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The Relative Pollen Productivity and Pollen Representation of North European Trees, and Correction Factors for Tree Pollen Spectra

Determined by Surface Pollen Analyses from Forests

By

Svend Th. Andersen

Dansk sammendrag:

Nordeuropæiske træers relative pollenproduktion og pollenrepræsentation
samt korrektionsfaktorer for træpollenspektre,
bestemt ved pollenanalyse af overfladeprøver fra skove

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ANDELSBOGTRYKKERIET I ODENSE

Draved forest, section 386. Mainly *Tilia cordata*. *Quercus robur* to the left, *Betula pubescens* to the right. Phot. H. Krog, may 28., 1955

Draved forest, section 370. Old *Quercus robur*. Phot. I. Brandt, may 9., 1951

Longelse forest. *Fagus silvatica*, *Quercus robur* and *Ulmus glabra*. Phot. P. Chr. Nielsen, march 11., 1966

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ABSTRACT

The present work deals primarily with a determination of the relative pollen productivity of various trees from North Europe by means of their representation in pollen analyses of surface samples from forests, with the aim to calculate correction factors for pollen diagrams.

Surface samples from 2 forests in Denmark were examined. The forest composition was determined by tree crown areas and tree basal areas in small sample plots. The relation of the tree crown areas to the tree basal areas was determined for the various tree species, and the data for crown area composition, basal area composition and tree frequency were compared.

The pollen preservation in the various surface samples was examined.

Data on wind conditions are mentioned in the chapter about pollen dispersal in the forest, and the various modes of pollen transfer are discussed. The amount of exotic pollen in the samples is used as a calculation basis for the tree pollen frequencies, and the occurrence and composition of the exotic pollen is discussed.

The relationship of the forest composition to the tree pollen deposition is discussed. Pollen deposition and pollen productivity is expressed by a regression equation. The relative pollen productivity of the tree species is expressed in relation to a reference species, in the present case *Fagus silvatica*. Pollen representation and relative pollen representation are determined by a comparison of pollen percentages with percentages for areal frequency.

Pollen productivity factors, pollen representation and correction factors were determined for Danish species of *Quercus*, *Betula*, *Alnus*, *Carpinus*, *Ulmus*, *Fagus*, *Tilia* and *Fraxinus* by means of the pollen frequencies in the surface samples. Corrected pollen percentages were compared with the tree areal percentages in the sample plots. Data for the pollen frequencies of forest plants other than the trees are presented. The data on trees from Denmark are compared with other data from Northern Europe, and correction factors were calculated for species of *Pinus*, *Picea* and *Abies*.

Tree pollen spectra from outside the forest are discussed and the relative pollen representation is calculated. The present calculations of the relative pollen productivity of the trees are compared with previous estimates, and the application of the correction factors to pollen diagrams is discussed.

I. INTRODUCTION

The immediate goal of pollen analysis must be the tracing of past vegetational composition and its changes. The elaborate recording of the pollen content of sediments becomes meaningsless unless it is interpreted in terms of the contemporary vegetation. The recognition of the problems of such a procedure is as old as pollen analysis itself, as they were mentioned already at von Post's lectures in 1916 (VON POST 1916, 1918), and discussed, although with varying intensity, ever since.

VON POST (l.c.) realized that the ability of fossil pollen spectra to record vegetational composition truthfully may be influenced by the effect of disproportionate pollen productivity and dispersal capacity of the plant species, particularly the important trees. He suggested a calculation of pollen representation rates by comparison of surface pollen spectra with vegetational composition. HESSELMAN (in VON POST 1916) maintained that pollen diagrams showing absolute pollen content may record changes in species abundance more truthfully than von Post's percentage diagrams, however, as von Post pointed out, absolute pollen values would be misleading due to the insufficient knowledge of the sedimentation rate. The solution of this problem suggested by G. de Geer (in VON POST 1916), a calculation of absolute pollen frequencies in postglacial annually varved sediments, remained unheeded and was forgotten.

Absolute pollen diagrams corrected for variation in sedimentation rate by means of C-14-datings have been established by DAVIS (1967) and others. Such pollen diagrams should record changes in pollen output more faithfully than percentage diagrams, however, as recognized by DAVIS (l.c.), the changes demonstrated by the absolute pollen diagram are almost identical to those appearing in the percentage diagram, for the period of forest vegetation at least. This surprising and somewhat reassuring observation may be explained by a relatively well balanced total tree pollen output not seriously affected by the interchange of single species of various pollen productivity. In spite of their usefulness as a check of the truthfulness of changes in pollen percentages, absolute pollen diagrams tell us little about the vegetational composition, for the evaluation of which corrections for disproportionate species representation are necessary.

II. SURFACE POLLEN SPECTRA AND VEGETATION

von Post (1918) mentioned a few surface pollen spectra from the bogs investigated by him, and since that time numerous surface pollen spectra have been investigated. However, the methods vary greatly and the application of the results may be viewed with a good deal of scepticism.

