A STUDY ON POLLEN DISPERSAL AND SEDIMENTATION IN THE WESTERN PART OF THE NETHERLANDS

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SUMMARY

The interpretation of palynological data into a history of the plant communities in a region requires (1) the estimation of the pollen density in the samples, (2) the knowledge of the relative representation rates of the vegetation elements in the pollen spectra and (3) a careful distinction between air-borne and water-borne pollen because of their different recording values. In the present article, a method is described for pollen density determination which is convenient when cores have to be analysed consisting of peat, gyttja and clastic sediments. This method involves the addition of a foreign pollen. Examples are given of the variation which may occur in the pollen density of sediments in a horizontal series of samples. In three cores the pollen densities were determined and the use of this additional information for the interpretation of the analysis data is demonstrated.

In a number of nature reserves a comparison was made between the composition of the local stand of vegetation and the pollen sedimentation. To this purpose moss samples were analysed. The representation of the plant communities was generally found to be fair.

The dispersal of water-borne pollen was studied by a comparison of the regional vegetation types with the pollen precipitated on river banks and tidal flats; there was also made a series of analyses of the pollen content of the water, which shows that the seasonal variations are so small that the pollen which is precipitated from the water in the regions investigated is not representative for the regional vegetation type. The pollen which is deposited in such conditions may originate from three different sources: (1) the local or regional stand of vegetation, (2) forests or other plant communities in remote upstream areas and (3) peat or gyttja layers or other pollen containing deposits which are eroded by the water currents. A number of examples of these dispersal mechanisms is described in this article. In a few cases it is demonstrated how the determination of pollen density may contribute to the solution of the problem, in which proportion these three dispersal mechanisms have been responsable for the presence of the pollen in the sediment under investigation.

1. INTRODUCTION

The Holocene of the Western part of the Netherlands has been deposited on Pleistocene sediments, the surface of which slopes down towards the North Sea (Burck *c.s.* 1956). Successive periods of alternatingly higher and lower sea levels (Burck *c.s.* 1956: 120, 128, 131–135; Jelgersma 1961) resulted in the deposition of several layers of peat, gyttja, clay and sand. In consequence almost any core obtained by sounding, and also every artificially exposed profile, contains different layers of some or all of these sediment types. If a palynological analysis is performed and a pollen diagram is drawn, the question arises how the palynological data, obtained from such a complex core, may be interpreted in terms of the vegetational history of the region. As will be explained, the solution of this problem requires *(a)* the gathering of all the information the palynological investigation of deposits may yield, *i.e.*, not only the percentual composition of the pollen content, but also the pollen density of the samples and *(b)* the investigation of the relations existing between the composition of a deposit of air-borne pollen and the composition of the local or regional stand of vegetation which acted as the source of the precipitated pollen; the sedimentation of water-borne pollen requires a separate consideration (FAEGRI & IVERSEN 1963: 120; ZAGWIJN & VEENSTRA 1965: 83). The principles of these two types of investigation will be considered previous to the discussion of details regarding the methods followed and the material studied.

1.1. Determination of pollen densities in samples

The desirability of performing density determinations was discussed by VON POST as early as 1916 (DAVIS 1963), but the subject was again brought up by the discovery of radio carbon dating (DAVIS 1967).

If a sufficient number of radio carbon data is available, the pollen sedimentation rate can be calculated in terms of a certain number of grains sedimented per year per unit of surface area in each interval between ^{14}C datings. The differences in the velocities of sediment deposition, or of peat formation, which affect the pollen density of the deposit, would have no influence on this number. But this holds only true, if the mean sedimentation rate, calculated for the interval between the dated levels, is equal to the value for the sedimentation rate in each sample in the interval, *i.e.* if the sedimentation rate was constant in the entire interval. It is obvious, however, that it is only allowed to suppose this in those circumstances where the radio carbon data show, that there has been an unchanging sedimentation rate over long periods.

A rather large number of such data is, therefore, required. Otherwise, rectilinear interpolation between the dated levels is not justified, and even in the most favourable cases this procedure will have to be handled with caution. The investigations described by DAVIS (1967) were carried out under ideal conditions, which will seldom or never be encountered in the Netherlands. It is to be expected that it will seldom be possible to obtain sufficient ^{14}C data from the complex cores, obtained by soundings in the Western Low Countries, for the estimation of the pollen sedimentation rate throughout the core. Even in a case in which all the sand and clay strata are bordered by sediments of which the age can be determined by the ^{14}C method, the rectilinear interpolation of the sedimentation rate of the sediment within an interval representing a clay or sand deposit is unreliable, considering the variable sedimentation rate of the matrix in these sediment types.

On the other hand, the determination of the pollen density in sediments is useful, even in cases in which no exact age determination is possible. This will be discussed in detail in the description of the cores in which pollen densities were determined.

1.2. Dispersal of air-borne pollen

The dispersal of pollen may be conceived as occurring according to three principles, namely, (1) direct sedimentation, (2) fractional sedimentation from

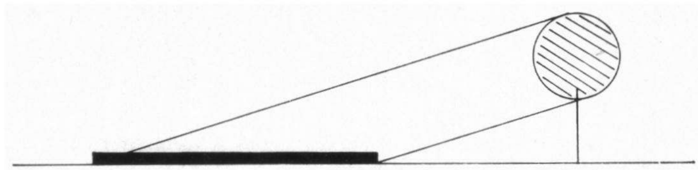

Fig. 1. Pollen shadow formed by direct sedimentation from air.

a vortex in the air and (3) transport by, successively, a thermal air current, the wind, and rain. (TAUBER 1967; FAEGRI & IVERSEN 1964: 31–41).

(1) It is to be expected that direct sedimentation will result in a "pollen shadow" formed at a distance from the pollen source (fig. 1). This distance depends on:

a. the height of the pollinating tree or plant,
b. the velocity of the local air current and
c. the velocity of the vertical component of the movement (FAEGRI & IVERSEN 1964: 35), which in turn depends on the resistance of the air. The resistance which is met with by the grain depends on the pollen type and on the density of the air. The influence of the pollen type on the braking resistance of the air depends on (α) the size of the grains, (β) the external structure of the exine, *e.g.* a certain type of sculpture, and (γ) the fraction of the total quantity of disseminated pollen which remains stuck together to form clumps of different size. The fraction of the pollen produced in the anthers which is disseminated and the tendency of the grains to stick together both must be expected to depend on the prevailing climatic conditions. The density of the air is to a certain extent equally dependent on climatic factors which prevail at the time of pollination, but also on the altitude.

The area over which the "shadow" will extend is dependent on the horizontal and vertical dimensions of the source of the pollen rain – *e.g.*, the crown of a certain tree – and on the direction of the resultant of the components (b) and (c).

From these considerations it follows that the type of sedimentation, referred to as direct sedimentation, depends on a multitude of factors, which may vary according to different geographic circumstances and to changes in the climate.

(2) Fractional sedimentation from a vortical air current (fig. 2): One may assume that, provided the pollen grains are transported along a solenoid-shaped trajectory, every time a pollen grain is swept through the stand of vegetation

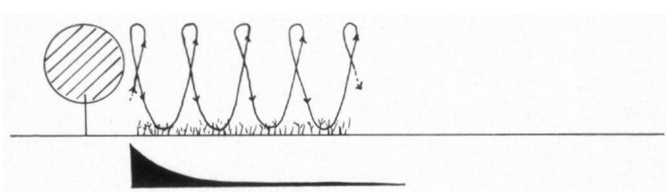

Fig. 2. Pollen sedimentation from an air vortex.

there is a certain probability for it to be caught and immobilized. At each revolution of the air current a certain fraction of the pollen will be substracted from the air. Accordingly, the pollen content of the air current will show a decline of the absorption type

$$C_t = C_o \cdot e^{-nt},$$

C being the pollen concentration of the air; C_0 at the start and C_t after t seconds; the determining factor (n) in the exponent is highly complex. The factors composing it vary according to climatic conditions, pollen type and landscape structure (SCHMIDT 1967; TAUBER 1965). It is, therefore, unlikely that it will be possible to determine accurately the value of this factor (n) as it was at the period of formation of a deposit under investigation.

(3) Pollen may be lifted up by a thermal air current, subsequently be carried over a certain distance, to be finally precipitated in a remote area *(fig. 3)*.

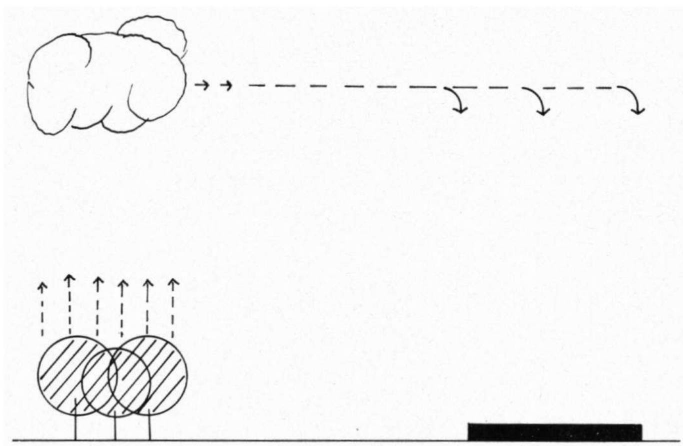

Fig. 3. Pollen transport by a thermal air current.

The distance over which the pollen is transported in this way may amount to 100 km (FAEGRI & IVERSEN 1964: 36, 37). It is obvious that minor quantities of pollen may be transported over even longer distances (*e.g.*, ERDTMAN 1937: 186). As they may contribute to the pollen content of the sea sediment, even such small quantities of air-borne pollen must be taken into consideration in cases where the density of the pollen in the water is also low – or must be expected to be so – *i.e.* at long distances from the land (ZAGWIJN & VEENSTRA 1966: 549).

The total pollen rain in a certain area can be expressed in a mathematical form as the sum of three terms. These terms refer to the pollen precipitation which takes place according to the three principles described (TAUBER 1965). The contribution of each individual term to the total pollen sedimentation varies all the time according to the different climatic conditions, the different pollen types composing the local pollen rain and the local vegetation structure and composition.

The influence of irregularities in the climatic conditions is conceivably levelled out in the course of time if the sample, which is to be compared with a plant community, represents the pollen sedimentation of a time interval which is long enough to allow the disregard of such irregularities. This will (1) hold true for a sample of peat or gyttja which may be supposed to represent the deposits formed during a sufficiently long time interval. It will (2) sometimes be allowed when moss samples are used for the study of the quantitative relation between the recent pollen sedimentation and the local plant community, *viz.* in those cases in which the sample represents a period long enough for the influences of climatic irregularities to be levelled out. It will (3) be possible to use the empiric data on the recent relations for the interpretation of a spectrum from the Holocene, if no major differences in climate exist between the two elements of the comparison.

1.3. Representation and representation rates

A plant community produces pollen grains of different types in a certain proportion. The composition of the pollen rain, of which this plant community is the source, is studied by means of the recent local pollen sediment found in an appropriate surface sample, *e.g.* a moss cushion. The precipitated pollen is expected to represent the local plant community according to some quantitative relation, which, for the moment, will be called the representation. The representation is always the result of two separate factors, namely, the productivity and the dispersal.

The productivity is the pollen production per annum, expressed in numbers of grains, in the anthers of a given plant species per unit of surface area covered by plants of that species.

The pollen productivity would be relatively simple to investigate (Faegri & Iversen 1964: 32–33), but – as has been explained – the dispersal of air-borne pollen is highly complicated and its quantitative analysis meets with serious difficulties. Hence the representation must be studied directly, in its entirety, from empirical observations; this should be done in the same region as that in which the vegetational history has to be reconstructed from palynological data with the aid of the information obtained in this way.

Apart from the need for a sufficient amount of empirical data, it is necessary that the appropriate arithmetical treatment is applied for the conversion of the empirical data into generalities which can eventually be used for the interpretation of palynological data obtained by the analysis of Holocene sediments.

1.3.1. Arithmetical treatment of the empirical data

A pollen diagram usually represents percentages, based on the numbers of pollen grains of certain types as fractions of a sum, *e.g.* the sum of all the arboreal pollen grains counted from each sample. If from these percentages, a reconstruction of the vegetational history is attempted a correction is needed for the conversion of the palynological data into the quantitative composition of the stand of vegetation which was the source of the pollen present in the sample. Many authors agree on this (DAVIS 1963; FAGERLIND 1952; HEIM 1962; JONASSEN 1950; P. MÜLLER 1936; POHL 1937; STEINBERG 1944; TEUNISSEN 1962; TSUDAKA 1958). As was already stated, the conversion factors must be derived from observations concerning the recent pollen sedimentation. Now, if the percentage (p) in which a certain pollen type is present in a sample is called p_1, and the percentage (v) in which the corresponding vegetational element is present in the stand of vegetation is called v_1, the specific correction factor is not the representation rate p_1/v_1, for – as a calculation would show – this quotient is not independent from the composition of the stand of vegetation. The specific conversion factor, as has been pointed out by DAVIS (1963), is the ratio

$$\frac{P_1}{V_1} : \frac{P_2}{V_2} : \text{etc.},$$

i.e. the conversion has to be performed according to the mutual ratio of the representation rates (p/v) of the various pollen-producing taxa. If the representation rate of a pollen type, occurring in the majority of the samples collected in a region, is chosen as a unity, the representation rates (p/v) of other pollen types can be expressed in terms of this unity. This may be done with p/v *(Betula pubescens)* as a unity. In this way a "*Betula* index" can be calculated for every species from appropriate observations. [It is obvious, however, that in many cases the difficulty will present itself that a pollen type corresponds to several species, of which the representation rates may be different.]

1.3.2. Values found for the conversion index[1]

The following table comprises the data published by FAEGRI & IVERSEN (1964: 105–107), here expressed as values of the *Betula* index:

	Müller	Steinberg	Pohl	Iversen
Alnus	–	–	1.3	1.4
Pinus	1.1	0.97	–	–
Corylus	–	–	1	–
Picea	0.1	0.1	1	–
Carpinus	–	–	0.6	–
Quercus	0.47	0.23	0.12	–
Fagus	0.08	0.03	0.07	–
Abies	0.13	0.13	–	–
Salix	–	–	–	0.13
Empetrum	–	–	–	0.33
Ericaceae	–	–	–	0.07
Cyperaceae	–	–	–	0.17
Gramineae	–	–	–	0.10

[1] A possible source of variations found in the conversion indices is the destruction of pollen grains, obviously by biochemical processes, in certain mosses (HEIM 1962). Some pollen types may be more subject to this kind of loss than others. When moss samples are used for the study of the representation of a plant community by the precipitated pollen, this may constitute a complication. It is, however, also possible that this destruction forms a kind of automatic correction for differential destruction during fossilization, when the conversion indices found are applied to samples of fossil pollen. It is even possible, therefore, that for this reason the use of moss samples has to be preferred to the use of artificial devices for the collection of pollen. This is one of the problems about which sufficient information is still lacking.

In the same way, the following values for the *Betula* index can be derived from the data published by JONASSEN (1950):

P-Q-R:	*Fagus* 0.74	*Quercus* 1,07 in forest	median values
	Fagus 0,15	*Quercus* 0.27 in open spaces	
N-O	*Fagus* 0.26	*Quercus* 0.44 in forest	
N	*Fagus* 0.25	*Quercus* 0.66 in open spaces	

The characters P, Q, etc. refer to the sampling sites.

The author's personal calculations based on the data published by P. MÜLLER (1936) (the same data as referred to in FAEGRI & IVERSEN (1964: 105–107), used directly from the original publication) yield the following values for the *Betula* index:
Pinus 1.4; *Picea* 0.17; *Abies* 0.16; *Alnus* 0.15; *Fagus* 0.10; *Quercus* 0.40; *Corylus* 0.40.

From the data published in STEINBERG (1944) the *Betula* index takes the following values if the mean is used of each set of three values given:
Pinus 0.43; *Picea* 0.16; *Abies* 0.003; *Quercus* 0.10; *Fagus* 0.02:

It should be borne in mind that, if as was done in the case of the data published by FAEGRI & IVERSEN (1965: 106) the calculations are based on p/v *(Betula nana)* as a standard, the resulting *Betula* indices may differ from results based on, *e.g.*, p/v *(Betula pubescens)*.

ANDERSEN (1967) calculated the following correction factors, originally based on p/v *(Fagus)* as a unity, here recalculated as based on *Betula*:

Fagus	0.23	0.24
Quercus	0.82	1.00
Tilia	0.11	0.17
Alnus	0.52	0.32
Fraxinus	0.09	0.15

The second column of figures contains the indices after correction for pollen from outside the area (vide infra).

These figures refer to observations in Jutland.

ANDERSEN (1967) applies a correction for pollen from outside the area. The underlying principle is the following: let p be the pollen frequency of a species (frequency defined as the number of grains, divided by the number of extraneous grains), p_0 the frequency of this species (as a fraction of the total number of extraneous grains) outside the area, a the surface of the area and P the productivity, then P follows from the equation $p = P.a + p_0$, hence $P = \frac{p - p_0}{a}$. The area, on which the calculations were based, was circular and had a radius of 30 m.

For the moment it appears to be difficult to decide if this correction for extraneous pollen will eventually be applicable to the analysis of Holocene sediments. In the ideal case the procedure is to be performed as follows:

1. A great number of Holocene cores are analysed after addition of foreign pollen, so as to enable not only the usual percentage calculations but also density determinations.

2. From the densities which have been calculated it is possible, by the mutual comparison of the values found in the different soundings in levels which are correlated in time, to evaluate the density of the ubiquitous rain consisting of certain pollen types. This ubiquitous rain is substracted from the density values found for these pollen types in the different soundings.[1]
3. In a suitable area, *e.g.* on a lake – in the Netherlands the IJsselmeer would probably be suitable – the ubiquitous pollen rain existing in the present time is investigated. This value, for every pollen type involved, is substracted from the local pollen rain in the areas where the recent sedimentation of pollen is investigated in relation to the local plant communities.
4. The representation rates, found in areas where the recent pollen sedimentation is compared with the composition of the plant community, can now be corrected for extraneous pollen. (It is to be noted, that the conception of "extraneous pollen" is here not the same as the definition of the concept given by Andersen, which is based on a circular area with a restricted radius; it may, however, be possible to apply an additional correction in Andersen's sense).
5. From the corrected representation rates conversion indices are calculated for the different pollen types, expressed in the terms of p/v of a suitable pollen type or species, *e.g.* in a *Quercus* index.
6. The conversion factors calculated from the empirical data on the recent pollen sedimentation are applied for the conversion of the palynological data, which have undergone the corrections described in (2), into percentages of coverage of the fossil plant community in each level in every core. These final results are the elements to be used for vegetation maps showing the composition of the vegetation in the whole region under investigation in different time periods[2].

