and VI, and reasonably well with some of the IVa stations. Thus, it does not express its intermediate geographical position, but this is not unexpected, since Ninette is situated in oak-aspen gallerie forests on the north side of a large glacial channel, with cultivation and aspen parkland on the adjacent uplands.

Between Zones V and VIII

The only station here, at Camp Shilo, lies on the west side of the Upper Assiniboine Delta. To its immediate west is an extensive area of prairie; to the east and north extend large plantations of jackpine and scots pine; further east is the open spruce parkland area; and the regions to the north and south bear aspen parkland. All these different elements contribute to the spectrum (Appendix, Table 20) with a preponderance of Artemisia and Pinus. The correlation coefficients show high positive values among Zone I, II and V stations, reflecting the heterogeneous, somewhat artificial conditions of the vegetation.

The main discrepancies between the Camp Shilo spectrum and the sediment sample from Zone VIII (Appendix, Table 11) are explicable in terms of the depressed birch production in 1963 and the proximity of the Camp Shilo station to continuous pine plantations.

TABLE 4

A comparison of the relative amounts of the main pollen types in petri dish samples from successive years. The sampler was located on the roof of the Buller Biological Laboratories during the seasons 1962 and 1963.

	1962	1963		1962	1963
Picea	2.4	2.2	Alnus	3.4	0.3
Pinus	15.7	18.2	Corylus	0.5	1.3
Betula	7.0	1.8	Salix	1.7	4.2
Populus	27.7	8.2	Total shrub	5.6	6.6
Quercus	4.1	12.0	Gramineae	8.5	8.2
Ulmus	10.3	9.5	Cheno-Amar.	2.0	6.1
Fraxinus	2.0	6.7	Ambrosieae	4.7	5.9
Acer	4.9	7.0	Artemisia	2.8	1.8
Total AP	74.1	65.6	Total NAP	19.7	27.8

D. Seasonal Variation

Before attempting to draw conclusions from the above results, some attention should be given to one of the main sources of variability in atmospheric pollen spectra. As other palynologists have observed (e.g. Hyde 1952), and as earlier studies at Winnipeg have shown (Ritchie and Lichti-Federovich 1963), meteorological conditions during floral development and at the time of anthesis may produce significant fluctuations in pollen production and dispersal. Thus the seasonal total pollen count of one or more types may vary from year to year, and of course the relative amounts of the other components of a spectrum are altered. Hyde (l. cit.) suggests that a minimum of five successive seasons are required to derive an accurate average spectrum.

On the basis of previous studies (in 1962 and earlier, Ritchie and Lichti-Federovich 1963) it was suspected that the relative amounts of Betula and Populus in 1963, particularly at stations in the Deciduous Forest and Aspen Parkland zones, were inordinately low. More specifically, a comparison of the relative amounts of the main components of the Winnipeg spectrum for 1962 and 1963 (Table 4) shows a discrepancy for the poplar and birch values, suggesting that the 1963 season was less favourable for these species, or that the conditions governing floral development during the previous summer, had been adverse. An inspection of the meteorological records for the periods of birch and poplar anthesis substantiates the former suggestion; the times in question were characterized by low temperatures (below freezing in the case of poplar) with high precipitation. A similar phenomenon has been demonstrated for *Quercus* during the 1962 season (Ritchie and Lichti-Federovich 1963).

It is likely, of course, that these seasonal irregularities in pollen production are insignificant for spectra from surficial sediment samples, since annual increments of pollen for not less than 10 years are represented in 1 ml of sediment.

IV. CONCLUSIONS

The most direct evaluation of the above results is obtained by applying them to a re-examination of the fundamental problems of pollen analysis in this area. This concluding section will be arranged accordingly, in an attempt to answer the three critical questions:

1. Is there a relation between vegetation-landform and pollen spectra?

The most general comparison of the pollen spectra with change in vegetation is between grassland and forested areas, and in fact there is strong evidence for a notable shift in the preponderance of the main pollen types from grassland to forest. Grassland spectra, corrected for poplar (Table 3), are characterized by the following composite totals: herbs 60-70%, composed chiefly of Gramineae, Chenopodiineae, _Artemisia_ and Ambrosieae; shrubs, about 5%, and trees 20-25%. The chief elements in the arboreal sum are accountable in terms of long-distance dispersal (_Pinus_), plantings (_Acer_, _Fraxinus_, _Picea_, _Pinus_) and local riparian forests (_Fraxinus_, _Ulmus_ and _Populus_). By contrast, continuously forested landscapes are characterized by spectra with less than 40% herbs and more than 50% tree types.

Considering the more specific differences between the major landform-vegetation zones, and with due regard to the several sources of variability discussed above, an inspection of the data reveals generally positive results.

It is likely that an extension of this study over several years, with a greater number of stations, would yield less variable data showing more marked differences between zones, and be adequate for a more critical statistical analysis. However, the results here indicate that sufficient data are at hand from atmospheric samples and that future efforts should be concentrated on surficial limnic sediment samples. The atmospheric studies reported here, together with earlier investigations (Ritchie and Lichti-Federovich 1963), have served the purpose of clarifying the nature and extent of the problem of poorly preserved pollen types in west-central Canada. It is concluded that only Populus of the more important types is subject to such excessive decomposition that its representation in contemporary spectra, if present at all, is entirely unreliable. The role of poplar in Holocene landscapes can be suggested only from macrofossil records (cf. Ritchie and de Vries 1964) or from the plant assemblages indicated by certain pollen spectra. In particular, it would be reasonable to suggest for west-central Canada that the vegetation yielding pollen spectra dominated by birch and oak with less than 50% herbaceous types probably contained substantial amounts of Populus. These three trees are associated consistently in deciduous forests on upland sites in Manitoba today. It would be more difficult, in the absence of macrofossils, to distinguish between the fossil spectra from mixed spruce-poplar forests and pure spruce forests.

The problem of poplar pollen preservation would merit further study, particularly since certain highly laminated late-glacial limnic sediments show relatively high Populus values (e.g. Ritchie and de Vries 1964, Wright et al. 1963). A comparison of poplar pollen frequencies between surficial sediments from shallow and deep, thermally stratified lakes might be a useful beginning to such an investigation.

2. What is the relevance of the findings to the interpretation of Holocene pollen spectra?

It might be useful to state briefly the limitations involved in applying knowledge of present-day phenomena to the reconstruction of the past.

a) The basis of paleoecological reasoning - uniformitarianism - is only partly tenable. It assumes (Ager 1963, p. 33) that particular species have remained largely unchanged in their ecological amplitudes, so that knowledge of contemporary forms can be applied directly to reconstruct past environments. There is an apparent conceptual paradox involved here, since uniformitarianism in its strict application precludes the possibility of such well known evolutionary processes as ecotypic differentiation. However, it is likely that for Quaternary floras, the migratory responses of plants to environmental change have outweighed their adaptive responses.

b) As others have suggested (e.g. Davis 1963), it is possible that there are no modern communities analagous with certain late- or post-glacial assemblages.