Livingstone (1968) pointed out that essentially two methods have been employed in attempts to utilize comparisons of surface pollen spectra with vegetational composition for the interpretation of pollen diagrams, (1) the matching of fossil pollen spectra with surface pollen spectra leading to identifications of earlier vegetation types with present day ones, or (2) a determination of correction factors to transform a percentage pollen diagram into a diagram showing the vegetational composition and changes truthfully.

The first mentioned method may be particularly useful where boundaries of vegetational formations are passed and has been successfully applied in such respects, however, as pointed out by Livingstone (l.c.), this method is too coarse for an explanation of the changes which characterize many pollen diagrams, and it is hampered by the lack of comparable vegetational combinations in the present day. Hence, methods of transforming pollen diagrams into diagrams recording vegetational composition and changes are highly desirable (cp. Jessen 1920, Iversen 1947, Fægri 1941, Fagerlind 1952, Davis 1963).

The present work is concerned mainly with the pollen representation of the trees. Previous attempts have dealt with determinations of the pollen productivity of trees directly and with comparisons of surface pollen spectra with forest composition.

The unique and elaborate pioneer work of Pohl (1937) was founded on determinations of the pollen content of stamens, inflorescences, branch systems, whole trees, and tree stands, a method which, however illuminating, contains many elements of uncertainty. Rempe (1937) collected pollen on vertical cylinders placed in the crown space of free-standing specimens of various trees during one season. The sequence of pollen productivity obtained in this investigation may be influenced by variations in the collection efficiency of the cylinders, and the flowering intensities may have been untypical in the year in question, as pointed out by Firbas (1949).

In the application of surface pollen spectra it should be realized that various kinds of surface samples record vegetations of different magnitude. Von Post (1918) pointed out that surface samples from wooded bogs may be locally

Table 1. Forest composition and surface pollen spectra (from JONASSEN 1950, table Q, forest composition in percentages of the timber volume), %

	Fagus	*Picea*	*Quercus*	*Betula* + *Alnus*	*Pinus*
forest composition (0,6 × 0,3 km) .	82	4	6	5	–
pollen spectrum, forest..........	79	3	9	7	2
pollen spectrum, glade in forest . .	44	10	7	28	11

influenced and that only surface samples from treeless bogs may be expected to record the regional forest vegetation. The contrast between locally and regionally influenced surface samples is illustrated in table 1 (from JONASSEN 1950). The tree pollen spectra shown there obviously record the forest vegetation in areas of greatly differing sizes.

The tree pollen spectra of surface samples from bogs, ponds or lakes surrounded by unforested country record the forests in very large areas as shown by the data in table 2 from STEINBERG (1944), who compared the pollen spectrum of the surface mud of Seeburger See, Unter Eichsfeld, with the forest composition in Kreis Duderstadt (27.3 km^2). The area is unforested up to 3–4 km from the lake, and it may be seen that the pollen of *Picea* and *Pinus* found in the lake mud obviously came from the forests in a much larger area than recorded in the forest analysis.

Table 2. Forest composition in Kreis Duderstadt (27.3 km^2) and surface pollen spectrum (from STEINBERG 1944), %

	Fagus	*Picea*	*Quercus*	*Betula*	*Pinus*
forest composition..............	55	28	13	4	0.2
pollen spectrum, lake mud.......	8	67	5	4	15

Some investigators compared the composition of pollen collected from the air with vegetational composition (BERTSCH 1935, FIRBAS und SAGROMSKY 1947, LEIBUNDGUT und MARCET 1953, POTTER and ROWLEY 1960, BOROWIK 1963, RITCHIE and LICHTI-FEDEROVICH 1963, LICHTI-FEDEROVICH and RITCHIE 1965). Such data confined to one season may be misleading due to irregularities in flowering intensity as pointed out by FIRBAS (1949) and LICHTI-FEDEROVICH and RITCHIE (l.c.).

As shown by the example from JONASSEN (1950) above, the tree pollen content of surface samples from forest can be considered mainly to be derived from the local forest. Besides the study of JONASSEN (l.c.), surface samples from forests have been studied by several authors (e.g. BORSE 1939, AARIO 1940, ERDTMAN 1943, MULLENDERS 1962, KRIŽO 1963, 1964, 1966, HEIM 1963, BASTIN

1964, POP 1967, ANDERSEN 1967 in Europe, CARROLL 1943, HANSEN 1949, POTTER and ROWLEY 1960, KING and KAPP 1963, MAHER 1963, BENT and WRIGHT 1963 and JANSSEN 1966 in North America, and WRIGHT, McANDREWS and VAN ZEIST 1967 in western Iran).