From observations in the Oosteinder Poel the following values were calculated for the *Betula* index:

OEP 1	*Alnus* 1.3	*Gramineae* 0.33 (almost exclusively *Phragmites*)
3	1.4	
5	1.6	
6	3.9	

The value for *Alnus* in OEP 6 deviates strongly from the other three figures obtained, which do not differ appreciably from the values based on the observations of other authors.

The variation found in the *Betula* index may be partly due to differences in dispersal rate. According to HEIM (1962) *Betula, Alnus,* and *Pinus* tend to be over-represented at a certain distance from the pollen source as a result of transport over a longer distance than is the case with other pollen types.

Apart from the complication, caused by the dependence of the representation rate of a species on the composition of the vegetation on account of a different dispersal in different vegetation types, the variations found in the "specific" conversion index may be the result of confusion of pollen types with botanical species. Moreover, what is called a botanical species may consist of various genetical stocks differing in pollen productivity and, perhaps, also in dispersal rate.

[1] A pollen rain has the dimension $n/cm^2.sec.$, density has the dimension n/cm^3. Hence, the ubiquitous pollen rain must be changed into a density by the relation between time and difference of depth, before it can be substracted from the estimated density of the sample.

[2] It is obvious that this reconstruction can often not be founded solely on calculation. If different vegetation types are represented in a sample, the interpretation requires the distinction between these vegetation types, in such a way that the corresponding plant communities are reconstructed separately.

From these considerations it follows that reliable conversion factors are still lacking. This is due, not to defectuous calculation, but to still insufficient information.

1.4. Transport of pollen by water

Pollen transport by water offers a problem different from that which is constituted by dispersal through the air. The first difference, which is obvious, is that there is, in streaming water, no dispersal proper, as it takes place in the air. Apart from tidal estuaries, the direction of the current is always the same, with the result that the pollen, once precipitated into the water, is not dispersed in all directions – as is more or less the case with air-borne pollen – but it remains within the river bed or it is deposited on the bank. The second difference to be mentioned here is, that the pollen is bound to be transported over much longer distances than in the case of air-borne pollen. These two differences together will account for at least a part of the remobilized pollen which must be expected to be present in the water in appreciable amounts. To this may be added pollen which is liberated from Holocene deposits by erosion, or from older deposits which may contain pollen grains which are indistinguishable from recent or Holocene pollen except by means of special methods which shall not be considered here.

GROOT (1966) analysed the pollen isolated from water of the Delaware River and found a fair representation of the vegetation type occurring in the area in a majority of the samples. The samples were all collected in August. The river water is supposed to contain only little pollen from older deposits.

STANLEY (1965) determined the pollen density of the continental shelf off the E coast of the U.S.A.. No pollen types were identified, however. Sand was found to contain less pollen per unit volume than silt or clay.

MULLER (1959) studied the transport of pollen and its sedimentation in the Orinoco delta and in the sea to within 50 miles offshore. A generally fair representation of the vegetation elements of the delta region was found.

INGRAM *c.s.* (1959) examined the pollen sedimentation in Semerwater, North Riding, England, in comparison with the regional vegetation type. Apart from the analysis of cores, two surface samples from the river bed were analysed. The area studied was about 500 metres in diameter. The pollen distribution showed that no local differences are found within the area, probably owing to the turbulence of the water. The composition of the surface samples resembles that of the cores so closely that presumably no important changes in the vegetation type took place in the period represented by the length of the cores. The data published by INGRAM *c.s.* can not be used for the calculation of correction factors.

The study by INGRAM *c.s.* was carried out in a hilly area and consisted of pollenanalytical observations concerning the water from the upper course of the rivers, which can not possibly contain any appreciable quantities of pollen hailing from distant areas with a different pollen production.

In the Netherlands conditions are different from those present in Semerwater, as the lower courses of the rivers Rhine, Waal, and Meuse dissect a country with a vegetation type which is highly different from that of the regions which supply the major part of the water in the rivers.

In the case of the Orinoco delta studied by MULLER (1959) the differences with the conditions in the Netherlands are (1) that in Zeeland, and to some extent also in the other parts of this country referred to in the present paper, old peat layers are an important source of secondary pollen precipitated with the clay and the sand which are deposited by the rivers, whereas in the Orinoco delta the contribution of reworked pollen to the total pollen precipitation seems to be much smaller, and (2) that the dimensions of the delta region studied by MULLER are larger – it has a diameter of about 250 km – in proportion to the upstream areas, with the result that the stands of vegetation in the Orinoco delta must make a relatively much more important contribution to the total pollen content of the river than can be the case in the Netherlands, where the pollen contribution from upstream areas is more important as compared to the pollen which is locally precipitated into the water. (An additional difference between the two regions is, probably, that the pollen productivity of the Orinoco delta vegetation is higher).

2. METHOD FOLLOWED FOR DETERMINATION OF POLLEN DENSITY

The pollen density in sediments can be estimated in several ways.

(1) A counting chamber is used for the determination of the pollen density in the final pollen suspension obtained by processing of the sediment sample, after the total quantity of this final suspension has been measured.

(2) The pollen grains contained in a certain volume of the final suspension are distributed on slides and counted by means of a special device on the microscope.

(3) A known quantity of foreign pollen is added to a measured volume of original sediment. The sediment sample is then processed and analysed in the usual way. The pollen density of the sediment is calculated from the proportion, which the number of originally present grains bears to the number of the foreign grains counted (BENNINGHOF 1962).

The methods (1) and (2) differ only in the microscopic technique. They may be subject to errors arising from the loss of pollen caused by the decanting of supernatant fluid after centrifugation. Débris present in the counting chamber or on the slides may hide pollen grains from sight. A third possible disadvantage is that, in all cases in which part of the original sample is discarded after filtration, pollen which is discarded with this material is not incalculated; it seems to be impossible to determine how many pollen grains are lost in this way. (This error may be avoided in samples of clay which are treated with HF.)

The method based on the admixture of foreign pollen has the advantage that the foreign pollen can be added previous to the further preparation of the sample, so that the probability of being lost or becoming obscured from view is the same both for the foreign pollen grains and for the pollen grains originally present in the sediment sample. This method is only subject to statistical errors, which can be estimated.

The method based on the admixture of foreign pollen is similar to that based on the addition of commercial *Lycopodium* powder to pharmaceutical products previous to analysis (HALLER 1946). For the present study, pollen was added of *Aesculus hippocastanum* which pollen has two advantages over *Lycopodium* spores; (1) the possible natural presence of *Lycopodium clavatum* spores in the sediment is not obscured, nor can it give rise to errors in the calculated density; (2) the *Aesculus* pollen does not have a tendency to float, in contrast to *Lycopodium* spores.

2.1. Preparation of the *Aesculus* pollen suspension

Inflorescences of *Aesculus hippocastanum* are taken from a tree in full flower. The stamina are collected and boiled for 5 minutes in a 10% KOH solution, passed through a copper wire filter, repeatedly rinsed in destilled water, once with 30% acetic acid and with water again; the suspension is subsequently passed through a cloth or a very fine filter, so as to eliminate conglomerates of pollen grains. Finally the pollen is supended in 50% glycerol in water with a drop of phenolum liquefactum added for every 20 ml of suspension (ZINSSER & BAYNE-JONES 1939). The suspension is kept in a carefully closed bottle.

2.2. Determination of the density of the *Aesculus* pollen suspension

The bottle containing the suspension is shaken for three minutes. A blood sugar pipette of 0.05 ml is filled with the suspension up to just over the mark; the pipette is withdrawn from the bottle which is closed without delay. The pipette is wiped with a clean piece of cotton wool and the surplus suspension is absorbed to adjust the volume to the mark.

So far, the process has to be repeated lateron previous to the admixture of the suspension to the sediment samples.

The pipette is half emptied on a piece of cotton wool. A *small* drop of the suspension is transferred from the pipette into a Bürker or Türk counting chamber. No fluid must be allowed to flow from the plateau into the groove. (If too much fluid enters the resulting count may be too high). The pollen is allowed to settle down during the time needed for cleaning the pipette. With the aid of a suction pump the pipette is rinsed consecutively with (1) 10% commercial Lodaline detergent in water, (2) 30% acetic acid in destilled water and (3) acetone, after which it is air dried. The pollen grains, which have settled down on 25 squares of 1/25 square millimetre, are counted. As the chamber has a height of 0.1 mm, the volume of suspension in which the grains are counted is 0.1 microlitre.

After each count the two glass parts of the counting chamber are consecutively cleaned with detergent solution, destilled water and alcohol, and wiped dry with a clean cotton cloth. The chamber is then fitted together again. After this, Newton rings should be visible on the bottom side, indicating that the chamber has the required height of 0.1 mm. If no Newton rings appear, the chamber is once more cleaned and put together.

The first count gives a preliminary estimate of the density, which should preferably be about 300 grains per 0.1 microlitre. If necessary the density of the suspension is adjusted by centrifugation and decanting, or by addition of a water-glycerol mixture. After this a series of counts is performed.

The purpose of this series of counts is twofold: first, the density of the pollen suspension must be estimated by means of a sufficient number of counts. Secondly, this series of counts serves as a check on the uniformity and accuracy of the performance. If the standard deviation is too large, the cause has to be found. This may be (1) insufficient shaking of the bottle, (2) insufficient cleaning of glassware or (3) overfilling of the counting chamber.

2.3. Determination of the pollen density of a sediment

According to the expected density, 0.5–2 ml of sediment is transferred into a narrow cylindric glass vessel bearing a mark which indicates a certain volume, which has been determined beforehand. From a burette a 10% KOH solution is added up to the mark. After this, 0.05 ml of the *Aesculus* pollen suspension is added to the sediment in the KOH solution; the solution is repeatedly sucked up into the pipette and blown down again (in contrast to the usual proceeding in the use of pipettes). The contents of the vessel are transferred into a beaker. This requires repeated washing of the first glass vessel with destilled water, which is then added to the contents of the beaker. The pipette is cleaned in the way described and the new level in the burette is noted down. The processing of the sediment is completed in the usual way.

The author used no HF. After boiling in KOH followed acetolysis, bromc form separation, suspension in 50% glycerol in water and mounting (all this with the usual transitionary steps).

After the pollen grains have been mounted on slides, counting is performed in the usual way. Not only the pollen grains naturally present are counted in a number sufficient for accuracy, but also the *Aesculus* grains.

The pollen density of the sediment is calculated by means of the following equation:

$$n = \frac{TP \cdot 500 \cdot a}{f \cdot v}$$

in which TP = number of non-*Aesculus* grains counted
a = number of *Aesculus* grains contained in 0.1 microlitre of suspension
f = number of *Aesculus* grains counted
v = volume of the sediment sample
n = number of non-*Aesculus* grains contained in one unit of volume (the same unit as in which v is expressed).

The density figures obtained in this way are subject to statistical errors. These errors are kept within certain limits by an appropriate choice of a and of TP.

In the present study f was at least 150. Assuming for f a Poisson distribution with parameter 150, it follows that its coefficient of variation V_f (defined as: the standard deviation divided by the average) is $V_f = \frac{1}{\sqrt{150}} = 0.08$. Therefore the precision of f is $2 \cdot V_f = 0.16$.

Generally not less than 200 AP grains were counted in the sample. Usually the TP count was higher than 200, but taking this minimum value of 200 as the the parameter of the Poisson distribution of TP it follows that

$$V_P = \frac{1}{\sqrt{200}} = 0.07.$$

For the sediment volume v the coefficient of variation is calculated at $V_v = 0.025$. The resulting coefficient of variation of the expression $x = \frac{TP}{f \cdot v}$ can be calculated from the formula:

$$V_x = \sqrt{V^2_{TP} + V^2_f + V^2_v}$$

and turns out to be $V_x = 0.11$. So the precision of n, due to the statistical variability of TP, f and v, is 0.22 or 22%.

The accuracy of the determination of the pollen density in the stock suspension of *Aesculus* pollen was 5%. This has to be taken into account if density determinations, performed with the aid of a different stock suspension, must be compared with the values published in this paper.

Apart from statistical errors, the possibility of a selective loss of certain pollen types during processing has to be considered. An extensive investigation of this problem is outside the scope of the present paper. Selective loss of pollen is a possible source of error in pollen analysis in general. When density is determined, a loss of pollen of certain types will lower the TP density, but it will not affect the calculated density of other pollen types. Hence, only a few remarks will be made here.

The factors which may cause pollen grains to disappear can be distinguished into chemical and physical causes. Chemical destruction of pollen grains, which were already in a poor state of conservation in a sediment, may cause certain pollen types to become under-represented. As far as percentages are concerned, other pollen types may become over-represented as a consequence.

Luzula pollen is hardly ever recovered from fossil sediments. *Ceratophyllum* pollen is completely destroyed by acetolysis. Apart from these two pollen types, it is likely that pollen grains of other thin-walled types are the first to disappear when the general state of conservation of the pollen in a sample is poor.

Apart from chemical destruction of pollen in the laboratory there may have occurred "differential destruction" (FAEGRI & IVERSEN 1964:120) in the sediment during fossilization. Although this distinction is made theoretically, these two ways in which pollen of certain types may be entirely or partially lost are not discernable, and the problems they entail for the interpretation of palynological data are the same.

One of the possible physical causes for loss of pollen grains is their precipitation together with sediment matrix particles during bromoform separation. This may take place even though the specific gravity of the grains is lower than that of the bromoform-alcohol mixture used (2.00). The probability of disappearance due to this cause may be higher for one pollen type than for another. owing to differences in size or sculpture.

A second possible physical cause of loss of pollen of certain types is the repeated decanting of fluid from the centrifuge tubes. The author repeatedly checked the pollen content of the decanted fluid and found some pollen grains to be present in all cases. It proved to be impossible to avoid this, even when the centrifugation was prolonged and the decanting was carried out with the utmost care. It is probable that the smallest pollen grains will be the first to be lost in this way, because due to slower precipitation they must occupy the most superficial position in the precipitate. Here, too, a certain sculpture may have the same effect as a small size.

It must therefore be expected that of the smaller grains a larger fraction is lost than is the case with the larger grains. Due to this, and apart from differences in dispersal, the pollen of *e.g. Myosotis* and – to a lesser extent – *Urtica* and *Solanum* species may be under-represented in the count.

It is obvious that, if the added foreign pollen suffers a selective loss, this must result in false density values. As far as pollen loss is dependent on grain size, this error can be avoided by the choice of a pollen type of average grain size, which may be expected to suffer a loss which is equal to the mean loss of originally present pollen. The author tried to meet this requirement by the choice of *Aesculus hippocastanum* pollen.

Through the same cause which may be responsable for a selective loss of smaller grains from a sample, the larger grain types may tend to become over-represented. Although this presents no serious problem as far as rarely represented pollen types are concerned, *e.g. Linum catharticum, Malva* or *Geranium,* it may be a more serious source of error in the case of *Abies, Picea* or *Pinus* pollen.

3. SURFACE OBSERVATIONS

In this chapter the results of the analysis of the pollen content of surface samples are discussed in their relation to the surrounding plant communities.

3.1. Nederhemert

In the small nature reserve which consists of the forest around the Castle Nederhemert a sample was taken from a moss cushion. The pollen which collects in this forest bottom originates from different sources. The forest covers an area of about 12 hectares. From this area has to be substracted the part in the immediate vicinity of the castle, which was laid in ruins in 1944. The remains of the garden and part of the ruins of the castle are covered mainly by grass. The surrounding countryside consists of arable land (used for growing potatoes,

Fig. 4. The Western part of the Low Countries
1 Sint-Annaland; 2 Bergen op Zoom; 3 Campinase Heide; 4 Nederhemert Zuid; 5 Geldermalsen; 6 Schipluiden; 7 Kwintsheul; 8 Meye; 9 Nieuwe Wetering; 10 Oosteinder Poel; 11 Vlieter; 12 Oude Vlie; 13 Nes; 14 Holwerd; 15 Schiermonnikoog; 16 Vlieland; a Mastgat; b Krabbenkreek; c River Meuse; d River Waal; Geographic coordinates of sampling sides: see p. 42.

cabbage and other vegetables but also cereals) and of pasture. The soil consists of clay.

The different species, growing within a radius of 20 m around the sampling site in the forest, were represented as follows, their contribution being expressed as degrees of coverage:

trees: *Quercus* sp. 50%, *Fagus sylvatica* 40%, *Acer* sp. 10%; NE of the sampling site, at a distance of 20 m, there is a row of *Populus* trees.
shrubs: *Sambucus nigra* 10%. (90% without any shrubs)
herbs: *Geranium robertianum* 80%, *Urtica dioica* 5%, *Aegopodium podagraria* 2%, *Hedera helix* 3%. In addition, 20% of the surface of the tree trunks is covered by *Hedera helix*.

The composition of the recent tree pollen rain, as it is recorded by the pollen recovered from the sample, shows a strong under-representation of *Fagus*. *Pinus* pollen is present, though no *Pinus* trees are found within a radius of 18 km. The shrub layer, which locally consists of *Sambucus nigra* only, is fairly well represented. The lowest angiospermous layer does not find itself truly represented in the pollen spectrum, the dominant *Geranium robertianum* being entirely absent from the sample. The occurrence of three cereal pollen grains on 88 gramineous pollen grains represents the influence from surrounding vegetation outside the forest. Noteworthy is the presence of 11 *Hedera* pollen grains on 143 NAP grains, *i.e.* 7.7%. The sampling site had been intentionally chosen for the purpose of testing the representation of *Hedera* in the local deposit, because *Hedera* is generally not frequent in pollen spectra. As far as it is permissible to draw conclusions from a single case, it seems that the usual scarcity of *Hedera* in pollen spectra is not to be attributed to a low representation rate.