However, the present investigation now permits a direct comparison of contemporary spectra with those from late-Pleistocene deposits. Apart from a report by Martin and Gray (1962), working in southwestern United States, this approach has not been attempted in North America. There are now available for west-central Canada the first Holocene pollen data, reported by Ritchie (1964), who has reported four distinctive pollen assemblages in chronological sequence, from limnic sediments in the Riding Mountain area. It is possible to examine his preliminary interpretations in the light of the results of this thesis.

His uppermost pollen zone (IV) has remained constant to the present day, so there is no problem about the reconstruction of vegetation. The pollen zone III, shows the following assemblage (main types only): *Picea* 1-2%, *Pinus* 15-20%, *Betula* 20-40%, *Quercus* 5-10%, *Alnus* 1-4%, *Corylus* 4-6%, *Salix* 1-5%, and 30-40% non-arboreal types. In Table 3 of this thesis, the spectrum which fits this assemblage most conformably is that for the Deciduous Forest on Uplands. Thus Ritchie's (1964 p. 191) interpretation of the type III spectra in terms of "a deciduous forest dominated by *Populus*, *Quercus* and *Betula*" is strengthened by the results obtained here.

Pollen zone II from the Riding Mountain deposits is characterized by "a preponderance of non-arboreal pollen types, making up about two thirds of the pollen sum, represented mainly by *Artemisia*, Chenopodiaceae-Amaranthaceae, Ambrosiae and Gramineae". The main tree types are recorded as *Picea* (1%), *Pinus* (5-15%), *Betula* (2-4%). The shrubs are *Alnus* (1-2%), *Corylus* (1-3%) and *Salix* (2-4%). The closest similarity to this spectrum type in Table 3 is the atmospheric-minus-poplar, from grassland areas. This again corroborates to some extent the conclusion that the spectra of zone II represent grassland vegetation.

Regarding the lowest pollen zone (I) from the Riding Mountain, also found in a late-glacial deposit from the Missouri Coteau, (Ritchie and de Vries 1964), and with slight variations, from southern Minnesota (Wright *et al*. 1963), there is no closely similar spectrum among those reported in this thesis. These late-glacial spectra are dominated by *Picea* with considerable quantities (10-30%) of *Artemisia*. It is not entirely surprising that no regional analogue can be found at present, since the potentially dominant spruce element of the boreal forest has been reduced by disturbance factors (fire and felling) with a concomitant increase in secondary dominants, particularly *Betula*, *Populus* and *Pinus*. The effects of forest fires in the boreal regions of Manitoba (Ritchie 1958) and elsewhere in western boreal North America (Lutz 1956) has been to increase the frequency of these secondary dominants and reduce the abundance of spruce.

3. How is the pollen sum determined?

The total of pollen types to be included for calculating percentages has been the subject of a continuing debate (cf. Faegri and Iversen 1950). Recently, Wright and Patten (1963) have suggested that pollen diagrams might show curves calculated from two or more pollen sums, so that the reader might choose whatever curve he considers most relevant or accurate. However, as the adoption of this proposal will entail considerable publication costs, it is likely that many diagrams will continue to be based on one pollen sum.

One group, the Cyperaceae, is included by some workers and excluded by others. The former contend that while Cyperaceae are primarily aquatic or lake-margin plants, some are found on uplands, and they should be included if one seeks a complete registration of upland vegetation. The results reported here (Appendix, Tables 1-20) are relevant to this discussion. In those areas where upland Cyperaceae occur most frequently - the Aspen Parkland and Grassland Zones - the proportion of pollen is consistently low (1-2%) in atmospheric samples, as it is in forested areas where there are fewer upland forms. However, sediment samples in the Aspen Parkland and Grassland Zones have 4 to 15% Cyperaceae pollen, suggesting strongly that the majority of Cyperaceae are derived from local aquatic or lake-margin communities. A notable exception to this generalization is the Bird station, where the Cyperaceae pollen amounts to about 25% of the total. However, this accords with the composition of the regional vegetation, in which there is a large element of lowland bog and fen communities with abundant Cyperaceae. Thus, it is concluded that Cyperaceae pollen should be recorded but excluded from the pollen sum in Holocene studies from west-central Canada.

SUMMARY

The aim of this study is to characterize the main landform-vegetation zones in the forest-grassland transition region of Manitoba. This is necessary to provide a basis for the objective interpretation of pollen spectra from Holocene deposits in the area.

On the basis of existing published information, the southern two thirds of Manitoba was divided into large units, each distinuished in terms of the prevalent landform and plant communities.

A simple sampler for atmospheric pollen was devised, after initial testing with an automatic, volumetric spore trap. Atmospheric samples for the 1963 season were collected at each meteorological station in the province, a total of 52 stations yielding suitable samples for analysis.

Surficial sediments were taken from 19 lakes scattered across the grassland-forest transition. For each atmospheric and sediment sample a pollen sum of 1000 was recorded.

The results from the 71 samples confirm the initial hypothesis that the landform-vegetation zones can be distinguished in terms of pollen spectra. Conclusive evidence

is offered to support the earlier suggestion that poplar pollen is largely destroyed in sediments. Discrepancies caused by planting and disturbance and by seasonal fluctuations in pollen production related to weather conditions, are assessed. The atmospheric sample data are further analysed by calculating correlation coefficients between the spectra from each station.

The significance of the results is illustrated by a brief comparison of Holocene spectra with the general spectrum types derived from this study.

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APPENDIX

TABLE 1

Complete data of pollen percentages from the atmospheric samples of the Main Boreal Forest Region (Zones Ia and Ib)

	Stations			
	1	42	37	49
Picea	3.8	12.0	4.7	6.9
Pinus	8.4	46.6	22.5	67.1
Abies		0.1		0.3
Larix	3.3		0.8	0.5
Betula	13.4	10.3	16.1	7.5
Populus	0.9	2.5	12.2	4.4
Ulmus			0.1	0.2
Fraxinus			1.9	
Juglans	0.1		0.1	
Total AP	29.9	71.5	58.4	86.9
Alnus	35.7	19.0	23.7	4.9
Corylus	0.1	0.6	1.1	
Salix	5.0	3.5	3.2	1.1
Myrica	0.9	0.3		
Juniperus-Thuja	1.4	0.1	0.3	0.2
Total shrub	43.1	23.5	28.3	6.2
Gramineae (n)	17.3	3.1	3.9	2.9
Gramineae (c)	0.8	0.2	1.4	0.6
Cheno-Amar.	1.2	0.1	1.2	0.9
Ambrosieae	0.2	0.1	0.7	
Artemisia	1.6	0.3	2.2	0.5
Liguliflorae				0.2
Tubuliflorae	0.9			
Plantago		0.1	0.2	0.2
Thalictrum	0.2		0.1	
Rumex	0.1			
Leguminosae	0.1	0.1		0.5
Cruciferae	0.1		0.7	0.1
Caprifoliaceae			0.7	
Epilobium		0.1		
Rosaceae	0.1			
Urticaceae	1.0	0.3	2.0	0.6
Equisetum	3.1	0.5	0.1	0.4
Lycopodium ann.	0.1			
L. clavatum	0.2		0.1	
L. complanatum		0.1		
Total NAP	27.0	5.0	13.3	6.9
Cyperaceae	25.3	2.9	1.1	1.7
Ericaceae	1.0	0.1		
Sphagnum	25.4	9.0	1.6	0.4

TABLE 2

Complete data of pollen percentages from the atmospheric samples of the Southern (Mixed) Boreal Forest Region (Zone II)

	Stations									
	51	50	44	48	35	31	58	14	30	15
Picea	14.6	2.9	2.2	4.9	7.2	2.3	10.5	10.2	3.8	3.5
Pinus	23.3	13.8	9.6	15.7	26.2	12.6	9.2	41.5	21.6	26.2
Abies								0.1		
Larix		0.5		0.3	0.4	0.1		0.3	0.1	
Betula	6.1	9.4	4.4	5.2	10.9	3.5	7.7	8.5	8.1	4.0
Populus	30.0	19.6	14.7	21.3	16.4	15.6	41.9	11.4	23.8	8.0
Quercus						0.2	0.5	2.4	0.9	3.0
Ulmus		0.2	0.3	9.0			0.2	4.3	1.0	2.8
Fraxinus	0.2		0.1				0.3	1.0	7.9	10.4
Acer	0.3	0.2	0.5	8.3	0.6	1.4		2.9	0.4	
Juglans				0.1						
Total AP	74.5	46.6	31.8	64.8	61.7	35.7	70.3	82.6	67.6	57.9
Alnus	5.4	3.4	1.4	1.6	1.5	1.1	1.1	0.6	2.1	0.9
Corylus		0.9	0.6	0.2		0.4	1.7	0.3	0.5	0.2
Salix	3.4	8.8	3.9	3.0	6.4	4.4	1.7	2.4	4.0	2.8
Myrica		0.5	0.6	0.1	0.4		0.1			
Juniperus-Thuja		2.6	0.5	0.1		0.1	0.3	0.3	0.3	0.7
Viburnum			0.1							
Ribes								0.1		
Total shrub	8.8	16.2	7.1	5.0	8.3	6.0	4.9	3.7	6.9	4.6
Gramineae (n)	6.9	11.6	13.3	5.5	14.2	31.6	9.3	4.1	11.0	6.6
Gramineae (c)	4.4	5.0	29.0	12.2	5.7	9.1	1.5	5.1	2.5	7.5
Cheno-Amar.	1.6	2.5	1.8	3.5	0.8	2.7	1.8	1.2	2.4	2.8
Ambrosiae		0.2		0.2	0.2	1.4	0.9	0.6	3.3	3.4
Artemisia	0.6	3.5	2.6	1.6	1.1	3.0	2.9	0.3	1.4	2.7
Liguliflorae	0.5	0.6	2.0	0.4		0.4	0.2	0.2	0.1	
Tubuliflorae	0.1	1.8	0.6		0.9	0.1	1.6	0.1	0.1	0.7
Plantago	0.6	0.4	0.4	0.6	0.1	1.0	0.2	0.3	0.3	0.4
Thalictrum		0.1			0.1		0.2			0.1
Rumex		0.1		0.3	2.2	0.8			0.1	0.2
Galium		0.1								
Leguminosae	0.2	4.3	7.1	0.2		1.8	0.1	0.4	1.0	9.2
Umbelliferae					1.3					
Cruciferae	0.1	0.2	2.1	0.1	0.1	0.3	0.1		0.2	0.6
Caryophyllaceae		0.1								
Labiatae		0.2	0.1							
Epilobium	0.1									
Rosaceae	0.1		0.1			0.4	0.3		0.1	0.3
Cannabinaceae			0.1	0.2			0.1		0.1	
Urticaceae	0.6	5.6	1.4	4.9	3.1	5.6	4.9	1.3	2.6	2.9
Equisetum	0.9	0.8	0.5	0.5	0.1	0.1	0.7	0.1	0.2	0.1
Lycopodium clavatum		0.1			0.1					
L. complanatum									0.1	
Total NAP	16.7	37.2	61.1	30.2	30.0	58.3	24.8	13.7	25.5	37.5
Cyperaceae	2.7	9.3	4.0	3.3	1.6	1.6	1.3	0.5	1.6	1.6
Sphagnum	1.2	2.4	0.3	1.0	1.2	0.5	0.5	0.2	0.6	

TABLE 3

Complete data of pollen percentages from the top sediment samples of the Southern (Mixed) Boreal Forest Region (Zone II)

	Stations						
	70	71	72	73	74	75	76
Picea	24.6	26.6	10.4	18.6	16.7	10.4	10.9
Pinus	14.4	12.2	23.2	9.4	24.1	31.6	40.1
Abies					0.2	0.2	0.9
Larix	1.6	0.6		0.3	0.5	0.6	1.7
Betula	19.4	14.6	26.1	32.2	26.0	25.6	14.5
Populus	1.6	2.0		1.0	1.6	1.6	
Quercus	0.6	0.2	1.6	1.3	1.4	1.0	0.2
Ulmus	0.4		0.4	0.3	0.2	2.0	
Fraxinus	0.4	1.0	0.1		0.8	1.2	
Acer	0.4	0.4					
Juglans						0.4	0.8
Carpinus-Ostrya						0.6	
Tilia						0.2	0.2
Total AP	63.4	57.6	61.8	63.1	71.5	75.4	69.3
Alnus	5.8	12.0	22.1	15.0	12.4	8.4	10.4
Corylus	2.6	0.8	3.9	1.0	1.3	0.4	1.1
Salix	2.8	3.0	1.0	2.8	2.4	1.8	0.8
Juniperus-Thuja					0.2		
Viburnum		0.2					
Lonicera							0.2
Total shrub	11.2	16.0	27.0	18.8	16.3	10.6	12.5
Gramineae (n)	5.6	5.8	2.6	2.3	3.1	4.6	1.3
Gramineae (c)		1.2	0.7	0.5			0.2
Cheno-Amar.	1.4	4.4	0.7	3.0	0.8	0.8	1.1
Ambrosiae	0.8	1.6	1.6	1.3	1.1	2.2	1.9
Artemisia	9.2	9.8	5.1	8.2	5.7	5.2	10.6
Liguliflorae				0.3			
Tubuliflorae	3.2	1.4	0.4	2.5	0.8	0.6	1.7
Thalictrum	0.6	0.4					
Rumex		0.2					
Leguminosae	0.2						
Umbelliferae	0.2		0.1		0.2		0.2
Cruciferae		0.2					
Epilobium		0.2					
Rosaceae					0.2	0.4	0.2
Ranunculaceae	0.6	1.0				0.2	0.2
Urticaceae					0.3		
Equisetum	3.6	0.2					0.4
Lycopodium clavatum							0.4
Total NAP	25.4	26.4	11.2	18.1	12.2	14.0	18.2
Cyperaceae	2.3	1.8	0.8	0.6		0.7	0.4
Ericaceae			0.2				35.5
Sphagnum		0.1				0.3	many
Polypodiaceae		0.3					