3.2. Oosteinder Poel *(Fig. 5)*[1]

The nature reserve Oosteinder Poel near Aalsmeer consists of a complex of small artificial rectangular islands intersected by canals. In former years some of the islands were in use for the cultivation of ornamental trees and shrubs, *e.g.* of *Syringa* and *Aronia* species. *Aronia* shrubs are still abundant throughout the region. Other islands were in use for the harvest of *Phragmites*, which is used as a winter cover in bulb growing areas. In order to preserve the stands of *Phragmites*, the local inhabitants regularly took away the young trees which tend to take root in the *Phragmites*-covered areas. After 1927, when the insular complex became a nature reserve, this elimination of trees has been continued in some of the islands for the preservation of the existing vegetation type. In all the places where natural processes are allowed to take their course the land is soon occupied by *Betula* or mixed *Betula-Alnus* forest containing minor quantities of *Quercus*, *Fraxinus*, *Acer*, *Sorbus* and other trees. No *Pinus* is present, though *Pinus* pollen is found in the samples.

All the samples also contain charcoal particles. This phenomenon is probably connected with the presence of *Pinus* pollen, which indicates a contamination of the region by extraneous pollen.

[1] Complete records of the analysis are obtainable on request.

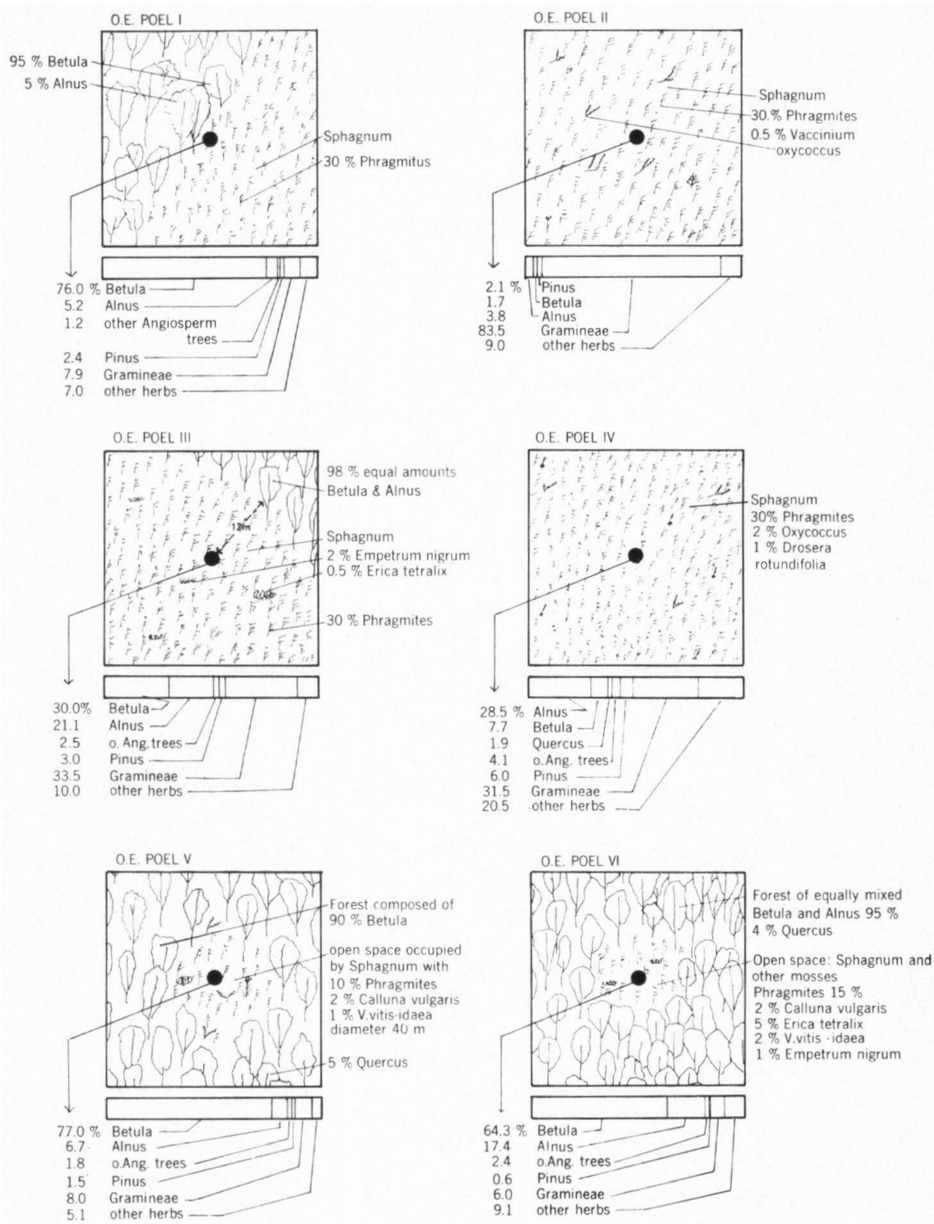

Fig. 5. Vegetation survey and pollen sedimentation in the Oosteinder Poel. In V and VI the diameter of the open spaces is approximately 50 m.

The following herbaceous species were noted: *Phragmites australis, Erica tetralix, Calluna vulgaris, Vaccinium vitis-idaea, Oxycoccus palustris, Empetrum nigrum* and *Drosera rotundifolia.* The sampling took place in October, so that not all the herbaceous species growing in the area could be identified.

A comparison between the composition of local stands of vegetation and the pollen found in the samples, taken at various sites as is shown in the diagrams, yields the following general results:

1. There is a fairly true representation of the proportion between the areas covered by forest and by open vegetation.
2. *Alnus* and *Betula* are more strongly represented by their pollen than *Quercus.*
3. *Empetrum* is strongly under-represented.
4. *Pinus* pollen is present, though *Pinus* does not occur in the forest.

Most of the gramineous pollen was *Phragmites* pollen, as was to be expected. In all the samples minor quantities of wheat pollen were found. Wheat is grown in the Haarlemmermeerpolder to the NW, at a distance of 1.5 km from the centre of the reserve.

3.3 Meye *(Fig. 6)*

The polder Nieuwkoop en Noorden consists of a complex of rectangular islands, much of the same type as in the reserve Oosteinder Poel, separated by narrow canals and some small lakes. Three samples were collected. The composition of the local stands of vegetation is shown in the diagrams. Here, too, there is a generally true representation of the vegetation type in the pollen spectrum. An exception is the important difference in the *Alnus/Salix* ratio between the samples Meye I and Meye II. It is possible that this difference is caused by the difference in the sampling technique, as one sample was taken from the soil and the other from a tree stump. Samples from the soil may be contaminated with pollen which was deposited in an earlier period. The trees in the immediate vicinity of the sampling site are all *Alnus, Salix* only occurring at a distance of some 100 m.

Here also *Pinus* pollen is found, though *Pinus* does not occur in the area, which lies at a distance of 25 km from the nearest *Pinus* stand of any importance.

The regular occurrence of *Pinus* pollen in superficial pollen deposits so far from the origin is probably attributable to thermal air transport. This phenomenon possibly has some bearing on the high *Pinus* content of the superficial North Sea sediment (ZAGWIJN & VEENSTRA 1966), but when water transport is also involved, the floating tendency of *Pinus* pollen (FAEGRI & IVERSEN 1964: 110) may also be responsible for the long-distance transport of the pollen.

3.4. Kampinase Heide (often written: Campinase Heide) *(Fig. 7)*

In contrast to the other two reserves which have been described, the Kampina'se Heide is a complex of forests, lakes and open landscape on a basis of Pleistocene sand. In some of the lakes and small marshes *Sphagnum* vegetation occurs and peat formation takes place. Sample Kampina I is from such a wet spot. There is a fair accordance between the composition of the local stand of vegetation

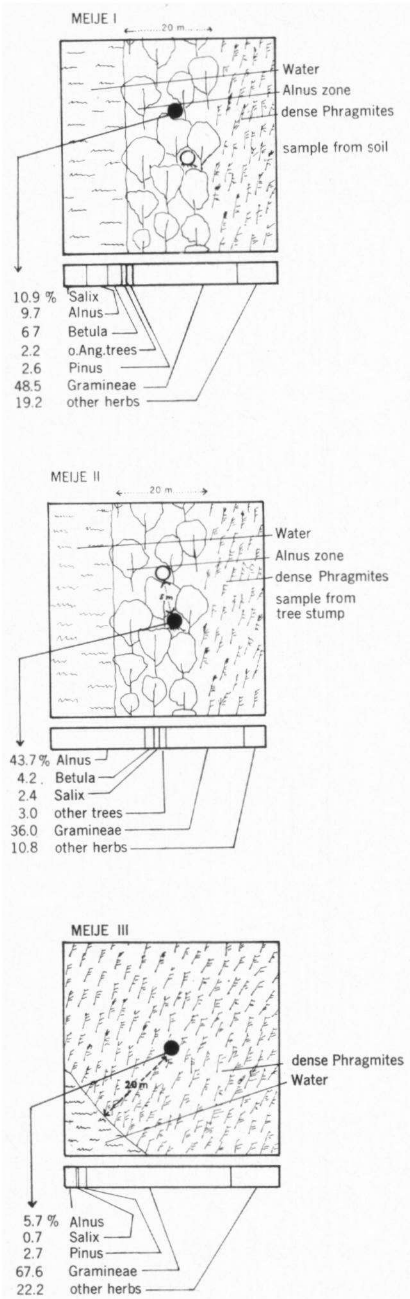

Fig. 6. Vegetation survey and pollen sedimentation in polder Nieuwkoop en Noorden, near Meye.

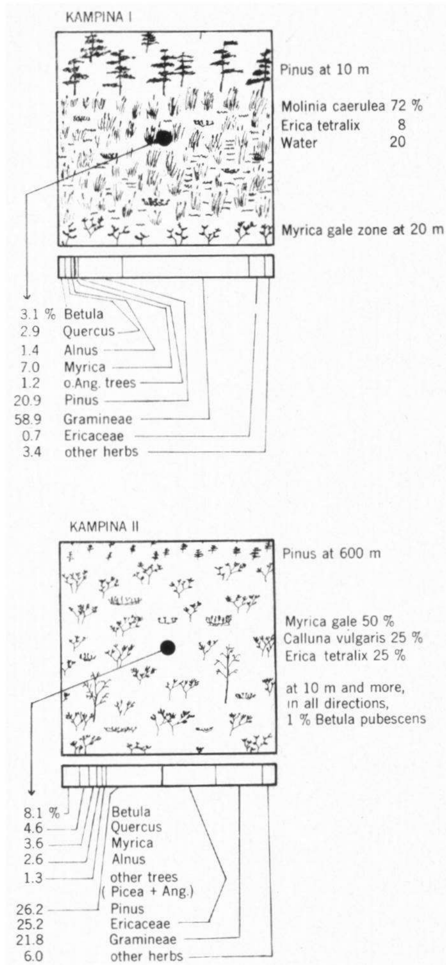

Fig. 7. Vegetation survey in Kampinase Heide

and the pollen content of the sample, but it should receive attention that *Myrica* has a low representation as compared to *Betula*, *Quercus*, and *Alnus*. Kampina II is an example of a drier spot, in a *Myricetum*. The representation of *Myrica* by 3.6% of the pollen in the sample is low.

In both of the Kampina samples *Quercus* pollen is present in percentages which are not far below those of *Betula*, though the nearest forest containing *Quercus* lies at a distance of 1 km. This is not surprising if the dispersal of the pollen from a *Quercus* tree is taken into account. If it is assumed that the velocity of the sedimentation of this pollen is 10 cm/s, that the tree is 20 m high and that the wind velocity is 10 m/s, the direct transport of the pollen from the top of the tree will be sufficient to cause the pollen grains to be precipitated at a distance of 2 km from the tree.

3.5. Kwelder near Sint-Annaland *(fig. 17)*

East of the village of Sint-Annaland, on the northern coast of the island of Tholen, lies a "kwelder", *i.e.* a salty mud flat which is only flooded when the water level is abnormally high. The term "kwelder" is taken from ABRAHAMSE *c.s.* (undated), though the local name in Zeeland for such a mud flat is "schor". A schor may, however, also be a mud flat which is regularly flooded at high water. The highest parts of the kwelder near Sint-Annaland are only flooded when high water at spring tide coincides with a strong NW wind, or else when high water coincides with a NW gale. The lower parts of the kwelder are, however, inundated regularly twice every 25 hours, as the mean tidal difference is about 3 m. It is evident that such conditions must cause a typical zonation in the vegetation. The kwelder is intersected by gullies, in which the kwelder is eroded by the currents, but in other places the deposition of sediment prevails; as a result, the course of the gullies is continually changing. Besides this, the area occupied by the kwelder becomes gradually narrower as the kwelder is washed away at the side of the main channel, the Krabbenkreek. In the course of time, the kwelder also becomes gradually higher by the deposition of fresh sediment on the occasions when it is flooded. In the same way as the other islands of the region, the island of Tholen was formed by the reclaiming of successive parts of the kwelder, which occupied the entire area. This process was started about 1200 A.D. (HOLLESTELLE 1878) when the polder Oudeland was formed. Shortly afterwards the castle was built in which Jacoba of Bavaria lived two centuries later. Within the enclosure formed by the remains of the main building of the castle, the author found a lump of peat embedded in the clay. Since all over the island agriculture has disturbed the superficial layers, this lump of peat was considered to be a rare witness of the transport of peat by tidal currents which took place before the building of the dyke, wherefore a sample was preserved. The following numbers of pollen grains were counted from this sample (percentages of AP and of NAP sum between brackets):

Quercus 23 (10), *Ulmus* 4 (2), *Tilia* 7 (3), *Fraxinus* 1 (1), *Fagus* 7 (3), *Salix* 3 (1), *Betula* 15 (7), *Alnus* 94 (42), *Carpinus* 3 (1), *Corylus* 58 (26), *Frangula* 1 (1), *Pinus* 11 (5), AP 224 (78% of TP), *Gramineae* 20 (31), *Cyperaceae* 3 (5), *Chenopodiaceae* 18 (28), *Ericaceae* 11 (17), *Compositae* *tub.* 3 (3), *Glaux* 1, *Artemisia* 2 (3), *Umbelliferae* 2 (2), *Hydrocotyle* 1, *Rubiaceae* 1, *Plantago lanceolata* 1, *Potamogeton* 1, *Lychnis* 2 (3), *Typha ang.* 1, NAP 65, *Polypodium vulgare* 2 (3), *Polypodiaceae* 73 (112), *Sphagnum* 34 (52). Diatoms: *Diploneis bombus* Ehr. 1, *Coscinodiscus centralis* Ehr. many fragments, *Rhaphoneis amphiceros* Ehr. 1. Total pollen 2 grains per microliter.

The polders in the Sint-Annaland region are younger than those of the Sint-Maartensdijk group. Damming up was started in the 15th century (A. HOLLESTELLE 1878), but the Suzannapolder, which borders the Krabbenkreek west of the village of Sint-Annaland, was not reclaimed before 1670. In 1860 the Johanna Maria polder, east of the village was reclaimed; from this time onwards the situation existed which is found in our time, the kwelder north of the dyke of the Johanna Mariapolder being left unreclaimed.

From a consideration of the conditions in the Krabbenkreek and on the mud flats it may be expected (1) that the lower parts of the kwelder will contain pollen of various types in the same proportion as present in the water at the time of deposition of the sediment, and (2) that the higher parts of the kwelder will be composed of clay and sand with not only the same organic elements as are found in the water, but, at the level where angiosperm vegetation begins to develop, also some pollen produced by these plants. The first angiospermous species to appear on a mud flat when it becomes sufficiently high is *Salicornia.* When the mud flat becomes progressively higher, other Chenopodiaceae follow, accompanied by *Triglochin maritimum.* (*Spartina townsendii,* though usually common in such habitats, is not abundant in the vicinity of the sampling site). On the kwelder, in still higher places, there is found *Limonium vulgare* and on the highest parts, which are only flooded by exceptionally high tides, there are *Aster tripolium* and various Gramineae. Chenopodiaceae are present everywhere (*e.g., Halimione portulacoides*). At the higher levels there occur also some less abundant species, *e.g. Spergularia media* (L.) C. Presl. The stand of vegetation on the kwelder around the place in which the samples were taken is composed as follows: *Triglochin maritimum* 15%, *Limonium vulgare* 44%, *Halimione portulacoides* 15%, *Gramineae* 24%, *Spergularia media* 2% (together 100%), total coverage 85% of the surface of the area, the remainder being bare or algae-covered clay.

At the side of a deep gully a profile was exposed from 0.5 to 1.0 m below the highest point of the kwelder. From this profile samples were taken in a vertical series at 10 cm distance apart from each other. The results of the analysis of the samples is shown in *fig. 17.* Although the regional vegetation elements are represented in the pollen from the kwelder profile, the elements deposited by the water prevail. The relatively high percentage of tubuliflorous *Compositae* in the two topmost layers is in accordance with the presence of *Aster tripolium* on the more elevated parts of the kwelder. It is quite clear, however, that owing to the considerable proportion of extraneous pollen introduced by tidal water currents, a reconstruction of the local flora from the palynological data would be unreliable. The tidal streams contain pollen from plants growing in the area itself, pollen introduced by the rivers and pollen leached out of the layers of clay, sand and peat in the region.

In the Keeten and the Mastgat the channels locally attain a depth of 40 m. The channels constantly change their course and thus large quantities of sand, clay and peat are displaced. It is probable that part of the pollen found in the kwelder sediment was redeposited from peat washed out in the channels of the larger streams. This may account for the Ericaceous pollen in the kwelder sediments, Ericaceae being abundantly present in the near-by peat deposits at Bergen op Zoom.

All the samples from the kwelder consist of clay mixed with some sand. They were collected on 10-6-1966. All the layers contained roots of the living plants growing on top of the deposit and also plant remains indicating that vegetation had started its development at a much lower level. The highest level in the diagram corresponds with a point 1.5 m above mean water level.