TABLE 4

Complete data of pollen percentages from the atmospheric samples of the Upland Deciduous Forest Region (Zone III)

	Stations						
	40	11	20	46	25	56	34
Picea	1.3	0.1	0.2	0.9	0.3	1.0	0.6
Pinus	5.9	1.6	3.3	7.7	0.8	12.5	2.8
Betula	0.4	2.0	0.7	1.1	0.2	0.7	0.1
Populus	28.0	30.3	35.8	31.3	57.2	20.6	6.9
Quercus	0.2			1.6	0.1	2.9	3.6
Ulmus	5.7	0.3		0.2	0.3	0.3	1.2
Fraxinus	0.9	0.5	0.6	0.1	0.2	0.6	5.6
Acer	2.5	11.7	0.5	1.4	4.4	2.0	2.9
Juglans		0.1					0.1
Total AP	44.9	46.6	41.1	44.3	63.5	40.6	23.8
Alnus	0.5	0.1		0.7	0.3	0.7	0.3
Corylus	0.7	0.3	0.3	0.7	0.1	0.6	0.2
Salix	3.9	3.6	4.6	8.8	2.5	4.1	2.9
Juniperus-Thuja	0.4	0.1		0.2	0.1	0.6	1.3
Symphoricarpos occ.			0.3				0.2
Cornus			0.2				
Elaeagnus		0.1					
Viburnum							0.1
Sambucus				0.1			
Syringa				0.1			
Total shrub	5.5	4.2	5.4	10.6	3.0	6.0	5.0
Gramineae (n)	11.8	9.8	24.2	8.7	10.5	11.4	10.3
Gramineae (c)	15.2	14.9	5.2	17.9	16.8	9.2	20.6
Cheno-Amar.	5.8	8.1	3.8	7.2	1.9	6.8	18.9
Ambrosiae	1.0	1.0	1.7	1.0	1.0	3.3	7.8
Artemisia	4.7	7.1	5.3	5.2	1.4	9.9	6.6
Liguliflorae	0.1	0.5	1.7	0.6	0.1	0.3	0.5
Tubuliflorae	0.2	1.2	2.3	0.4	0.3	0.6	0.5
Plantago	0.1	0.2	0.1			0.1	0.9
Thalictrum	0.1		0.2	0.4			0.2
Rumex	0.4	0.5	0.3	0.4	0.1		0.1
Leguminosae	1.3	2.1	0.6	0.7	0.3	7.9	1.4
Cruciferae	0.9	0.3	2.7		0.3	0.7	0.6
Labiatae						0.1	
Fagopyrum							0.1
Rosaceae	0.5	0.1	1.3	0.2			
Ranunculaceae			0.1				0.3
Urticaceae	6.6	2.3	3.2	1.5	0.3	1.0	0.8
Cannabinaceae						0.1	0.2
Equisetum	0.9	1.0	0.7	0.9	0.5	1.9	1.4
Lycopodium complanatum		0.1	0.1			0.1	
Total NAP	49.6	49.2	53.5	45.1	33.5	53.4	71.2
Cyperaceae	4.1	3.1	2.5	2.1	0.7	1.5	1.7
Sphagnum			0.1		0.1	0.4	0.1
Other Pteridophyta		0.1					

TABLE 5

Complete data of pollen percentages from the top sediment samples of the Upland Deciduous Forest Region (Zone III)

	Stations		
	77	78	79
Picea	2.2	1.7	2.4
Pinus	6.8	8.5	8.2
Betula	23.6	22.7	16.8
Populus	0.8	1.6	0.8
Quercus	15.2	12.8	14.8
Ulmus	0.8	2.0	1.2
Fraxinus	1.0	2.0	2.8
Acer	0.2	1.0	0.2
Juglans	0.4	0.3	
Total AP	51.0	52.6	47.2
Alnus	2.8	2.8	1.6
Corylus	2.2	3.7	3.4
Salix	2.8	3.2	3.6
Viburnum	0.2	0.2	
Total shrub	8.0	9.9	8.6
Gramineae (n)	7.4	11.2	14.4
Gramineae (c)	0.6	0.3	0.6
Cheno-Amar.	4.8	3.5	4.4
Ambrosiae	4.0	3.5	3.8
Artemisia	15.4	15.0	18.0
Liguliflorae		0.2	
Tubuliflorae	5.6	1.5	2.4
Thalictrum	0.4	0.8	
Rumex	0.2		
Leguminosae		0.3	
Liliaceae	0.4		
Rosaceae	0.8	0.2	0.2
Ranunculaceae	0.4	0.5	0.2
Urticaceae		0.3	
Cannabinaceae		0.2	
Equisetum	1.0		
Lycopodium complanatum			0.2
Total NAP	41.0	37.5	44.2
Cyperaceae	2.3	3.3	1.8
Polypodiaceae			0.1

TABLE 6

Complete data of pollen percentages from the atmospheric samples of the Lowland and Alluvial Deciduous Forest Region (Zones IVa and IVb)

	Stations									
	9	60	54	10	8	28	57	2	17	33
Picea	2.7	2.2	1.1	1.0	1.0		1.2	0.2	2.2	0.3
Pinus	7.4	18.2	10.6	6.7	8.9	2.0	10.6	4.6	28.9	12.5
Tsuga	0.1									
Betula	2.6	1.8	3.3	0.5	0.8	0.6	1.7	1.5	0.8	0.5
Populus	7.8	8.2	10.1	7.4	10.1	10.7	6.1	7.8	16.7	8.2
Quercus	8.1	12.0	10.4	4.1	1.5	30.0	6.1	3.2	2.0	1.1
Ulmus	19.3	9.5	3.9	2.7	7.6	6.1	1.4	0.8	2.5	0.8
Fraxinus	8.0	6.7	3.9	12.9	3.8	2.5	4.5	1.5	3.6	5.8
Acer	21.0	7.0	2.7	9.3	17.1	10.6	2.6	1.4	7.2	5.5
Juglans			0.1							0.2
Carpinus-Ostrya	0.1						0.1			
Tilia	0.4					0.1	0.2		0.3	0.1
Pterocarya	0.3									
AP Total	77.8	65.6	46.1	44.6	50.8	62.6	34.5	21.0	64.2	35.0
Alnus	0.3	0.3	0.4	0.3	0.1	0.2	0.5	0.5	0.3	0.1
Corylus	0.2	1.3	1.2		0.4		0.2	1.0	1.9	
Salix	0.9	4.2	2.8	0.9	2.0	0.9	4.3	2.0	2.8	1.6
Myrica		0.1						0.1		
Juniperus-Thuja	0.2	0.2	0.4		0.5	0.7	0.3	0.3	0.3	0.1
Symphoricarpos			0.1							
Viburnum	0.3	0.3								
Lonicera									0.3	
Cornus						0.1				
Sambucus	0.1	0.2	0.2						0.5	
Shrub Total	2.1	6.6	5.1	1.2	3.0	1.9	5.3	3.9	6.1	1.8
Gramineae (n)	6.9	3.8	12.7	6.3	3.9	2.0	22.5	11.2	7.9	7.1
Gramineae (c)	2.5	4.4	7.7	17.7	8.8	4.0	8.7	19.5	3.6	21.6
Cheno-Amar.	3.4	6.1	9.3	10.4	10.7	14.5	6.0	15.7	4.5	15.6
Ambrosieae	2.1	5.9	7.8	11.7	13.5	8.3	6.3	16.4	4.8	7.7
Artemisia	1.8	1.8	4.1	1.3	2.1	1.9	6.5	3.4	0.9	3.1
Liguliflorae		0.1	0.2	0.2	0.2			0.3	0.3	0.4
Tubuliflorae			0.7	0.2	0.5	0.2	0.1	1.4	0.4	0.6
Plantago	1.0	0.6	2.2		0.3	0.2	3.2	0.2	1.0	0.4
Thalictrum	0.1		0.1	0.1			0.6	0.2	0.1	
Rumex	0.1	0.4	0.3	0.3	1.2		0.1	1.2	0.1	1.2
Leguminosae	0.5	1.2	0.6	0.4	0.6	0.8	1.1	1.2	0.8	0.9
Umbelliferae						0.1			0.1	0.2
Cruciferae	0.2	0.4	0.8	0.2	1.9	0.6	0.7	0.9	0.3	2.9
Labiatae										0.1
Caryophyllaceae		0.1			0.1	0.3				
Rosaceae	0.1	0.2	0.2		0.5	0.1	0.7	0.5	1.6	0.2
Ranunculaceae	0.1		0.2		0.1	0.3	0.4		0.3	0.1
Polygonaceae pp.	0.1		0.2	0.1	0.4		0.1			0.2
Fagopyrum						0.1			0.2	0.1
Polygonum								0.3		
Cannabinaceae	0.1	0.2	0.1		0.2	0.1				
Urticaceae	1.0	2.0	1.2	4.8	1.0	1.5	2.2	2.1	1.9	0.7
Equisetum	0.1	0.6	0.2	0.5	0.2	0.4	1.0	0.6	0.9	
Lycopodium ann.						0.1				0.1
L. clavatum			0.2							
NAP Total	20.1	27.8	48.8	54.2	46.2	35.5	60.2	75.1	29.7	63.2

TABLE 7

Complete data of pollen percentages from the atmospheric samples of the Aspen Parkland Region (Zone V)

	Stations						
	47	38	52	39	43	53	12
Picea	2.5	1.1	0.7	2.1	0.6	0.3	0.2
Pinus	20.0	8.3	4.4	7.2	4.9	4.5	3.7
Betula	2.2	1.7	3.2	1.2	1.4	1.7	0.1
Populus	21.4	17.7	25.6	37.0	19.3	11.7	34.8
Quercus		0.5	2.9		0.4	3.3	3.8
Ulmus	2.0		1.0	0.1		0.3	0.6
Fraxinus	0.5	0.1	2.4	0.1	1.1	1.0	0.7
Acer	4.2	10.9	2.3		0.3	1.0	13.6
Juglans	0.1				0.1	0.1	0.1
Carpinus-Ostrya						0.1	
Total AP	52.9	40.3	42.5	47.7	28.1	24.0	57.6
Alnus	0.5	0.1	0.2	0.1	0.1	0.7	0.2
Corylus	0.1		0.5	0.3	0.1	0.7	0.2
Salix	0.7	4.6	3.2	3.2	2.6	3.5	1.7
Myrica			0.2	0.1			
Juniperus-Thuja		0.4	0.3				
Total shrub	1.3	5.1	4.4	3.7	2.8	4.9	2.1
Gramineae (n)	10.9	25.8	8.2	12.0	57.9	13.9	6.1
Gramineae (c)	11.5	15.2	8.8	2.0	2.1	10.0	11.6
Cheno-Amar.	10.0	2.1	5.5	2.2	1.4	16.2	7.2
Ambrosiae	0.3	0.8	3.5	0.6	0.7	5.5	3.4
Artemisia	2.9	2.1	13.3	0.3	2.7	11.0	6.2
Liguliflorae	0.5	0.3	2.3	0.2	0.1	0.1	0.4
Tubuliflorae		0.3	0.7	1.6	0.5	1.3	0.2
Plantago	0.6	0.1	0.1	0.2	0.1	0.3	0.1
Thalictrum						0.2	0.2
Rumex		0.3	0.1		0.1	0.2	0.3
Leguminosae	0.2	0.8	1.7	5.4	0.7	3.9	1.6
Umbelliferae	0.6					0.1	
Cruciferae	1.8	0.2	4.1	9.1	0.2	0.8	0.6
Labiatae				6.7	0.1		
Campanulaceae			0.1				
Polygonaceae	0.2	0.1	0.3				
Fagopyrum			0.3				
Rosaceae	0.4	0.1	0.4	6.8	0.1	0.1	
Ranunculaceae			0.1	0.2		0.2	
Cannabinaceae	0.1	0.1	0.3		0.1	0.1	0.1
Urticaceae	5.2	5.5	2.7	0.9	2.0	3.8	1.3
Equisetum	0.6	0.8	0.6	0.4	0.3	3.3	1.0
Total NAP	45.8	54.6	53.1	48.6	69.1	71.1	40.3
Cyperaceae	0.5		0.8	1.6	0.9	1.1	1.4
Sphagnum	0.8					0.3	0.2
Polypodiaceae							0.1

TABLE 8

Complete data of pollen percentages from the top sediment samples of the Aspen Parkland Region (Zone V)

	Stations	
	80	81
Picea	9.4	3.4
Pinus	45.8	12.4
Betula	3.8	1.2
Populus	1.2	0.2
Quercus	1.6	1.4
Ulmus	0.2	0.6
Acer	0.4	
Total AP	62.4	19.2
Alnus	1.8	3.6
Corylus	1.0	
Salix	2.2	1.2
Total shrub	5.0	4.8
Gramineae (n)	14.2	26.0
Gramineae (c)	0.4	1.0
Cheno-Amar.	7.2	17.8
Ambrosiae	1.0	6.4
Artemisia	5.8	16.4
Liguliflorae	0.2	0.6
Tubuliflorae	2.8	5.2
Plantago		0.2
Thalictrum		0.2
Umbelliferae		0.4
Rosaceae		0.6
Ranunculaceae	0.4	0.8
Cannabinaceae	0.4	0.4
Equisetum	0.2	
Total NAP	32.6	76.0
Cyperaceae	5.8	7.6

TABLE 9

Complete data of pollen percentages from the atmospheric samples of the Grassland Region (Zone VI)