3.6. The sand bank in the Krabbenkreek *(Fig. 8)*[1]

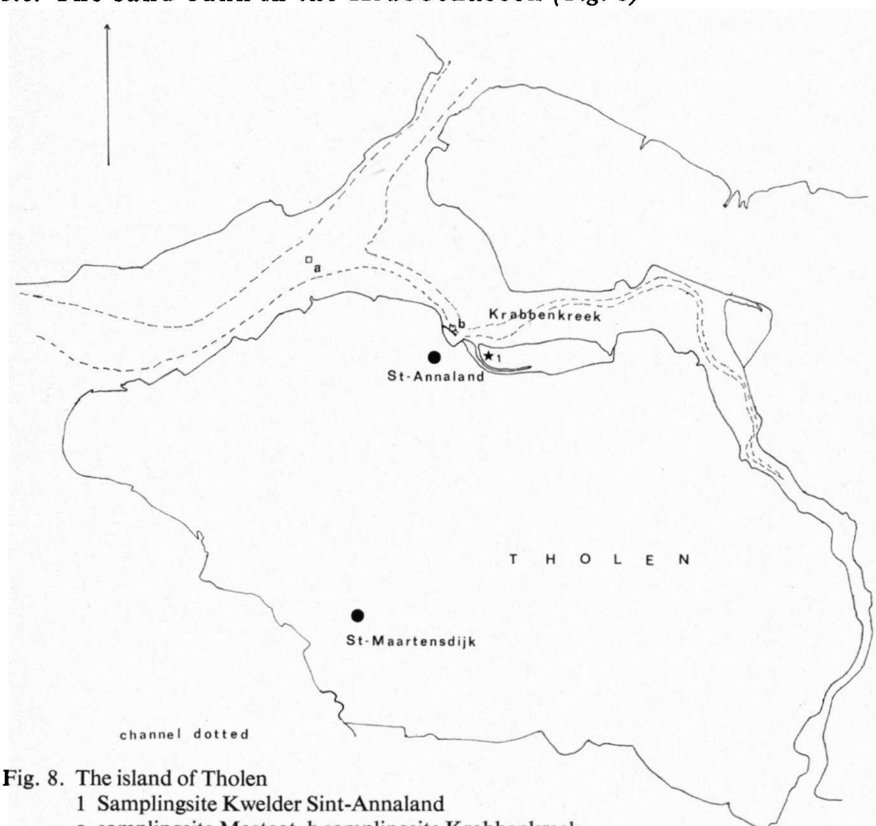

Fig. 8. The island of Tholen
1 Samplingsite Kwelder Sint-Annaland
a samplingsite Mastgat, b samplingsite Krabbenkreek.

The port side of the channel in the Krabbenkreek, in front of the harbour of Sint-Annaland, is bordered by a bank mainly consisting of sand and containing only a little clay. Two samples of this sand were collected at low water, one from

[1] complete records of the analysis are obtainable on request.

the top of the bank and one near the waterline. Here as in the kwelder the major part of the pollen content of the sediment appears to have come either from distant regions or from eroded more deeply lying layers. The percentage of *Pinus* pollen is remarkably low in comparison with the percentage of *Pinus* pollen in the water of the Krabbenkreek; this difference is greater than it is between the water and the clay of the kwelder, where it also exists. A possible explanation is, that *Pinus* pollen does not settle down as easily as pollen generally does. If this is indeed the case, *Pinus* pollen may be transported by water over greater distances than other pollen types. This constitutes an alternative explanation of the high *Pinus* percentage found by ZAGWIJN & VEENSTRA (1966) in samples from the North Sea bottom.

3.7. Banks of River Waal *(Fig. 4)*[1]

Near the place where the water samples have been taken (ferry station near Gameren) a sample of clay and one of sand were taken from two different spots in the river bank, where different types of sediment had been deposited. The analysis of the two samples was difficult due to the high charcoal content of the samples. (The term "charcoal" may here also comprise carbon particles accumulated from chimneys and black particles from shipping exhaust). Only a small number of pollen grains could be detected and, because the foreign particles kept the cover glass from the slide, the use of high magnifications was impossible. This renders the exact comparison of the pollen content of the sediment sample with the local vegetation type difficult. The riverside is covered by grass. The few trees in the vicinity are *Populus* trees. The pollen in the sediment shows no distinct relation to this vegetation type and it is probably a mixture originating from various regions.

No pollen was found in the samples taken from the river bank near Hedikhuizen.

3.8. Water samples from the Krabbenkreek and from the rivers Meuse and Waal *(Fig. 16)*

At monthly intervals samples were collected at the following places:
Krabbenkreek: northern side of harbour dam of Sint-Annaland.
R. Waal: Gameren ferry station.
R. Meuse: Hedikhuizen ferry station.
The basic idea started from was that, if the river water contains mainly pollen originating from the regional stand of vegetation, the composition of the pollen content will show seasonal variations. If, however, the river water contains mainly pollen originating from various regions and having been transported over long distances, the seasonal variations in the regional pollen production will not become manifest in the composition of the pollen content at the sampling site, but they will become masked.

As is apparent from the diagram *(fig. 16)*, the seasonal variation was slight. *Alnus glutinosa* produces its pollen in early spring, *i.e.* Februari and March

[1] Complete records of the analysis are obtainable on request.

(VAN OOSTSTROOM 1956). In the river Meuse a maximum of *Alnus* pollen is found in March and April. If a delay of a few weeks is taken into account, after which the pollen reaches the sampling site, there seems to exist a correlation with the flowering time of the trees. In the Krabbenkreek an *Alnus* maximum in Februari was recorded. In the river Waal, the *Alnus* spring maximum is present in Februari and March, but it is not so pronounced as the maximum in November, for which there seems to be no explanation.

The dominant tree pollen in all three series of observations is *Pinus*. The *Pinus* minima coincide with the *Alnus* maxima. This could not be otherwise, as the values represented in the diagram are percentages. *Pinus sylvestris* produces its pollen in May and early June (VAN OOSTSTROOM 1956). In the Krabbenkreek there is only a, hardly distinct, maximum in June. The summer maxima in the other two series are also insignificant. In the NAP columns a few maxima are distinct (Cereals in June in R. Waal; *Compositae tub.* in September in rivers Meuse and Waal; *Compositae lig.* in May in R. Waal; *Ranunculus* in May in River Waal) which present a slight evidence of a relation with the seasonal pollen production of some plant groups.

From all these considerations it follows that the effect of fluctuations in the pollen production by the regional vegetation on the pollen content of the river water is small. This forms an indication, that the pollen content of the water is not a true representative of the regional pollen production. As the pollen present in the river bank sediment is precipitated from this water, the conclusion must be that the pollen content of the river bank sediment is not a reliable source of information about the composition of the regional vegetation.

3.9. Clay and sand from channels in the Waddenzee *(Vide tables p. I-XII)*

The Waddenzee is an extension of the North Sea lying between the mainland and the Frisian Islands. The word "wad" signifies a tidal flat which is exposed at low water. The tidal flat is intersected by gullies.

A few of these gullies retain a depth of water sufficient for craft of shallow draught. The mean tidal difference is 16 dm (at Harlingen; Getijtafels 1967). Such channels are buoyed and bear names. The terms "Vlieter" and "Oude Vlie" are such names.

Four samples were taken from the bottom of such channels by kind cooperation of the Institute for Marine Biological Research at Den Helder.

The two samples from the Oude Vlie consist of sand and were collected at a depth of 8 m (OV 36) and 10 m (OV 34) respectively. The important contribution of *Betula* in OV 34 shows that the pollen must be largely derived from sources older than Holocene. It is probably for the greater part of Eemien origin. (or, possibly, the sand belongs to an Eemien deposit). The presence of Eemien at about this level has been established in the region of the Oude Vlie (personal communication by Mr. D. Eisma). OV 36 has a somewhat lower *Betula* content. Two of the 31 *Gramineae* grains were of a cereal type. Two grains of *Plantago lanceolata* were found. The sample contained also *Aesculus, Castanea, Juglans* and *Picea.* It may be concluded that this sand probably contains a mixture of pollen of Pleistocene origin with some Holocene and recent pollen, which is partly of foreign origin. The same probably holds true for the OV 36 sample, though in OV 34 the contribution of the Eemien is probably more important.

The samples V5 and V7, from the Vlieter, consist of clay. The sample OV 7 contained much charcoal.

The samples probably contain a mixture of recent pollen (cereals, *Castanea, Plantago lanceolata)* and pollen from Holocene – or, perhaps, older – layers (the most convincing feature is the high *Corylus* percentage). The *Ericaceae* pollen may have been introduced into the region in recent historical times, before the separation of the Waddenzee from the Zuiderzee, in which case it may have been produced in the Veluwe region.

3.10. Clay from mud flats in the Waddenzee

Apart from the samples taken from channels in the Waddenzee, clay samples from the surface of the mud flats were taken at low water. This was kindly done by Miss Reina Posthumus, and by Mr. J. W. Smit. The results of the analysis are as follows (the figures between brackets represent percentages):

HOLWERD:
Quercus 29 (20% of AP sum), *Ulmus* 3 (2), *Fraxinus* 1 (1), *Betula* 18 (14), *Alnus* 25 (18), *Salix* 5 (3), *Carpinus* 1 (1), *Corylus* 21 (15), *Acer* 2 (1), *Juglans* 1 (1), *Myrica* 1 (1), *Ilex* 2 (1), *Sambucus* 1 (1), *Pinus* 29 (20), *Picea* 4 (3), AP 143 (75% of TP).
Gramineae 17 (35% of NAP), *Cyperaceae* 2 (4), *Chenopodiaceae* 5 (10), *Ericaceae* 6, of which 2 *Vaccinium* type(12), *Artemisia* 2 (4), *Cruciferae* 2 (4), *Ranunculus* 1, *Lychnis* 1, *Typha angustifolia* 2 (4), *Plantago lanceolata* 2 (4), *Triglochin* 1, *Rumex acetosella* 1, unidentified 6, NAP 49, *Polypodium vulgare* 2, *Polypodiaceae* 10, *Sphagnum* 8. TP 12/microlitre.

NES
Quercus 19 (17), *Ulmus* 1, *Fraxinus* 1, *Fagus* 1, *Alnus* 29 (26), *Betula* 4 (4), *Corylus* 24 (22), *Salix* 1, *Pinus* 27 (25), *Picea* 2, AP 110 (71% of TP), *Gramineae* 14 (32), *Cyperaceae* 3 (7), *Chenopodiaceae* 8 (18), *Ericaceae* 8 (18), *Artemisia* 1, *Cruciferae* 2, cereal grass 1, *Solanum dulcamara* 1, *Lychnis* 1, *Rumex acetosella* 2 (5), NAP 44, *Polypodiaceae* 12, *Sphagnum* 7, TP 21/microlitre.

SCHIERMONNIKOOG
Quercus 31 (16% of AP), *Tilia* 1, *Fraxinus* 3 (2), *Ulmus* 2 (1), *Fagus* 1, *Betula* 19 (10), *Alnus* 22 (11), *Corylus* 46 (24), *Acer* 2 (1), *Salix* 4 (2), *Sambucus* 1, *Populus* 1, *Pinus* 53 (27), *Picea* 5 (3), *Abies* 2 (1), AP 194 (70% of TP), *Gramineae* 22 (34% of NAP), *Cyperaceae* 8 (9), *Chenopodiaceae* 9 (11), *Ericaceae* 13 (15), *Compositae tub.* 2 (2), *Compositae lig.* 2, *Artemisia* 1, *Mercurialis* 1, *Umbelliferae* 2, *Cruciferae* 4 (5), *Ranunculus* 1, *Plantago lanceolata* 2, *P. maior* 1, *Papaver* 1, *Liliaceae* 1, *Rumex acetosella* 4 (5), *R. acetosa* 1, *Linum catharticum* 1, *Typha latifolia* 1, *Scrophulariaceae* 1, *Filipendula* 1, *Labiatae* 1, *Potentilla* 1, undefined 1, NAP 85, *Polypodiaceae* 12 (14% of NAP) *Sphagnum* 4 (5), *Pediastrum* frequent, TP 475/microlitre.

VLIELAND, LANGE PAAL (Waddenzee coast of the island), close to the shore. Black mud with much organic material and a strong smell of H_2S.
Quercus 40 (18), *Ulmus* 7 (3), *Tilia* 1 (0,5), *Fraxinus* 1 (0,5), *Betula* 29 (13), *Acer* 2 (1), *Alnus* 33 (15), *Corylus* 26 (12), *Hippophae* 1 (0,5), *Populus* 1 (0,5), *Fagus* 2 (1), *Salix* 1 (0,5), *Aesculus* 1 (0,5), *Myrica* 1 (0,5), *Carpinus* 5 (2), *Rhamnus* 1 (0,5), *Castanea* 1 (0,5), *Pinus* 65 (30), *Abies* 2 (1), AP 220 (64), *Gramineae* 67 (53% of NAP), of which 4 cereal, *Cyperaceae* 8 (6), *Chenopodiaceae* 12 (9), *Ericaceae* 10 (8), *Compositae tub.* 1 (1), *Compositae lig.* 1, *Rumex*

maritimus 1, *Typha angustifolia* 2 (2), *Ranunculus* 1, *Labiatae* 1, *Papaver* 1, *Sanguisorba offininalis* 1, *Valeriana officinalis* 1, *Cruciferae* 4, *Plantago lanceolata* 4 (4), *Rumex acetosa* 4 (3), *R. acetosella* 2 (2), NAP 127, *Polypodiaceae* 21 (17), *Sphagnum* 3 (2). Slides densily occupied by frustulae of *Melosira* species and containing also some pennate diatom fragments.

WEST OF PIER KOEHOL, 10 m from the coast.
Quercus 32 (14), *Ulmus* 7 (3), *Tilia* 4 (2), *Fraxinus* 1 (0,4), *Betula* 25 (11), *Alnus* 42 (19), *Corylus* 37 (17), *Sambucus* 1 (0,4), *Fagus* 4 (2), *Salix* 3 (1), *Populus* 1 (0,4), *Myrica* 2 (1), *Carpinus* 2 (1), *Pinus* 58 (26), *Picea* 4 (2), *Abies* 1 (0,4), AP 224 (71), *Gramineae* 33 (35) of which 4 cereal, *Cyperaceae* 6 (6), *Chenopodiaceae* 9 (10), *Ericaceae* 17 (18), *Compositae tub.* 2 (2), *Cruciferae* 5 (5), *Plantago lanceolata* 4 (4), 1 (1), *Rumex acetosella* 5 (5), *Ranunculus* 2 (2), *Lychnis* 1, *Typha angustifolia* 3 (3), *Filipendula* 1, *Gentiana pneumonanthe* 1, *Plantago major* 1, *Typha latifolia* 1, undefined 1, NAP 94, *Polypodium vulgare* 1, *Polypodiaceae* 41 (44), *Sphagnum* 2 (2), *Pediastrum* in high quantity.

EAST OF PIER KOEHOL, 80 m from shore.
Quercus 20 (% same), *Ulmus* 3, *Tilia* 1, *Betula* 6, *Alnus* 16, *Corylus* 31, *Fagus* 3, *Pinus* 20, *Picea* 2, AP 102 (72% of TP), *Gramineae* 14 (36% of NAP), of which 2 cereal, *Cyperaceae* 5 (13), *Chenopodiaceae* 5 (13), *Ericaceae* 6 (15), *Compositae lig.* 1 (3), *Artemisia* 1, *Umbelliferae* 1, *Cruciferae* 1, *Plantago lanceolata* 1, *Typha angustifolia* 2 (5), *Rumex martimus* 1, unidentified 1, NAP 39, *Polypodiaceae* 15 (34), *Sphagnum* 3 (8).

EAST OF PIER KOEHOL, 10 m from shore.
Quercus 41 (17), *Ulmus* 9 (4), *Tilia* 3 (1), *Fraxinus* 5 (2), *Alnus* 40 (17), *Corylus* 47 (20), *Betula* 35 (14), *Juglans* 1 (0,4), *Fagus* 4 (2), *Acer* 1, *Salix* 3 (1), *Carpinus* 1, *Rhamnus* 1, *Aesculus* 1, *Pinus* 48 (20), *Picea* 2 (1), AP 242 (72), *Gramineae* 35 (% same) of which 3 cereal, *Cyperaceae* 4, *Chenopodiaceae* 18, *Ericaceae* 14, *Compositae lig.* 1, *Artemisia* 3, *Umbelliferae* 2, *Plantago lanceolata* 3, *Lychnis* 1, *Rumex acetosella* 1, *R. acetosa* 3, *Trifolium* 2, *Typha angustifolia* 2, *Ranunculus* 3, *Solanum dulcamara* 1, *Lotus* 1, undefined 2, NAP 96, *Polypodiaceae* 33, *Pteridium* 1, *Sphagnum* 6, *Pediastrum* present.

As only minor parts of the Frisian Islands are forested, the high AP/TP ratio (about 75% in the three samples) in the sediment samples can not be considered to represent the regional vegetation type.

The *Juglans* pollen present may have been brought down by the rivers Rhine or Meuse, but some *Juglans* trees occur in the Netherlands in the present time.

The presence of important quantities of *Corylus* pollen indicates that the pollen in the Waddenzee sediments is largely derived from other sources than the actually existing stands of vegetation in the entire region. *Corylus avellana* is of highly rare occurrence in the region; this applies to both the Frisian Islands and the coast of the mainland of Friesland and Groningen.

The percentages of Chenopodiaceous pollen are relatively low. It follows that, as was already to be expected from other considerations, the mud flats contain a mixture of pollen produced in a variety of regions and presumably also much secondary pollen.

As regards the samples from Nes and Schiermonnikoog it is equally difficult to assess which part of the pollen present in the sample is related to regional stands of vegetation. Some of the pollen may have been produced in the region in recent times, but the low content of cereal pollen suggests that the regionally produced pollen has no important share in the pollen deposited in the clay of the mud flats.