	Stations			
	6	5	21	23
Picea	0.9	0.6	0.1	0.7
Pinus	3.7	5.3	5.1	5.0
Larix				0.1
Betula	0.3	0.1	0.1	0.4
Populus	11.4	5.8	3.6	6.0
Quercus	0.4	0.2	0.5	1.8
Ulmus	2.4	1.0	3.0	2.3
Fraxinus	15.1	1.0	13.9	1.7
Acer	9.8	24.6	2.6	1.6
Juglans		0.2		0.4
Larix				0.1
Total AP	44.0	38.8	28.9	20.0
Alnus		0.1	0.1	0.2
Corylus	0.6	0.1	0.1	
Salix	3.9	1.2	1.2	2.9
Juniperus-Thuja	0.9	0.7		0.5
Symphoricarpos occ.				0.1
Viburnum			0.1	0.1
Sambucus				0.8
Total shrub	5.4	2.1	1.5	4.6
Gramineae (n)	14.1	7.1	8.7	11.0
Gramineae (c)	13.9	16.0	38.4	14.6
Cheno-Amar.	7.0	13.0	6.8	18.4
Ambrosieae	2.5	6.0	5.4	7.6
Artemisia	4.6	9.5	3.5	9.0
Liguliflorae	0.1			1.5
Tubuliflorae	0.1	0.9	0.9	1.1
Plantago	0.1		0.3	0.1
Thalictrum	0.2			0.1
Rumex	0.4	0.5	0.5	0.7
Galium				
Leguminosae	4.4	1.6	0.9	3.4
Cruciferae	0.4	0.7	0.6	1.0
Caryophyllaceae			0.1	
Campanulaceae			0.1	
Malvaceae				0.1
Linum	0.1			
Rosaceae	0.3		0.1	0.7

TABLE 10

Complete data of pollen percentages from the top sediment sample of the Sandilands Region (Zone VII)

	Station 82
Picea	7.7
Pinus	65.4
Larix	2.3
Betula	2.9
Populus	0.4
Quercus	0.4
Fraxinus	0.2
Total AP	79.3
Alnus	2.7
Corylus	0.8
Salix	1.5
Total shrub	5.0
Gramineae (n)	5.2
Gramineae (c)	0.4
Cheno-Amar.	1.3
Ambrosiae	3.9
Artemisia	0.8
Tubuliflorae	0.4
Thalictrum	0.4
Ranunculaceae	0.4
Cannabinaceae	0.4
Equisetum	1.9
Lycopodium clavatum	0.3
L. lucidulum	0.1
L. complanatum	0.2
Total NAP	15.7
Cyperaceae	2.8
Sphagnum	0.1

TABLE 11

Complete data of pollen percentages from the top sediment sample of the Spruce Woods Region (Zone VIII)

	Station 83
Picea	4.0
Pinus	10.2
Betula	21.6
Populus	1.2
Quercus	4.0
Ulmus	0.8
Fraxinus	0.2
Acer	0.8
Juglans	0.2
Total AP	43.0
Alnus	4.2
Corylus	1.4
Salix	5.6
Viburnum	0.4
Total shrub	11.6
Gramineae (n)	11.2
Gramineae (c)	2.2
Cheno-Amar.	2.8
Ambrosiae	2.0
Artemisia	21.6
Tubuliflorae	3.0
Thalictrum	0.4
Ranunculaceae	0.4
Equisetum	1.8
Total NAP	45.4
Cyperaceae	3.8
Sphagnum	0.1
Polypodiaceae	0.1

TABLE 12

Complete data of the pollen percentages from the atmospheric sample of the Boundary Region between Zones I and II

	Station 13
Picea	3.7
Pinus	83.6
Abies	0.2
Betula	1.4
Populus	2.3
Quercus	0.4
Ulmus	0.1
Fraxinus	0.5
Juglans	0.1
Total AP	92.3
Alnus	1.5
Corylus	0.2
Salix	0.2
Juniperus-Thuja	0.6
Total shrub	2.5
Gramineae (n)	2.0
Gramineae (c)	0.8
Cheno-Amar.	0.3
Ambrosieae	1.1
Artemisia	0.3
Liguliflorae	0.1
Tubuliflorae	0.1
Plantago	0.2
Urticaceae	0.1
Equisetum	0.2
Total NAP	5.2
Cyperaceae	0.8

TABLE 13

Complete data of the pollen percentages from the top sediment sample of the Boundary Region between Zones I and II

	Station 84
Picea	13.4
Pinus	49.4
Abies	0.4
Betula	5.0
Populus	1.8
Quercus	2.0
Ulmus	0.2
Fraxinus	0.6
Acer	0.6
Total AP	73.4
Alnus	7.4
Salix	0.4
Total shrub	7.8
Gramineae (n)	4.6
Gramineae (c)	
Cheno-Amar.	2.2
Ambrosieae	2.6
Artemisia	3.2
Tubuliflorae	0.8
Umbelliferae	0.2
Rosaceae	0.6
Ranunculaceae	0.4
Urticaceae	0.2
Equisetum	3.0
Lycopodium clavatum	0.2
Total NAP	18.8
Cyperaceae	0.9
Other Pteridophyta	0.1

TABLE 14

Complete data of the pollen percentages from the atmospheric samples of the Boundary Region between Zones II and V

	Stations		
	22	55	59
Picea	0.4	3.9	2.2
Pinus	1.2	42.8	24.9
Larix		0.2	
Betula	1.1	3.8	12.8
Populus	72.5	6.2	12.0
Quercus	1.3	1.3	1.3
Ulmus	0.3	0.4	0.1
Fraxinus	0.3	1.3	0.1
Acer	9.1	0.5	0.2
Total AP	86.2	60.4	33.6
Alnus	0.4	1.4	18.6
Corylus	0.5	1.2	0.5
Salix	1.2	4.2	0.8
Juniperus-Thuja			0.1
Total shrub	2.1	6.8	20.0
Gramineae (n)	4.2	15.6	18.8
Gramineae (c)	0.8	3.4	1.9
Cheno-Amar.	3.4	2.9	1.6
Ambrosieae	0.4	2.8	0.6
Artemisia	0.6	1.6	1.4
Liguliflorae	0.3	0.4	0.2
Tubuliflorae	0.3	0.6	0.1
Plantago	0.1	1.9	0.7
Thalictrum	0.1		
Rumex	0.2		0.3
Leguminosae	0.4	0.7	0.3
Cruciferae	0.1	0.8	
Umbelliferae			0.2
Polygonaceae		0.1	
Rosaceae	0.2		
Urticaceae	0.3	1.1	
Equisetum	0.3	0.9	0.3
Total NAP	11.7	32.8	26.4
Cyperaceae	0.4	2.5	0.2
Sphagnum		0.5	0.3
Polypodiaceae			0.5

TABLE 15

Complete data of the pollen percentages from the atmospheric sample of the Boundary Region between Zones II and VII