4. Determination of pollen density in horizontal series of samples

4.1. Pollen density in the kwelder near Sint-Annaland

In the kwelder near Sint-Annaland samples were taken at three levels which were about 15 cm apart in vertical direction; in each of the levels three samples were taken at horizontal distances of 4 m. The nine samples were processed after addition of *Aesculus* pollen. It was known from the previous analysis of samples from the kwelder that the natural *Aesculus* pollen content of the sediment is negligible. The density values found are represented in *fig. 9*. They give an impression concerning the variations which may occur in the pollen density of a sediment. Some of the variations observed are to great to be considered as statistical variations of samples from one population. They constitute a warning against basing conclusions on incidental variations occurring in a sequence of density values. This may, of course, also apply to vertical series. Hence, the interpretation of "absolute" pollen diagrams will require sufficient information on this type of variation in different deposits.

ST-ANNALAND

TP/mm³

36	67	33
85	46	38
15	27	15

sample order:

1	2	3
4	5	6
7	8	9

P. grains/mm³				% of AP		
4.1	6.9	3.8	Quercus	19	19	25
5.3	11.6	4.1	Alnus	24	32	27
4.8	10.0	2.8	Corylus	22	27	19
8.5	6.7	5.4	Q.	16	22	23
16.6	9.0	7.4	A.	32	29	31
14.6	7.4	4.1	C.	28	24	18
3.0	2.9	1.9	Q.	31	17	19
2.3	6.1	2.9	A.	24	36	30
1.7	3.4	2.3	C.	17	20	23

P. grains/mm³				% of NAP		
3.2	6.4	2.2	Gramineae	23	20	12
4.2	17.2	13.0	Chenopodiaceae	31	55	70
2.8	2.0	1.1	Ericaceae	21	6	6
4.7	4.1	3.6	G.	14	27	26
14.3	3.1	3.8	C.	42	20	27
10.2	3.9	2.5	A.	30	26	18
0.7	1.9	1.1	G.	15	19	20
1.9	3.4	1.6	C.	33	34	29
1.4	2.0	1.0	A.	24	20	18

Fig. 9. Pollen density in the Sint-Annaland profile.

4.2. Pollen density in a peat profile near Bergen op Zoom *(Fig. 10)*

The channel in the outer part of the harbour of Bergen op Zoom, outside the lock, is bordered by a peat profile which was cut out in the local peat deposits when the harbour was constructed. This peat layer is accessible at low water. At two stratigraphically determined levels at a vertical distance of 30 cm apart, four samples were taken in each of the levels at horizontal distances of 1 m. These peat samples were analysed after addition of *Aesculus* pollen. From an earlier analysis, performed by the Geological Survey of the Netherlands, it was known that no *Aesculus* pollen occurs naturally in this peat. The peat is considered to be of late-subboreal age (information obtained by courtesy of Dr. W. H. Zagwijn).

The data obtained from the density determinations in the eight samples are represented in *fig. 10*.

BERGEN op ZOOM

TP/mm³	21	39	55	17	
	73	107	91	98	
P/mm³	1.9	4.3	3.0	1.8	Quercus
	3.9	14.2	11.0	3.3	Alnus
	5.2	7.8	20.8	1.7	Ericaceae
	4.3	7.4	7.1	6.0	Q.
	29.2	29.5	27.1	39.6	A.
	10.6	35.0	23.0	18.2	E.
% of AP	18	16	10	18	Q.
	35	53	37	33	A.
% of NAP	51	69	81	52	E.
	8	11	11	8	Q.
	51	44	42	54	A.
	65	88	85	76	E.
sample order	1	2	3	4	
	5	6	7	8	

Fig. 10. Pollen density in the Bergen op Zoom profile.

Evidently there exist in this peat deposit differences in pollen density at one level, which are not smaller than those found in the clay near Sint-Annaland. It is possible that the differences found within one level are partly due to errors in the visual correlation of the levels in the peat.

As the information concerning the variations in pollen density within one level is still insufficient for the interpretation of incidental variations occurring in a vertical series of samples, the author has refrained from drawing complete "absolute" pollen diagrams relating to the cores from Schipluiden and Geldermalsen.

5. ANALYSIS OF CORES

5.1. Schipluiden 1966 *(Fig. 21)*

In June 1966 the Geological Survey of the Netherlands performed a boring near Schipluiden, Zuid-Holland. The top of the core corresponds to the level of 28 dm below Nieuw Amsterdams Peil. The composition of the core is given in *table 1*.

Table 1. Composition of the Schipluiden core.

0–30 cm	dark grey clay
30–50 cm	gyttja
50–110 cm	peat, mainly *Sphagnum*, some *Phragmites*
111–114 cm	gyttja
114–125 cm	transition gyttja to *Phragmites* peat
125–130 cm	amorphous peat
130–140 cm	peat with undefined plant rests
140–200 cm	*Phragmites* peat
200–235 cm	amorphous peat with much charcoal
240–315 cm	clay (with marine diatoms)
315–365 cm	peat
365–375 cm	peat with clay
375–435 cm	brown clay
435–445 cm	gyttja
445–480 cm	peat with much charcoal
480–800 cm	clay. At 600 cm some *Phragmites* (marine diatoms in the majority of the samples)

Table 2 gives the figures for the total pollen density of the samples from this section.

Table 2. Pollen density in the Schipluiden core.

Depth in cm	pollen grains per mm^3	Depth in cm	pollen grains per mm^3	Depth in cm	pollen grains per mm^3
20	101	205	15	475	221
35	368	215	9	482	56
45	295	225	18	495	108
59	74	230	–	515	73
68	81	240	70	535	143
75	14	259	80	555	646
85	11	280	123	575	71
95	28	300	280	592	43
105	11	320	32	615	67
111	493	330	103	635	88
115	171	340	81	655	12
121	115	350	95	675	60
125	19	361	46	695	82
136	6	369	121	715	53
145	3	580	63	735	81
155	1	398	41	755	80
165	1	412	96	775	116
175	2	430	274	795	113
185	4	440	155		
195	6	460	143		

Table 3. Radiocarbon datings in a number of levels in the Schipluiden core; depth of the levels are given also in relation to N.A.P.

cm	below N.A.P.	years	B.P.
105	385	3590	50
125	405	3220	75
225	505	4430	60
310	590	4785	60
360	640	5050	45
470	750	6020	70

Fig. 11. Pollen-analytical characterization of the Holocene in the Western part of the Netherlands, from Jelgersma (1961).

Subdivision by Blytt-Sernander	Zones and subzones used at the Palaeobotanical Laboratory of the Geological Survey		Pollen-analytical characterization in the Netherlands	Approximated age in years before present (correction for Suess effect added)
		Vb	Carpinus curve continuous; Fagus shows high values Sometimes Fagus shows a temporary decrease at the transition Va/Vb	
Subatlantic	V			2,000 B.P.
		Va	Increase of Fagus curve to above 5 %	
				2,900 B.P.
		IVb	Fagus curve continuous; reaches values of about 2 %	
Subboreal	IV			3,800 B.P.
		IVa	Decrease of Ulmus curve; Fagus with low values present	
				5,300 B.P.
Atlantic	III		Alnus and Quercetum Mixtum dominant. Ulmus important, Pinus present with very low values	
				8,000 B.P.
		IIb	Beginning of continuous Alnus curve	
Boreal	II			8,400 B.P.
		IIa	Expansion of Quercetum mixtum (Quercus);	
				8,700 B.P.
		Ic	Expansion of Corylus; Pinus high values	
				9,000 B.P.
		Ib	Pinus dominant	
Preboreal	I			9,700 B.P.
		Ia	Betula dominant	
Late-Glacial				10,300 B.P.

Radiocarbon datings were obtained from a number of levels. They are given in *table 3*, which gives also the depth of the levels in relation to N.A.P.

Fig. 11 shows the palynological characterization of the Holocene in this region in relation to the age of the deposits. By means of the radio carbon data obtained from the Schipluiden core, it can be determined to which of the zones of *fig. 11* the deposits in this core belong.

The upper gyttja deposit and the peat immediately below it belong to zone IVb or to zone V. The peat found at a depth from 125 to 235 cm belongs to zone IV, but it can not be read from the radio carbon data if both of the sub-zones IVa and IVb are represented. The third peat deposit, found at a depth between 315 and 365 cm, must belong to zone IVa. The lower limit of the fourth peat layer found between 445 and 480 cm from the top of the core was dated as 6020 years B.P., which indicates that this peat belongs to zone III. From the radio carbon data available it can not be determined if it extends into zone IVa. There is some contradiction found in the ^{14}C data ascertained from the levels 105 and 125 cm. Inversion of deposits is possible as a result of agriculture but in this case it seems more likely that the younger age, found for the 125 cm level, is due to a contamination of the sample.

Since the percentages of *Fagus* do not exceed 5% in the upper peat deposit and *Carpinus* is not continuously present there, it is not possible to deduce from the palynological data if this peat consists partly of deposits belonging to zone V. It can only be stated that it must be younger than zone IVa.

The base of the second peat layer, dated 4430 B.P., belongs to zone IVa. The low percentages of *Ulmus* and *Fagus* found here are consistent with the characteristics described for this zone in *fig. 11*.

Equally consistent with the usual features of *fig. 11* are the absence of *Fagus* and the low percentages of *Ulmus* in the third peat layer, which also belongs to zone IVa according to the radio carbon dating. Although this dating indicates that the peat started its development at the beginning of the period, a decrease in the representation of *Ulmus* can not be observed here.

The clay deposit between 375 and 435 cm is located between two peat layers both belonging to zone IVa. The high content of Chenopodiaceous pollen and the presence of marine diatoms make probable that this clay was deposited during a marine transgression, which may be identical with the early-subboreal transgression mentioned in *figs. 12* and *13*.

The lowest peat layer, which according to the radio carbon data belongs to zone III, contains *Ulmus* pollen in percentages which are consistent with the description of the palynological features in *fig. 11*. The percentages of *Pinus* are low and Quercetum mixtum is, together with *Alnus*, dominating in the forest pollen. All of this is in accordance with *fig. 11*.

There appears to be a slight discrepancy with the depth scale of *fig. 12* in that the peat deposit in the interval between 315 and 360 cm (595–640 cm below N.A.P.) is of subboreal age according to both the radio carbon data and the palynological features, but would be of late Atlantic age according to the depth scale.

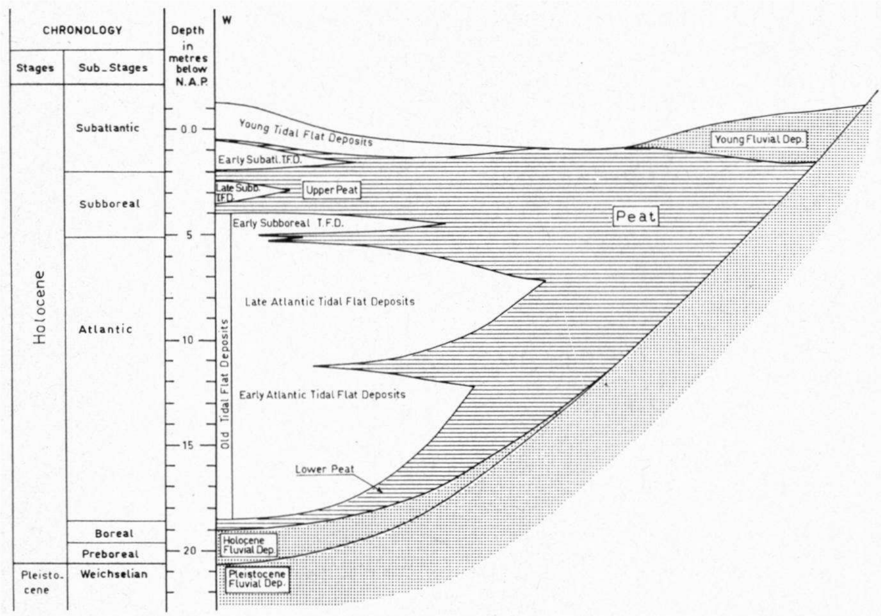

Fig. 12. Schematic section through the Holocene in the Western part of the Netherlands Horizontal distances not to scale. From Jelgersma (1961).

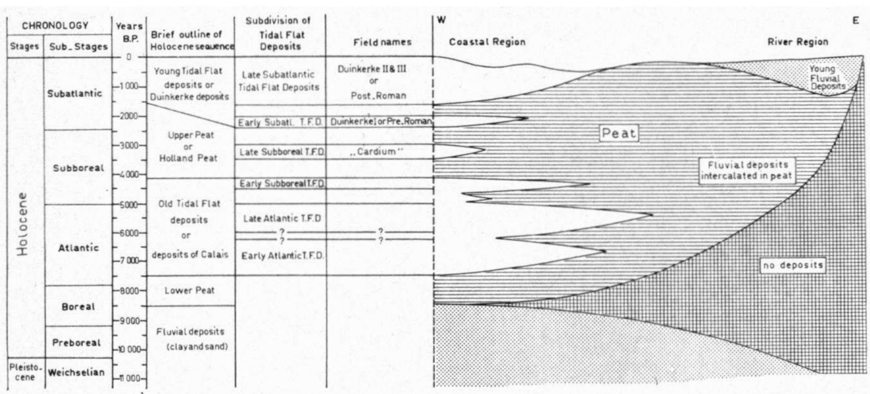

Fig. 13. The same section as in fig. 12, plotted on a time scale. From Jelgersma (1961).

A comparison of the third peat layer with the second one shows that in the third peat layer there is a strong representation of *Chenopodiaceae*, but in the second peat layer *Chenopodiaceae* attain only low percentage values; this peat starts its development with a high representation of *Cyperaceae*. Probably the lower of these peat layers developed in a brackish environment and the younger one in an oligohaline milieu. This indicates that either the sea level was lower in relation to the land or the sea had no longer access to the area.

In the series of samples from 225 cm to 111 cm there is a regular decrease of

Table 4. Number of pollen grains per cm^3 in the Schipluiden core.

Depth in cm	pollen grains per cm^3				
	Quercus	*Alnus*	*Pinus*	*Gramineae*	*Cyperaceae*
105	1890	2050	284	2140	790
111	25800	74000	660	256000	3970
115	10300	29000	930	78800	5800
121	6140	13500	1495	55900	7460
125	2780	4850	405	4110	1620
136	1160	1050	76	1310	943
145	630	995	41	529	345
155	114	130	–	114	211
165	291	446	–	795	680
175	259	282	23	164	1105
185	690	380	70	719	1269
195	10610	4315	1440	5460	30250
205	1970	918	230	918	8050
215	1230	700	308	615	4950
225	2420	1310		1010	8160

the pollen density as far as the 155 cm level; the density increases from 145 cm onward until at 111 cm a maximum is reached. This interval will be considered more closely. A calculation of the densities of *Quercus, Alnus, Pinus, Gramineae,* and *Cyperaceae* pollen is given in *table 4.*

As can be seen from the table the five pollen types all have their minimum density at the 155 cm level. The peat is mainly composed of remains of *Cyperaceae.* From 145 cm upwards the environment became drier; tree and grass pollen became more important in relation to *Cyperaceae* pollen. Between 225 and 145 cm the AP/TP ratio increases, whereas the pollen density decreases. This may signify that gradually less pollen was produced in the immediate vicinity and distant forests became relatively more important as a pollen source. The density figures suggest that the forest did not come nearer, or at any rate that the increasing percentage of forest pollen is not due to a rise in the amount of forest pollen.

More information about pollen density is needed for a reliable explanation of such density changes. It will, for instance, be desirable to know if certain climatic or other general influences changed the pollen productivity of all the vegetational elements in this country.

Fig. 14 represents the numbers of arboreal pollen grains (bars) and the numbers of herbaceous pollen grains (broken line) per microlitre of sediment. The broken line for the NAP density was chosen for the sake of legibility and it has the same meaning as a series of bars.

From 482 to 475 cm there is a sharp increase in the NAP density and there is another rise in the interval between 440 and 430 cm. The interpretation of these two phenomena is difficult in the absence of sufficient radio carbon data. The level of 430 cm is not dated and the sedimentation rate of the clay deposit below 480 cm is unknown. The interpretation of the combined phenomena is, therefore, difficult and even more so because in this case pollen precipitation

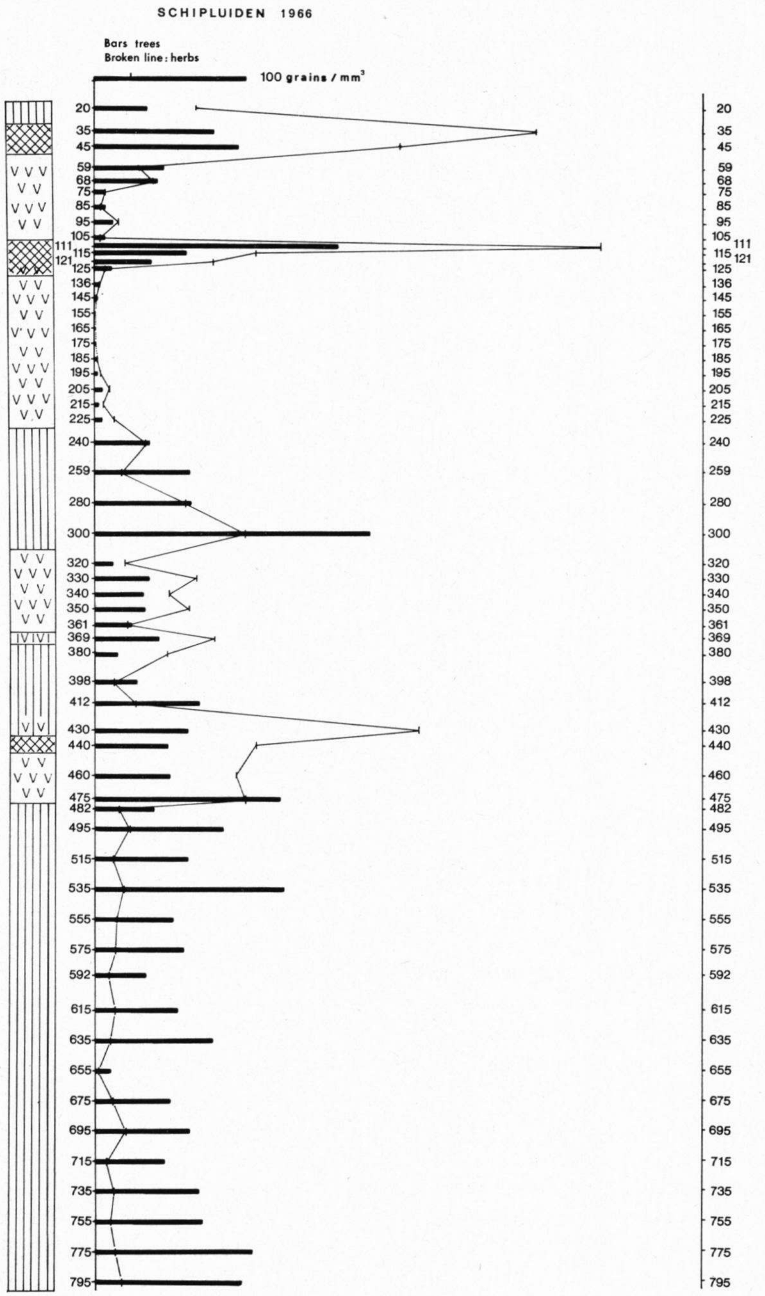

Fig. 14. AP and NAP densities in the Schipluiden core.

from the air has to be compared with the precipitation of water-borne pollen.