	Station 16
Picea	3.0
Pinus	32.2
Betula	1.3
Populus	2.6
Quercus	1.4
Ulmus	0.5
Fraxinus	16.9
Acer	7.0
Total AP	64.9
Alnus	0.7
Corylus	
Salix	2.7
Juniperus-Thuja	0.4
Total shrub	3.8
Gramineae (n)	10.6
Gramineae (c)	3.0
Cheno-Amar.	4.0
Ambrosieae	3.4
Artemisia	2.1
Liguliflorae	0.1
Tubuliflorae	0.2
Plantago	1.6
Thalictrum	0.2
Rumex	0.3
Leguminosae	0.1
Cruciferae	0.5
Umbelliferae	0.1
Cannabinaceae	0.2
Urticaceae	4.3
Equisetum	0.6
Total NAP	31.3
Cyperaceae	2.3
Sphagnum	0.2

TABLE 16

Complete data of the pollen percentages from the atmospheric samples of the Boundary Region between Zones III and IV

	Stations		
	24	3	7
Picea	0.9	0.3	0.1
Pinus	4.8	1.3	7.3
Betula	0.9	0.9	0.4
Populus	7.7	4.7	7.0
Quercus	1.5	1.0	5.1
Ulmus	13.2	3.0	2.7
Fraxinus	7.4	6.4	11.9
Acer	13.7	0.8	8.9
Juglans		0.1	
Carpinus-Ostrya		0.2	
Tilia	0.3		
Total AP	50.4	18.7	43.4
Alnus	0.7	0.1	0.1
Corylus	0.8	0.2	
Salix	1.9	1.3	1.2
Juniperus-Thuja		0.5	
Elaeagnus	0.1		
Oleaceae			0.1
Total shrub	3.5	2.1	1.4
Gramineae (n)	2.8	4.5	4.5
Gramineae (c)	10.7	36.9	24.0
Cheno-Amar.	11.1	24.1	15.0
Ambrosieae	9.6	5.3	4.7
Artemisia	5.1	4.0	3.1
Liguliflorae	0.3	0.3	0.1
Tubuliflorae	0.3	0.5	0.4
Plantago	0.2	0.6	0.6
Thalictrum		0.1	
Rumex	0.2	0.3	0.5
Leguminosae	0.5	0.5	0.4
Cruciferae	0.5	0.1	0.3
Fagopyrum		0.1	0.2
Polygonum		0.1	
Rosaceae	0.5		
Ranunculaceae	0.5	0.1	
Cannabinaceae		0.4	0.3
Urticaceae	2.8	0.7	0.6
Equisetum	1.0	0.6	0.5

TABLE 17

Complete data of the pollen percentages from the top sediment samples of the Boundary Region between the Zones III and V

	Stations		
	85	86	87
Picea	5.0	4.2	3.8
Pinus	11.0	15.4	16.8
Betula	5.8	3.6	4.6
Populus	0.8		0.2
Quercus	6.6	32.4	15.6
Ulmus	0.4	0.6	0.4
Fraxinus	0.6	0.6	
Acer		0.4	0.2
Juglans	0.2		0.2
Tilia			0.2
Total AP	30.4	57.2	42.0
Alnus	3.6	2.4	4.0
Corylus	0.8	0.4	0.6
Salix	2.8	0.6	3.6
Elaeagnus		0.8	
Total shrub	7.2	4.2	8.2
Gramineae (n)	15.8	1.6	15.2
Gramineae (c)	4.0	3.4	0.2
Cheno-Amar.	12.8	14.4	3.2
Ambrosieae	5.8	8.4	2.4
Artemisia	19.8	8.4	24.0
Liguliflorae		0.2	
Tubuliflorae	1.6	0.6	3.6
Plantago			0.2
Thalictrum	0.4	0.2	0.4
Leguminosae		0.2	
Cruciferae	0.2	0.2	
Liliaceae	0.2		
Caryophyllaceae		0.2	
Rosaceae	1.0	0.6	0.2
Ranunculaceae	0.2		0.2
Equisetum	0.4	0.2	0.2
Lycopodium complanatum	0.2		
Total NAP	62.4	38.6	49.8
Cyperaceae		0.9	4.6
Other Pteridophyta	0.2		

TABLE 18

Complete data of the pollen percentages from the atmospheric sample of the Boundary Region between Zones III and VI

	Station 4
Picea	1.0
Pinus	16.7
Betula	0.7
Populus	9.1
Quercus	35.0
Ulmus	1.0
Fraxinus	7.4
Acer	5.9
Total AP	76.8
Alnus	0.2
Corylus	2.2
Salix	1.1
Juniperus-Thuja	0.2
Total shrub	3.7
Gramineae (n)	3.1
Gramineae (c)	4.6
Cheno-Amar.	3.1
Ambrosieae	1.1
Artemisia	3.1
Tubuliflorae	0.6
Plantago	0.4
Thalictrum	0.1
Rumex	0.2
Leguminosae	0.6
Rosaceae	0.1
Cannabinaceae	1.0
Urticaceae	0.4
Equisetum	1.1
Total NAP	19.5
Cyperaceae	0.9

TABLE 19

Complete data of the pollen percentages from the top sediment sample of the Boundary Region between Zones III and VI

	Station 88
Picea	5.8
Pinus	11.6
Betula	7.0
Populus	1.8
Quercus	13.4
Ulmus	1.2
Fraxinus	1.4
Acer	0.6
Juglans	0.4
Carpinus-Ostrya	0.2
Total AP	43.4
Alnus	2.4
Corylus	0.4
Salix	2.4
Total shrub	5.2
Gramineae (n)	12.6
Gramineae (c)	0.4
Cheno-Amar.	9.2
Ambrosieae	7.0
Artemisia	16.6
Tubuliflorae	2.2
Thalictrum	0.4
Rosaceae	0.4
Ranunculaceae	1.0
Cannabinaceae	0.2
Urticaceae	0.8
Equisetum	0.6
Total NAP	51.4
Cyperaceae	3.4
Polypodiaceae	0.1

TABLE 20

Complete data of the pollen percentages from the atmospheric sample of the Boundary Region between Zones V and VIII

	Station 19
Picea	1.2
Pinus	34.7
Betula	1.0
Populus	7.1
Quercus	1.5
Ulmus	0.2
Fraxinus	0.7
Acer	0.1
Total AP	46.5
Alnus	0.3
Corylus	0.5
Salix	1.4
Juniperus-Thuja	1.8
Total shrub	4.0
Gramineae (n)	4.7
Gramineae (c)	12.7
Cheno-Amar.	5.5
Ambrosieae	1.2
Artemisia	18.5
Liguliflorae	0.2
Tubuliflorae	0.4
Thalictrum	0.1
Galium	0.1
Leguminosae	2.4
Rosaceae	0.3
Cannabinaceae	0.1
Urticaceae	0.1
Equisetum	3.2
Total shrub	49.5
Cyperaceae	0.8
Polypodiaceae	0.1

TABLE 21

Correlation coefficients between each of the 52 atmospheric samples, based on the 16 main pollen types listed in Table 3. The stations are grouped according to the landform-vegetation zones (as in Table 3). (Negative correlations are underlined; each value is a decimal).