Nevertheless, as this case will demonstrate, the estimation of pollen densities may contribute to our knowledge of pollen transport. The peat-gyttja complex is rich in herbaceous pollen. If it has functioned as a source of pollen deposited afterwards in clay, this clay deposit may contain an important fraction of NAP pollen. Accordingly the clay between the levels 430 and 369 cm shows a higher NAP density than the clay between 795 and 482 cm; this is at least so at the levels 430 and 412 cm and at 380 and 369 cm. This is in accordance with the fact that fragments of peat were seen to be present in the clay at naked-eye view, as is represented in the lithological column of *fig. 21*. Both the NAP/TP ratio and the NAP density seem to be correlated with the peat content. It is possible that some of the peat found between the levels 475 cm and 450 cm, or an overlying peat layer of about the same composition which has completely been washed away, was eroded and partly redeposited dispersed in clay. In the Sint-Annaland kwelder clay a comparable phenomenon was observed; there too the high percentage of NAP pollen in the clay may be attributed to a redeposition of pollen from peat.

Between the levels of 795 cm and 245 cm the tree pollen density remains approximately constant in the clay (the sample 300 cm excepted). This constancy of the pollen density, especially that of the tree pollen density, may be explained on the supposition that the proportion of the sedimentation rates of the pollen and of the mineral constituents of the clay remained approximately constant; as there is no reason to suppose that the sedimentation rate of the clay deposit itself was constant, the constancy of this proportion means that the pollen was probably largely extraneous pollen, brought down with the river water, and produced in distant forested regions.

From 430 cm upwards, herbaceous pollen appears as if superimposed upon the extraneous arboreal pollen. Possibly this may be traced back to the peat-gyttja complex between 475 and 440 cm, which is rich in NAP pollen.

In *fig. 21* the general pollen density in the interval between 225 and 115 cm at first decreases, *viz.* from 225 to 155 cm, to increase again from 145 to 111 cm. The column in *fig. 21* representing the AP/TP ratio shows almost the reverse of the density column. This leads to the question how this inverse relation between the AP/NAP ratio and the general pollen density may be explained.

The calculation of the AP density and of the NAP density in this interval, the results of which are represented in *fig. 14*, show that both the AP and the NAP densities first decrease to increase afterwards. There is no increase in the AP density in the interval where the AP/TP ratio increases. A tentative interpretation is, that but little pollen was produced *in situ* when the peat was being formed. Herbaceous pollen being usually an important constituent of the general pollen precipitation in an area where peat formation takes place, the arboral pollen coming from afar temporarily became a relatively more important, though not dominant, constituent of the pollen rain. The phenomenon can not be satisfactorily explained by assuming a higher rate of accumulation of the peat.

5.2. Geldermalsen 1967 *(Fig. 24)*

The core, obtained by means of Dachnovsky sounding, contains clay, mostly containing peat fragments, and two sand layers. As the topmost layer of about

Table 5. Composition of the Geldermalsen core.

125–160 cm	brown clay (i.e., colored brown by humus); some charcoal at 125 cm.	320–330	clay with peat and remains of *Phragmites*
160–260	grey clay	330–480	brown clay and some charcoal
260–270	grey sand with some plant débris	480–495	clay with peat
270–305	grey clay	495–632	brown clay
305–307	transition clay to peat	632–640	grey sand
307–320	black mixture of clay and peat	640–647	light grey, coarse sand

Table 6. Pollen densities in the Geldermalsen core.

depth in cm	pollen grains per mm³	depth in cm	pollen grains per mm³	depth in cm	pollen grains per mm³
125	9	320	487	475	430
143	9	325	235	490	497
155	36	330	235	505	357
165	53	330	291	522	165
175	92	340	414	542	195
183	137	350	593	557	531
195	363	365	240	570	182
205	162	378	128	583	391
240	25	385	170	598	453
265	12	397	93	609	286
280	237	415	165	624	176
290	314	430	107	630	212
300	804	445	502	638	8
307	610	458	1169	646	7

1 m thickness was considered to be disturbed by agriculture, the analysis was started with a sample from the level of 125 cm. From this level downwards the composition of the core is given in *table 5*. In *table 6*, the pollen densities found in this section are given.

Since this core does not contain any layers of pure peat, water-borne pollen produced at unknown distances must be expected to be present. The percentages of *Picea* and *Abies* are, however, low. Therefore, a comparison with the stratigraphy of *fig. 11* is permissible.

There is a weak evidence of the "*Ulmus* fall" being present between the levels 397 and 365 cm. This would mark the transition from zone III to zone IVa. *Fagus* is, however, present at much lower levels. This may be explained in two ways: either these levels belong to zone IV, or the *Fagus* pollen was brought down from regions where the presence of *Fagus* begins earlier.

In the vicinity of the place where this core was obtained, the Geological Survey of the Netherlands had already performed a boring in 1958. The pollen diagram representing the data obtained from this core closely resembles the diagram of *fig. 18*. In this core there was a peat band between 380 and 330 cm. A radio carbon dating at the level of 380 cm yielded an age of 5275 ± 90 (GRN 1941). This is the age of the transition between zone III and zone IVa.

Hence, the clay deposit at the level of 365 cm must be considered to belong to zone III, which implies that the *Fagus* pollen must have been brought down from remote regions.

In the interval between 205 and 583 cm there are several high percentage values for *Tilia*. The densities of *Tilia* pollen are given in *table 7*.

Table 7. Densities of *Tilia* pollen in the Geldermalsen core.

Depth in cm	grains per ml.	Depth in cm	grains per ml	Depth in cm	grains per ml
205	1495	385	11000	598	2850
240	2350	397	9650	609	17200
265	5250	415	700	624	14180
280	6450	450	3695	630	2850
290	1320	445	1029	638	265
300	22650	458	29500	646	0
307	3675	475	4610		
320	1785	490	16500		
330	4050	522	11284		
340	1330	542	16500		
350	1516	557	28150		
365	2700	570	11250		
378	7800	583	9560		

A comparison of *table 7* with the percentage diagram *(fig. 18)* shows that the percentage maxima for *Tilia* do not coincide with the density maxima for this pollen type. The high *Tilia* percentages coincide with a low general pollen density. This may be partly due to a lower *Alnus* density in the samples taken at the same levels.

In the sample taken at a depth of 490 cm and in the interval between 350 and 307 cm, where much peat is present in the clay, high densities of herbaceous pollen occur, as is shown in *fig. 15*. These NAP densities may be explained as being caused by the presence of the peat, in the same way as was suggested in the interpretation of the Schipluiden diagram. The form of the NAP density line in *fig. 15* requires a different interpretation, as no peat was present in the clay between 240 and 183 cm. Between 240 and 205 cm a few samples were found to yield no pollen. At the level of 205 cm a high NAP density suddenly appears, which reaches a maximum value at the level of 195 cm. Gramineous pollen is abundantly present at this level. Possibly the river had broad grass-covered banks. At the level of 195 cm there is also a high total pollen density, which may be explained by a low sedimentation rate of the mineral components of the sediment in relation to the pollen sedimentation rate. If this conjectural factor is accounted for, there remain a NAP density maximum at a depth of 195 cm and an AP/NAP ratio less than unity at 205 cm: the rise and fall of the "curve" in the interval between 265 and 143 cm would become less pronounced, but would not altogether dissappear. The tentative interpretation of the data as indicating grass-covered river banks could not have been deduced from the mere percentages in which the various pollen types occur, as without the densities being known the minimum in the AP/NAP ratio could be satisfactorily explained by assuming that a smaller quantity of tree pollen was deposited, whilst the NAP sedimentation rate remained constant.

5.3. Nieuwe Wetering 1958 *(Fig. 20)*.

The material obtained in 1958 at Nieuwe Wetering suffered from long storage and frequent handling. This would have rendered a determination of sediment volumes unreliable for density determinations. For this reason no density determinations were performed.

The composition of the cores obtained from Nieuwe Wetering is given in *table 8*.

Table 8. Composition of the Nieuwe Wetering cores.

Nieuwe Wetering 1958 first core 0 = 247 cm below N.A.P.	
0– 20 cm	peat with sand and brick gravel
20– 40	peat, *(Phragmites* and *Sphagnum)*
40– 60	*Phragmites* peat
60–100	peat and gyttja
100–140	gyttja
140–160	peat *(Sphagnum* and *Ericaceae)*
160–180	peat of unknown origin
180–260	*Phragmites* peat
260–280	clay with peat
280–340	light grey clay with vivianite and charcoal
340–400	clay with sand and containing *Scrobicularia*

second core, 0 = 630 cm below N.A.P.	
0– 40 cm	sand
40– 60	transition of sandy clay to sand; *Scrobicularia*
60–100	sandy clay with *Scrobicularia*
100–120	sandy clay with *Scrobicularia* and *Mytilus*
120–140	sandy clay with shells of *Mytilus edulis*
140–160	sandy clay with various unidentified shells and Bryozoa
160–340	clay with shells
340–360	peat and transition to clay with *Cardium*
360–380	brown clay, transition to *Phragmites* peat at 360
380–480	brown clay. Charcoal in 440–460
480–500	peat *(Phragmites* and *Cyperaceae)*. Shells at 480
500–540	*Phragmites* peat and sand

The radiocarbon datings are given in *table 9*.

Table 9. Radiocarbon datings of the Nieuwe Wetering cores.

1	GRN 2125:	1850	± 50 BP	Level:	375 cm below N.A.P.
2	2119	4515	45		506
3		6300			983
4		6500			1091
5		8700			1164

The peat at the levels 1155–1125 cm below NAP rests on Pleistocene sand. The Pleistocene age of this sand deposit is apparent from the very low percentage of *Quercus* pollen and the high percentages of *Betula* and *Pinus*. The expansion of the *Quercetum mixtum* and the beginning of the *Alnus* representation in the peat are usual for zone II, as can be read from *fig. 11*. The two phenomena occur together, which renders the distinction between zone IIa and zone IIb difficult. The low values for *Pinus* found in the samples at 1135 and 1125 cm may, however, indicate that these two samples represent zone IIb, but that the samples taken at the levels of 1145 and 1155 cm belong to zone IIa. The radio carbon dating, which yielded the age of 8700 B.P. for the base of the peat, equally indicates that it belongs to zone IIa.

The peat band at the level of 985 cm, dated 6300, must accordingly belong to zone III. Its pollen content is normal for this zone (high share of *Ulmus* in *Quercetum mixtum*, *Pinus* absent).

The peat deposit at a depth between 382 and 492 cm contains only small quantities of Chenopodiaceous pollen. *Fagus* attains low values, but it is present in all the samples within the interval excepted at 482 cm. The "*Ulmus* fall" can not be distinguished; the *Ulmus* values are low in the entire interval. According to the radio carbon dating of 4515 B.P. at 492, the base of this peat belongs to zone IVa. The almost continuous presence of *Fagus*, together with the continuously low percentages of *Ulmus* would, however, indicate that the peat deposit belongs entirely to zone IVb.

In the gyttja and in the peat overlying it the values for *Fagus* remain low; in the peat *Carpinus* is absent. The ^{14}C dating at the level of 372 cm yielded the value of 1850 B.P., which indicates that the sediments between this level and the top of the core belong to zone Vb. As can be read from *fig. 11*, here too exists a discrepancy between the palynological characteristics and the zonation if it is based on the radio carbon dating. This may be partly due to deforestation; this is, at least, a probable explanation in the case of the levels 262 and 252 cm, judging from the lower AP/TP ratio and the high percentages of Ericaceous pollen. It is obvious that in a region where human influences changed the flora no fixed rules can be applied.

The increasing percentage of *Pinus* in the interval between 302 and 352 cm can not be satisfactorily explained without the determination of pollen densities.

5.4. Kwintsheul 1958 *(Figs. 22 and 23)*

At Kwintsheul the Geological Survey performed a boring which was analysed in 1958. The data *(fig. 22)* were kindly put at the author's disposal by Dr. W. H. Zagwijn. Two *Pinus* maxima are present in the interval covered by the diagram. In order to ascertain if these *Pinus* maxima are attributable to an abundance of *Pinus* in the regional vegetation or to a general pollen poverty, the material from which the data of *fig. 22* were obtained was analysed once more, this time after addition of *Aesculus* pollen for the determination of density. A general analysis was performed, because this seemed to be desirable as a check on the state of preservation of the material, which had already been dissected and subsequently been stored for about ten years. The data obtained by the second analysis are represented in diagram *fig. 23*. A comparison of the percentages found in the two series showed that the results of the analyses were comparable in the interval between 1290 and 1470 cm.

A comparison of the two series of data shows that the *Pinus* maximum in the interval between 1390 and 1470 cm in the first series and the somewhat more pronounced maximum at 1430 cm in the second series are not coincident with a high *Pinus* density. This density was found to be highest at 1345 cm, though the percentual occurrence of *Pinus* pollen was found to be low in the same interval. Hence, it seems that the high *Pinus* percentage must be ascribed to a predominance of extraneous pollen transported from a distant source and that this predominance is caused by a poverty of the sediment in locally produced pollen.

6. SOME GENERAL CONCLUSIONS

The interpretation of palynological data, obtained from the analysis of cores, in terms of the vegetational history of a region can be rendered more precise in three ways, *viz.*,

(1) The determination of the pollen density, which in cores containing peat, gyttja, sand, and clay can be achieved by a method involving the addition of foreign pollen, yields information in addition to the pollen percentages as conventionally calculated. Even in the absence of sufficient chronological data, required for the calculation of the pollen sedimentation per year and per unit of surface area for the various pollen types occurring in the core, the determination of pollen density may contribute valuable indications for the interpretation of the pollen percentages found in a series of samples.

When interpreting the recorded pollen densities in a series of samples, one must take into account the statistical variation inherent to the method used as well as the variation occurring in the pollen density of sediments.

(2) For the evaluation of the percentual quantities of a certain pollen type present in a sediment in terms of actual floristic representation of the corresponding pollen-producing taxon, a correction factor is required which can only be determined empirically by a study of the relation between the recent percentual rate of pollen sedimentation and the stands of vegetation acting as the source, or the sources, of that pollen. A great deal of inquiry is still needed before any reliable phytohistorical interpretations can be given in a number of cases, and relevant information should preferably be obtained from studies of recent pollen sedimentation in its relation to pollen-producing vegetation in the same region as the one whose phytogeographical history is under investigation, or in a comparable area. Some examples of relevant studies are discussed in the present paper. The representation of a certain pollen type in a deposit being largely dependent on its specific dispersal rate, the correction factors to be used for the estimation of the floristic representation of the pollen-producing taxa at the time of sedimentation must be deduced from a study of recent vegetation types as closely comparable to the ancient plant communities as possible.

(3) Water-borne pollen may have travelled far. The pollen spectrum in sand or clay gives no direct information about the vegetation which existed in the region during the period of deposition of the sediment. There is, however, some evidence that the local stands of vegetation start being represented in the pollen contained in the sediment as soon as flooding of the area becomes rare. This can be reflected in a sudden change in the composition of the pollen content at a certain level.

In addition to the pollen, brought down by a river, which has been produced in remote regions in recent time, considerable quantities of secondary pollen may be included in sand or clay deposits. This must especially be expected in areas where tidal currents run in deep channels where they erode old peat layers. The resedimentation of pollen which was formerly contained in peat may be the cause of a higher herbaceous pollen content than is otherwise usually found in clay or in sand.

The present report clearly shows that there are still considerable lacunae in our knowledge of the relations between the recent pollen sedimentation and the regional stands of vegetation and in our knowledge of the factors causing different pollen densities in different sediments.

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ABBREVIATIONS

AP	arboreal pollen
NAP	non-arboreal pollen (N.A.P. in a depth scale means Nieuw Amsterdams Peil)
TP	total pollen, spores not included
O.A.	other angiospermous
H.W.	High Water
L.W.	Low Water
h.b.	hours before
P.	pollen
B.P.	before present, i.e. before 1950 A.D.
T.F.D.	tidal flat deposits

Throughout this article the metric system of measures is used, nautical miles for sitances at sea excepted. It is to be noted that synonyms exist in this system. 1 millilitre = 1 cubic centimetre. 1 microlitre = 1 cubic millimetre. The botanical names are according to VAN OOSTSTROOM (1956). The only exceptions are (1) *Phragmites australis* (Cav.) ex Steud. (= *Phragmites vulgaris* L. in VAN OOSTSTROOM) (CLAYTON 1968) and *Spergularia media* (L.) C. Presl (= *Spergularia marginata* (DC) Kittel in VAN OOSTSTROOM 1956) (STERK 1968).

Names of authors have been omitted from the botanical names which are in accordance with VAN OOSTSTROOM (1956).