	Ia	Ib			II										III							IVa						IVb				V							VI				Boundary cases									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52
1																																																				
2	16																																																			
3	45	93																																																		
4	72	64	81																																																	
5	08	66	55	54																																															
6	09	62	53	56	96																																													
7	25	25	18	19	68	61																																											
8	21	77	71	62	91	88	69																																									
9	23	46	42	56	87	87	73	88																																								
10	02	16	12	34	75	79	50	60	80																																							
11	02	16	08	12	57	40	62	50	56	38																																						
12	09	45	34	35	80	73	48	70	23	72	64																																					
13	12	48	57	60	87	88	50	84	84	86	42	79																																				
14	06	96	87	60	76	72	32	85	57	34	27	63	73																																			
15	23	16	30	33	10	01	32	03	06	02	60	17	07	14																																		
16	13	07	03	14	67	63	56	51	76	78	75	77	66	23	47																																	
17	12	07	14	12	63	63	48	40	69	89	57	74	67	11	27	92																																
18	12	03	08	08	68	63	63	48	72	79	74	80	64	20	46	95	93																															
19	18	12	22	01	52	49	50	33	61	74	62	72	52	04	46	90	92	91																														
20	07	32	17	22	79	75	71	66	79	74	64	72	71	42	44	87	77	86	80																													
21	03	02	10	12	67	68	78	52	79	84	52	60	63	11	27	82	87	88	82	84																												
22	15	29	08	02	60	52	66	48	45	34	46	39	33	34	55	50	39	53	41	70	56																											
23	32	65	44	11	50	48	12	43	21	13	06	47	36	68	07	15	09	16	04	32	05	58																										
24	29	02	11	23	13	02	01	05	13	01	13	34	04	09	15	08	07	09	15	05	02	09	51																									
25	36	18	30	33	10	11	15	24	20	01	14	03	12	14	21	08	12	07	14	08	03	49	47	32																								
26	40	09	09	21	18	15	08	05	02	11	16	45	09	15	40	27	29	32	45	29	16	36	43	54	29																							
27	36	02	19	29	20	12	16	01	05	02	49	25	03	02	75	33	26	35	39	28	13	48	29	18	23	67																						
28	10	22	09	03	49	40	88	49	44	16	51	21	19	23	48	34	20	41	29	59	56	80	23	01	04	14	35																					
29	18	08	22	23	19	08	37	07	12	06	58	18	01	06	89	45	29	42	41	45	31	63	05	22	19	50	74	52																				
30	22	24	07	06	40	26	34	27	23	09	70	46	20	27	87	53	31	50	49	54	24	59	31	03	11	58	84	46	83																							
31	04	83	67	46	85	84	49	82	66	51	33	73	75	87	03	06	39	45	35	67	42	56	75	22	01	42	23	40	13	42																						
32	09	06	19	13	34	27	59	23	41	33	50	27	19	03	80	61	45	62	61	74	62	70	01	20	18	28	39	67	78	64	21																					
33	03	56	41	37	88	81	67	79	79	69	66	87	80	66	41	79	68	80	70	89	69	66	49	10	03	42	37	51	41	65	33	59																				
34	08	10	01	04	61	51	90	56	65	50	74	61	44	21	42	67	62	74	72	72	78	59	11	18	44	32	37	77	43	48	45	57	69																			
35	18	02	14	07	60	59	50	39	68	80	53	62	58	11	37	88	88	88	86	89	86	49	08	04	12	23	22	35	35	35	38	67	68	58																		
36	24	06	17	03	54	53	39	31	57	79	49	72	58	10	34	86	93	87	96	78	79	42	18	23	28	51	36	19	33	40	43	50	69	62	87																	
37	02	12	06	26	76	80	61	59	82	96	45	73	80	29	12	85	93	87	81	82	93	48	19	05	07	20	09	32	18	20	55	46	75	63	85	85																
38	27	01	04	03	46	43	93	46	53	39	39	22	28	06	22	36	38	48	39	52	74	59	03	04	09	02	06	85	26	13	26	53	43	81	40	28	52															
39	28	17	31	22	34	24	42	19	35	33	81	50	20	06	81	78	64	76	78	62	53	44	01	01	06	42	73	41	70	79	17	66	56	65	66	66	45	27														
40	23	14	29	17	34	25	44	17	40	41	66	44	23	06	84	77	62	77	76	74	61	59	01	13	18	38	52	46	74	73	17	90	61	54	77	66	51	33	85													
41	23	14	25	25	13	03	21	01	05	03	77	25	06	09	85	47	28	45	44	36	16	33	07	16	01	28	75	34	76	82	03	54	33	39	36	30	05	07	87	74												
42	29	14	27	29	07	05	21	25	07	03	59	34	04	09	83	49	32	48	61	45	23	34	03	06	13	61	68	31	73	81	08	68	42	47	45	51	12	08	81	80	81											
43	09	99	90	56	63	59	24	73	41	11	14	44	54	94	13	06	08	02	12	33	03	33	70	05	14	14	03	25	05	20	34	04	55	09	02	06	10	01	15	13	12	11										
44	14	70	61	63	96	96	61	91	90	77	46	79	91	79	01	66	62	64	50	79	65	54	51	01	07	16	05	39	09	29	38	29	87	52	60	55	78	38	22	28	02	01	68									
45	02	82	69	36	60	59	34	62	31	04	14	31	39	77	01	02	09	02	08	29	03	38	66	17	16	22	30	43	01	36	78	02	50	23	03	05	09	18	01	12	01	05	85	55								
46	49	13	31	41	03	08	09	22	20	06	14	34	15	08	48	18	19	28	37	13	03	20	32	63	24	86	67	01	43	53	14	23	23	16	17	37	03	13	49	42	42	62	08	10	06							
47	23	15	25	27	02	11	10	09	04	10	65	20	11	12	21	40	19	38	36	25	06	32	04	16	10	32	73	23	79	85	06	57	31	26	22	23	21	03	78	72	92	79	13	10	07	48						
48	34	01	17	26	17	05	12	01	02	06	61	31	03	03	92	41	24	40	43	31	09	42	25	11	24	52	90	28	69	91	17	48	43	35	24	36	05	03	81	62	86	79	03	03	22	62	89					
49	22	28	15	07	22	19	01	14	03	06	01	18	13	29	85	07	05	01	01	18	01	51	68	21	76	01	10	17	06	05	31	02	17	01	08	13	09	04	06	06	07	12	31	25	28	12	09	14				
50	03	81	66	39	62	52	33	65	45	17	41	48	48	78	04	32	09	26	15	61	13	42	52	09	14	15	16	39	19	49	73	34	66	25	32	15	17	06	21	30	27	28	82	62	68	04	17	27	25			
51	14	05	13	12	54	59	38	34	61	86	29	68	63	11	09	76	91	78	88	67	81	32	16	28	24	41	15	10	10	15	43	35	62	55	79	94	89	32	44	45	05	05	07	58	05	05	05	05	05	05		
52	63	62	69	84	80	78	65	82	79	57	35	54	74	63	12	40	39	41	28	56	53	38	24	10	21	06	13	41	01	10	55	20	65	48	35	28	58	50	48	09	50	50	56	83	50	50	50	50	05	50	18	