Geographic coordinates of sampling sites (*fig. 4*): Oosteinder Poel, 52°16′N, 4°47′E.; Nederhemert, 51°45′25″N, 5°9′16″E; Meye, 52°7′3″N, 4°47′00″E; Kampinase Heide, 51°33′48″N, 5°15′18″E; Kwelder St. Annaland, 51°36′12″N, 4°7′18″E; Sand bank Krabbekreek, 51°36′27″-N, 4°6′35″E; Harbour St. A., 51°36′18″N, 4°6′33″E; Mastgat, 51°37′11″N, 4°4′00″E; Gameren 51°48′48″N, 5°13′50″E; Hedikhuizen, 51°44′36″N, 5°13′13″E; Oude Vlie 34, 53°7′3″N, 5°11′2″E; Oude Vlie 36, 53°7′24″N, 5°10′18″E; Vlieter 5, 53°1′6″N, 5°4′00″E; Vlieter 7, 53°1′36″N, 5°4′12″E; Holwerd, 53°23′48″N, 5°52′47″E; Nes, 53°26′1″N, 5°46′30″E; Schiermonnikoog, 53°28′7″N, 6°12′18″E; Bergen op Zoom, 51°29′54″N, 4°16′10″E; Schipluiden, 51°58′32″N, 4°19′28″E; Geldermalsen, 51°52′25″N, 5°16′5″E; Nieuwe Wetering, 52°12′59″N, 4°37′37″E; Kwintsheul, 52°0′5″N, 4′16′40″E. °

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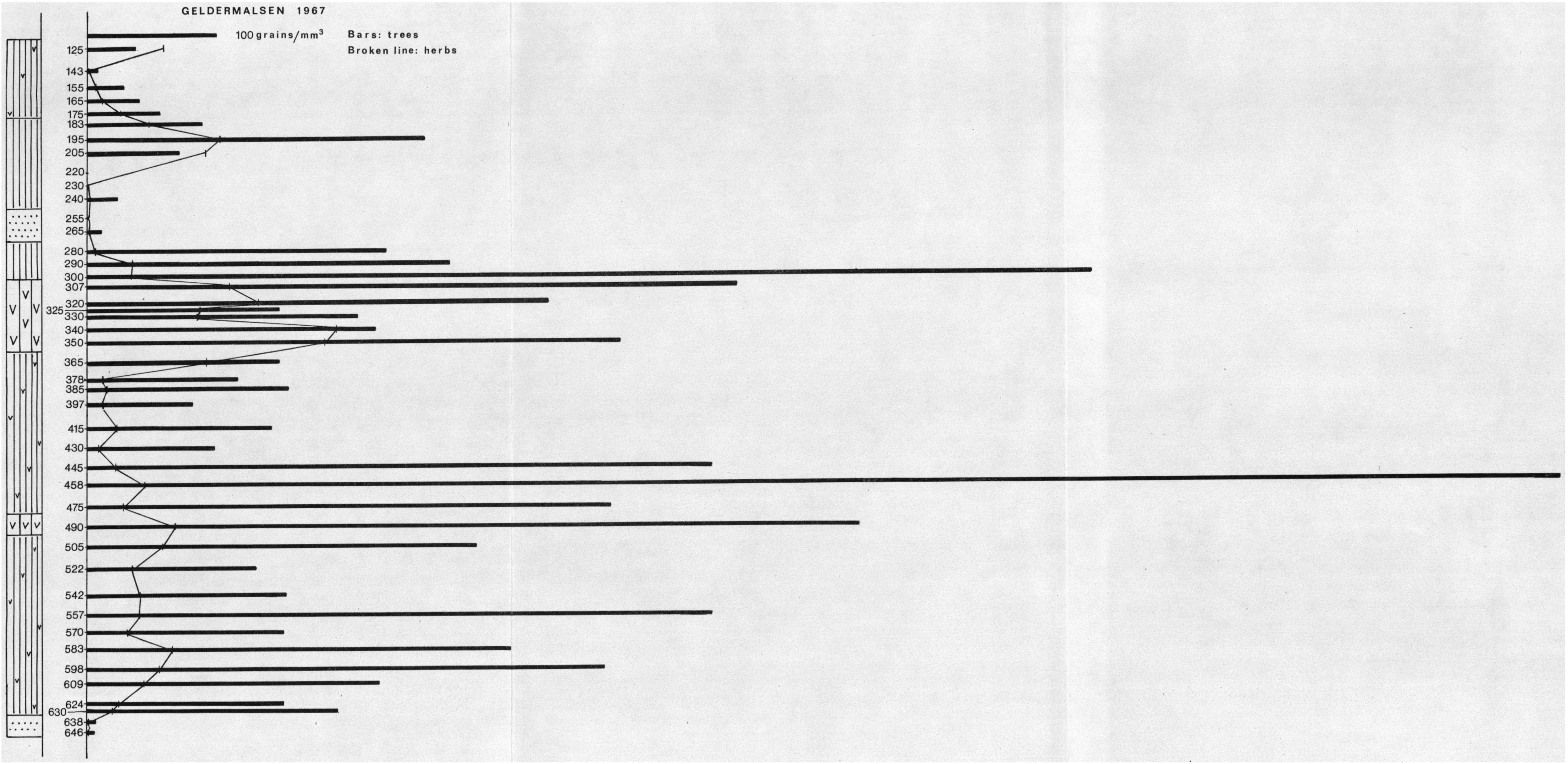


Fig. 15. AP and NAP densities in the Geldermalsen core

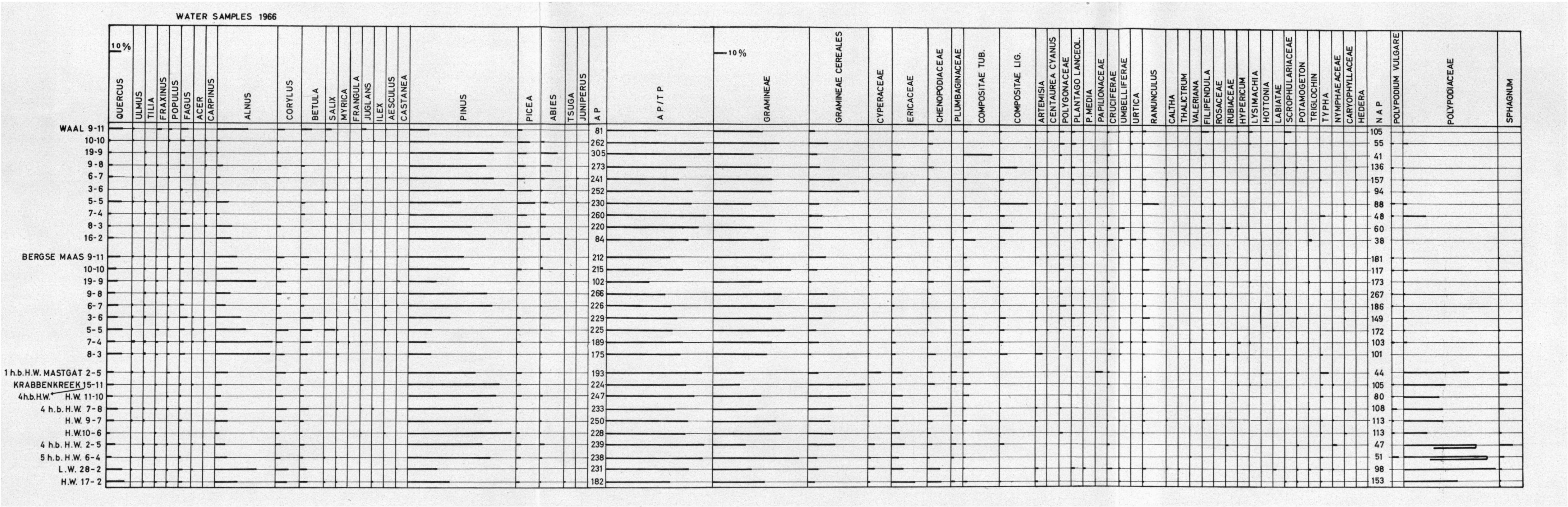


Fig. 16. Water samples

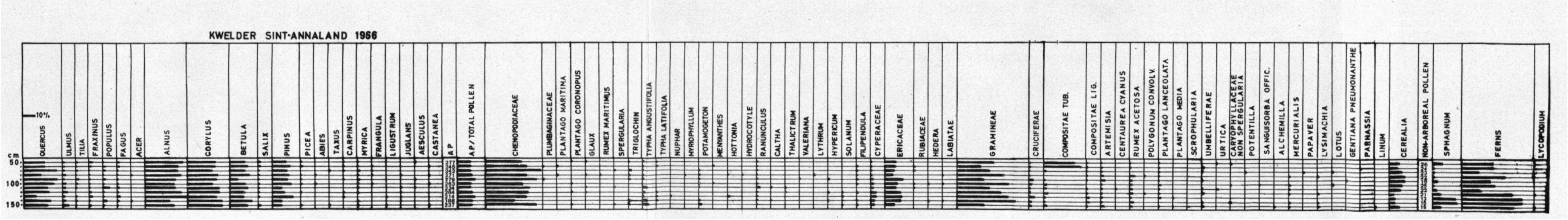


Fig. 17. Sint-Annaland 1966

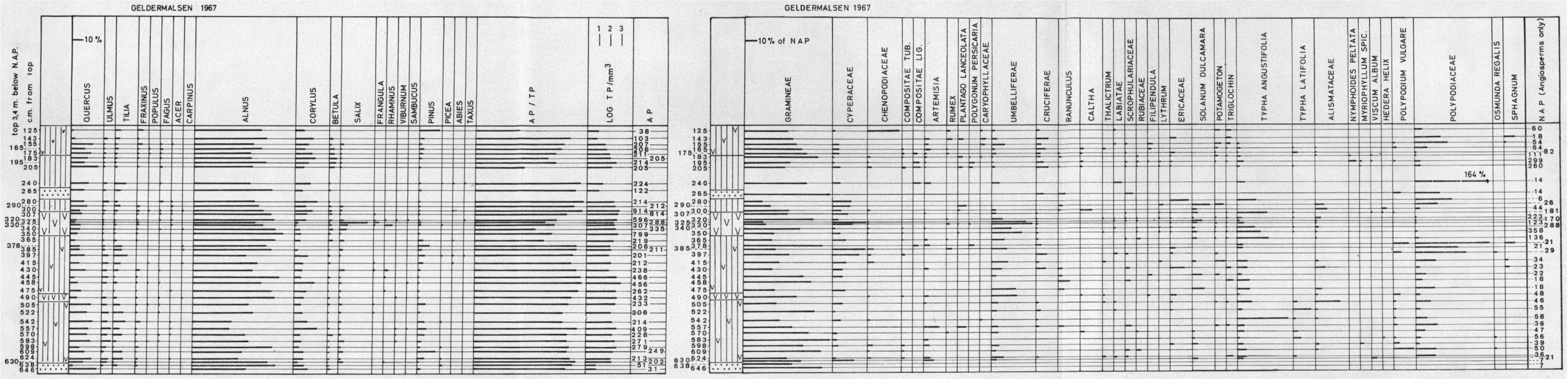


Fig. 18. Geldermalsen 1967

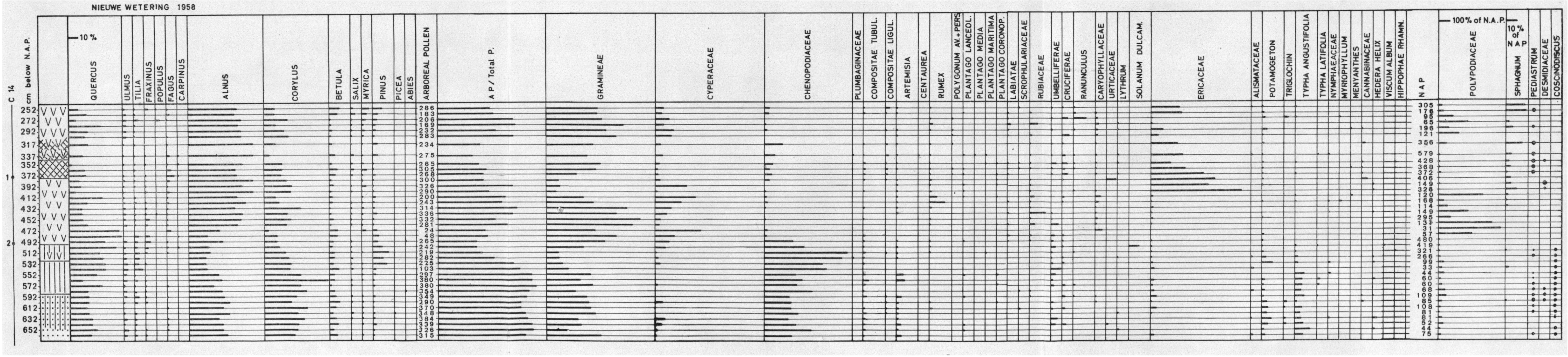


Fig. 19. Nieuwe Wetering 1958

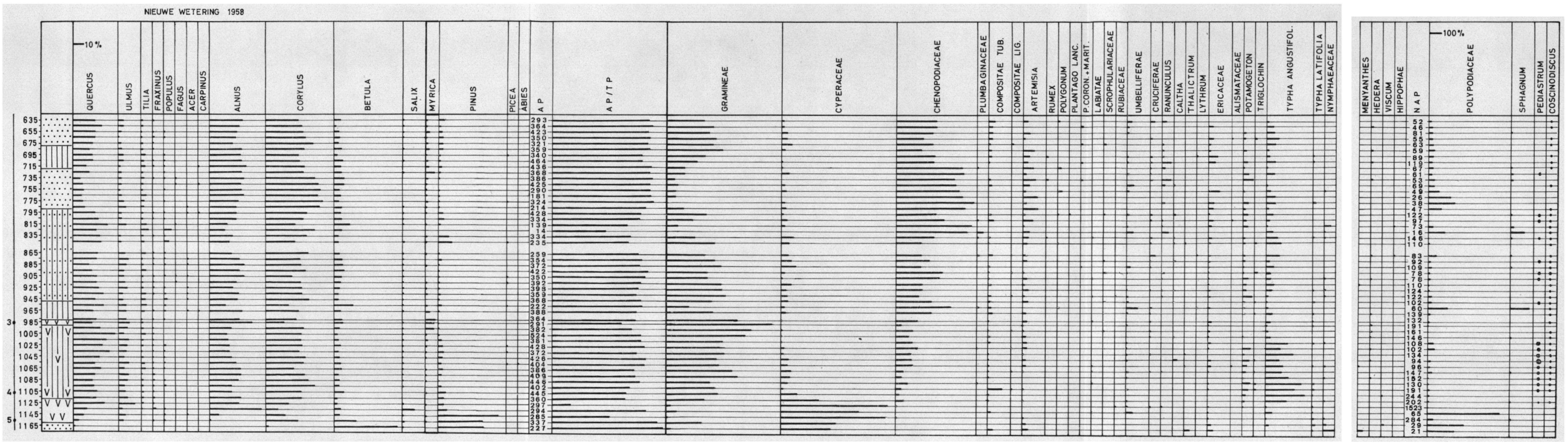


Fig. 20. Nieuwe Wetering 1958

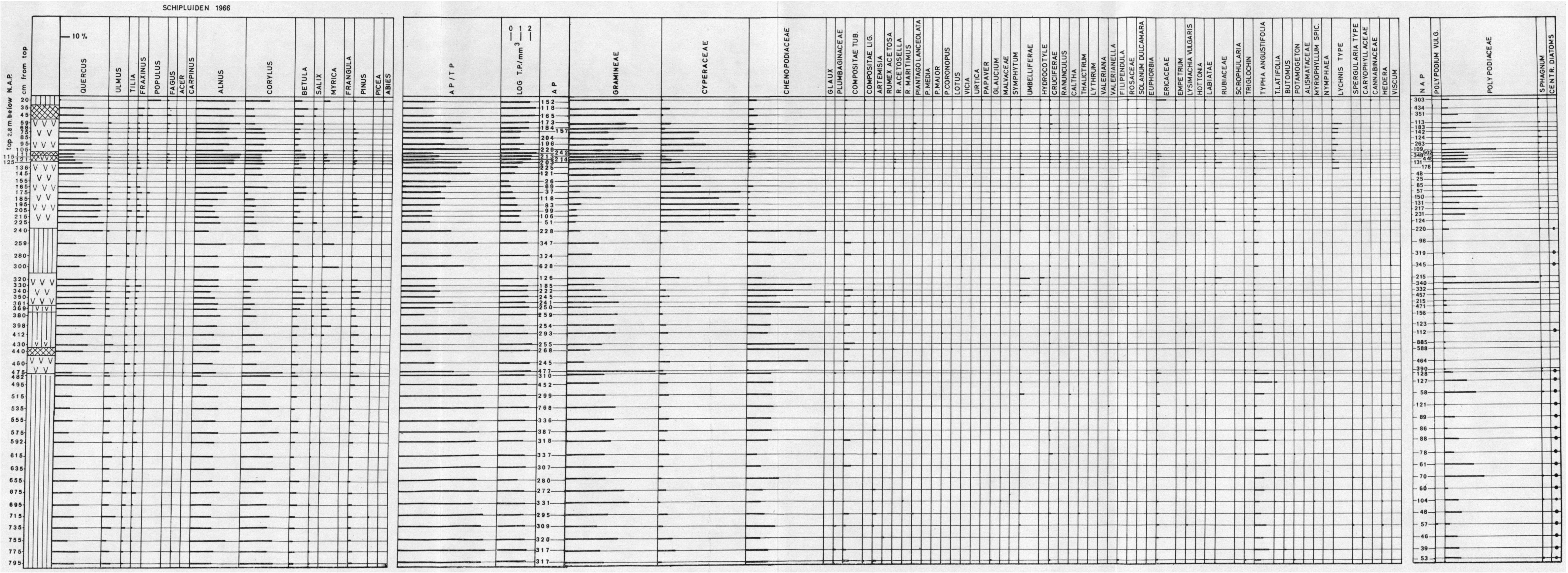


Fig. 21. Schipluiden 1966

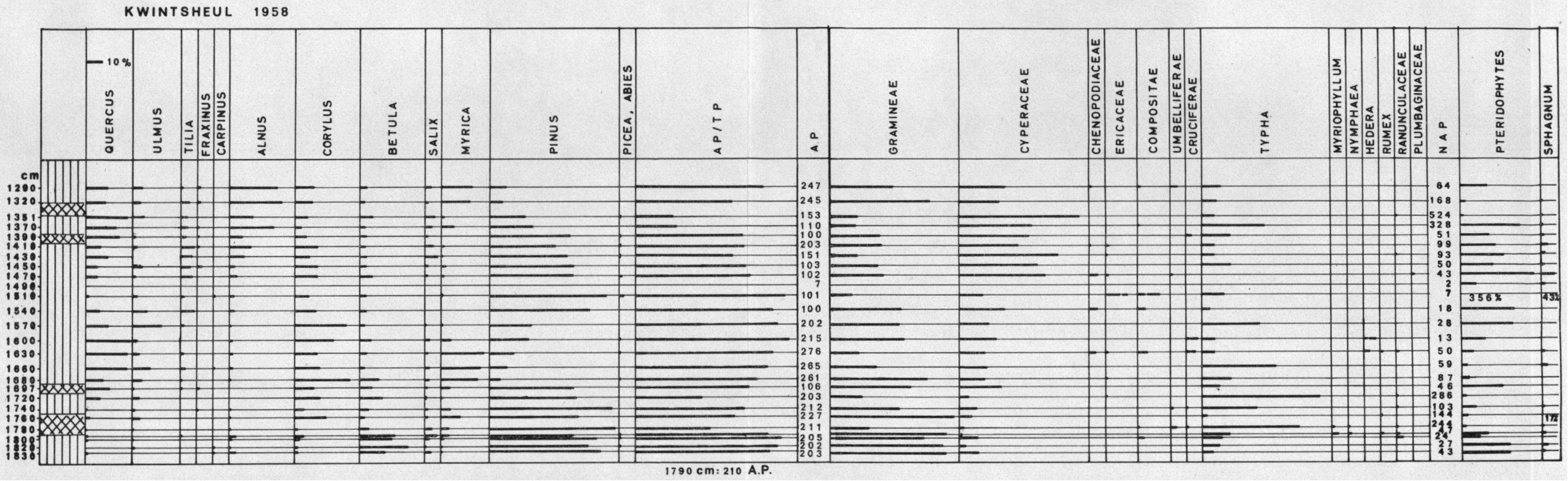


Fig. 22. Kwintsheul 1958. Data from the Geological Survey of the Netherlands at Haarlem

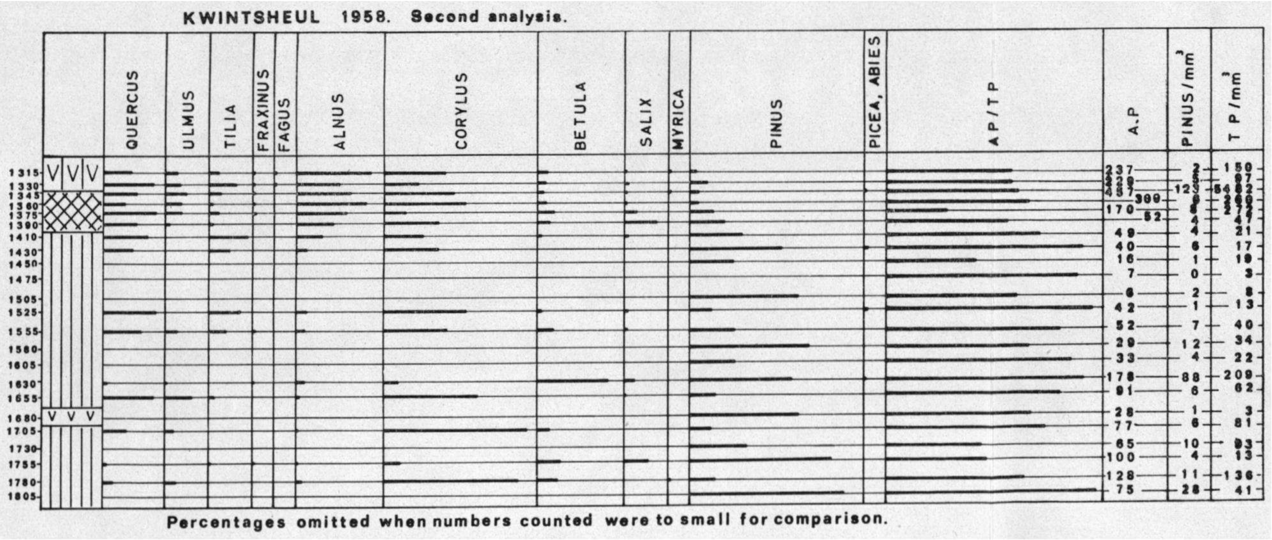
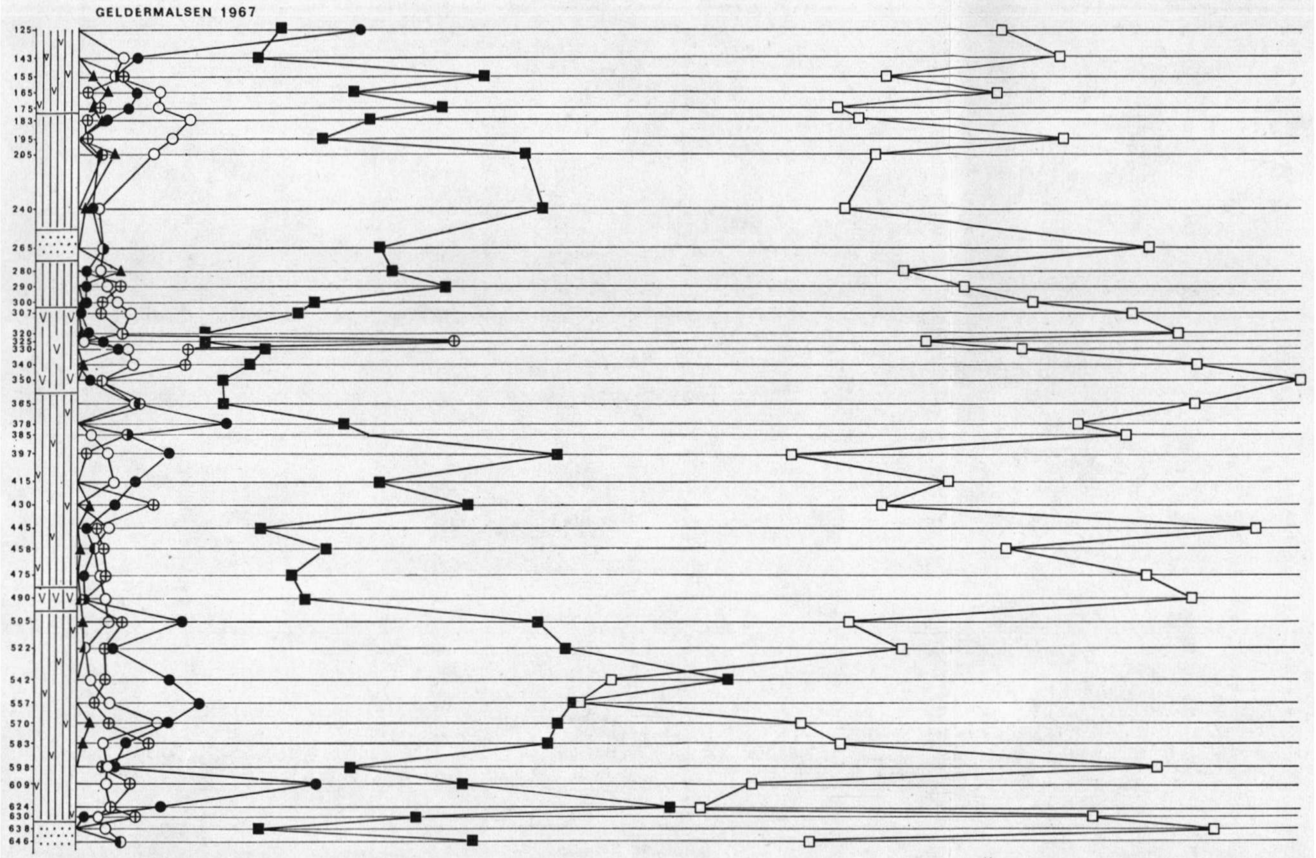
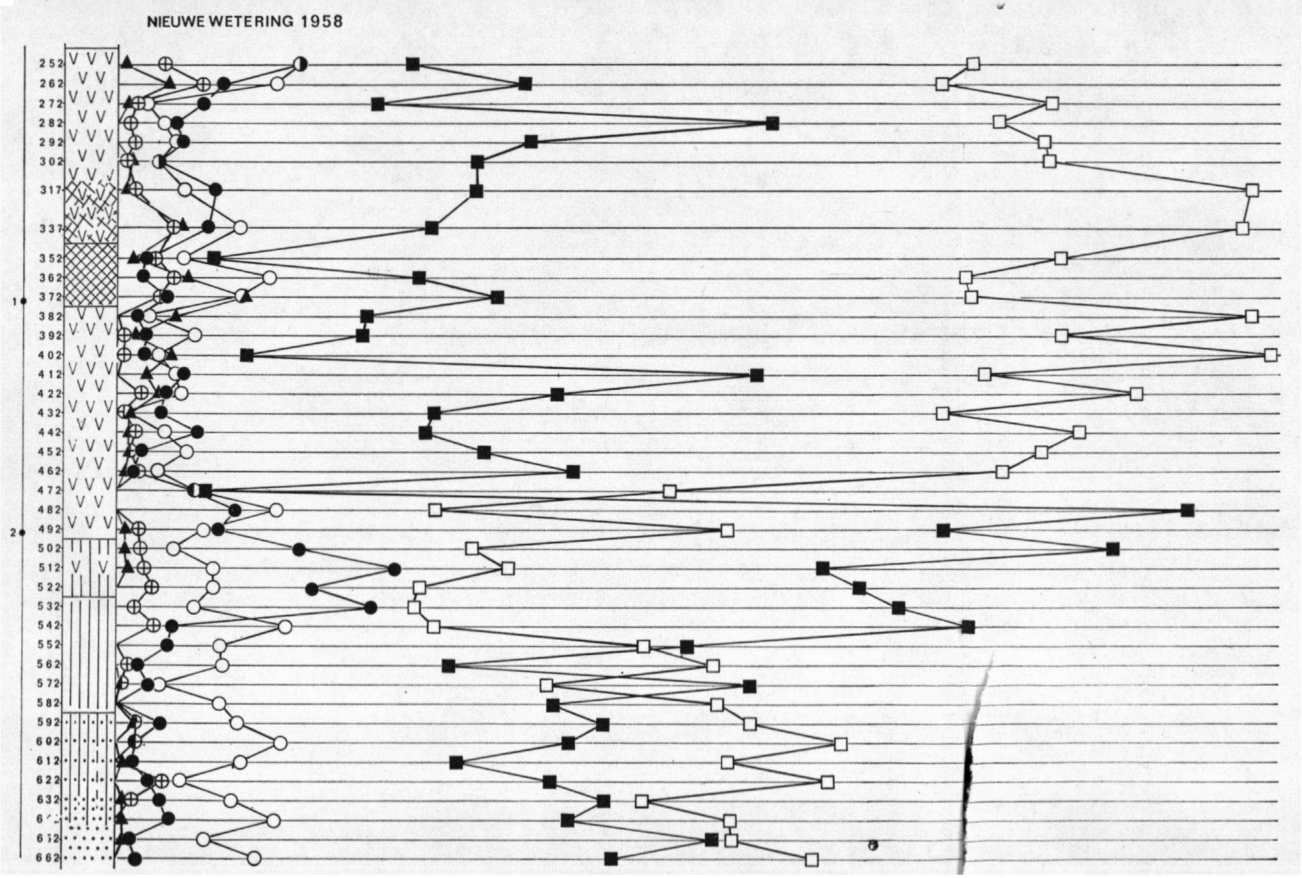
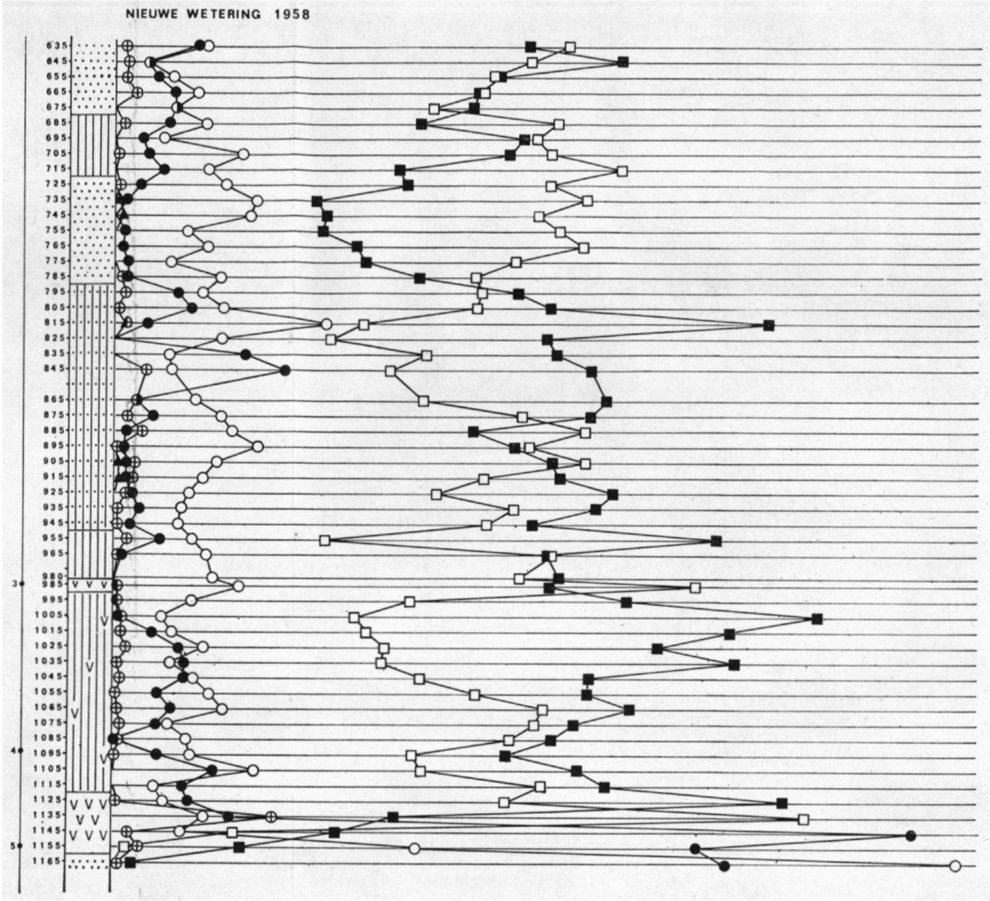
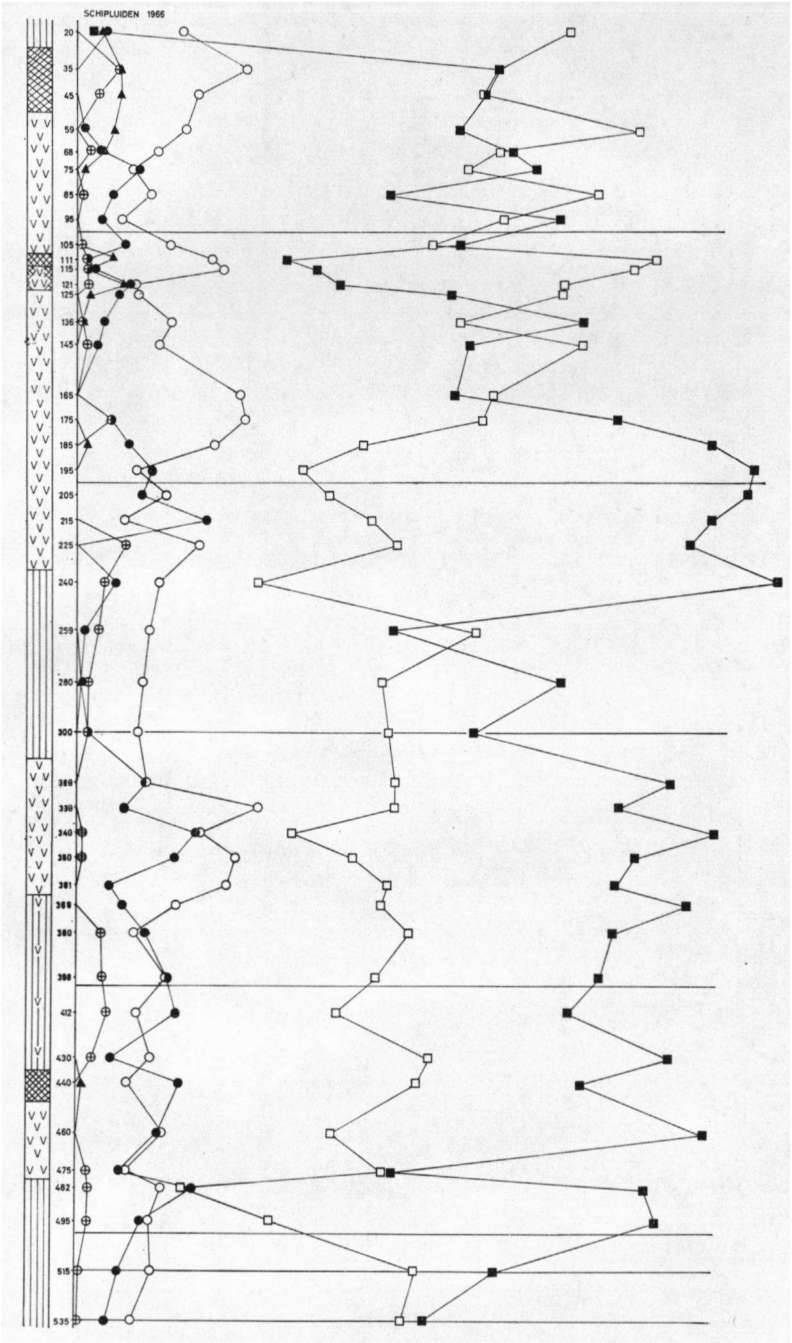


Fig. 23. Kwintsheul 1958, second analysis









○ Betula
⊕ Salix
● Pinus
■ Quercetum mixtum
▲ Fagus
□ Alnus

Fig. 24. Geldermalsen 1967 tree pollen curve
Fig. 25. Nieuwe Wetering 1958 tree pollen curve
Fig. 26. Nieuwe Wetering 1958 tree pollen curve
Fig. 27. Schipluiden 1966 tree pollen curve