It should be noticed in this connection that the pollen percentage of a tree species obtained in samples from pure or almost pure stands of the species depends on the amount of other tree pollen blown in from outside the stand and provide little information about the pollen production of the tree species in question. In mixed forests several authors have noticed that the pollen content of the samples is influenced by the nearest trees (e.g. KRIŽO 1963, KING and KAPP 1962, JANSSEN 1966).

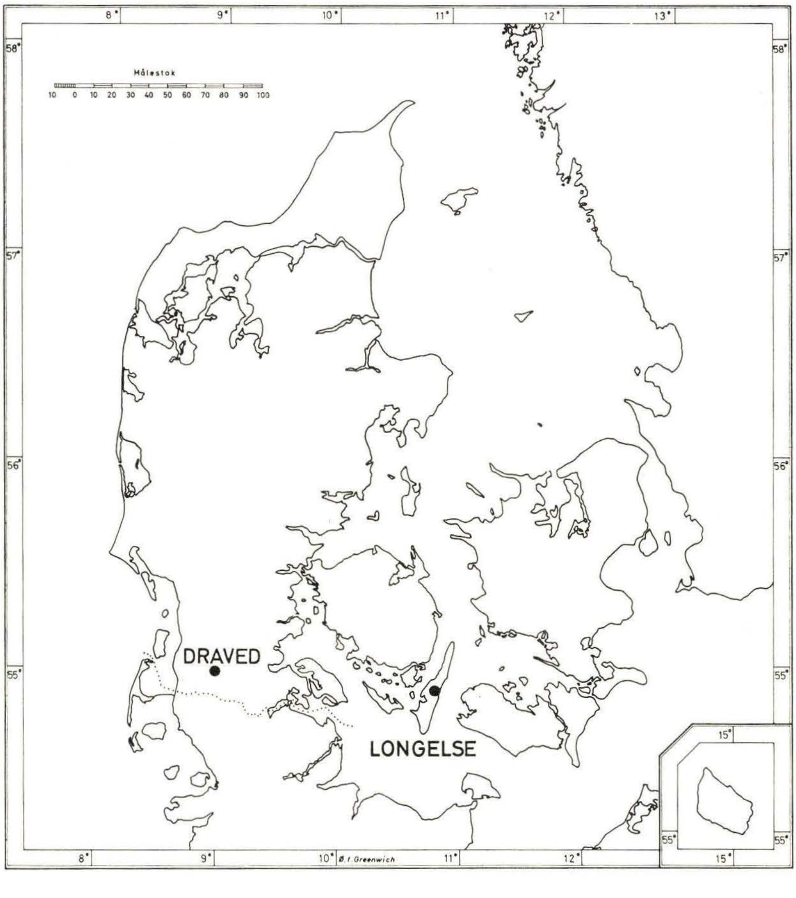
MÜLLER (1937), IVERSEN (1947, cfr. FÆGRI and IVERSEN 1964), JONASSEN (1950) and KRAL (1968) suggested correction factors for European trees. IVERSEN's correction factors have been employed particularly by Danish investigators for a correction of pollen diagrams (IVERSEN 1949, MIKKELSEN 1949, TROELS-SMITH 1954, JØRGENSEN 1954). Correction factors have also been calculated and applied to pollen diagrams in North America by DAVIS (1965) and LIVINGSTONE (1968), and in Japan by TSUKADA (1958).

The present author has studied surface samples from a mixed forest in Denmark (ANDERSEN 1967). The pollen spectra were compared with data on tree basal areas in small sample areas and correction factors were calculated. In the present work new pollen data are provided and data on crown areas have been determined by means of maps of the tree-crown projections. Another forest containing tree species not represented in the former one (*Ulmus*, *Carpinus*) was studied too.

III. NOTES ON THE FORESTS STUDIED

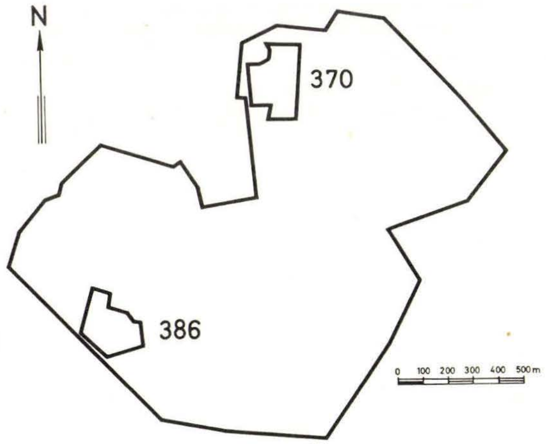
DRAVED FOREST

Draved forest is situated about 10 km northeast of Tønder in the southwestern part of Jutland, Denmark (see the map below). West of the forest the large bog Draved mose is found. On all other sides the forest is surrounded by cultivated land. Parts of the forest are *Picea* plantations. Otherwise it consists of deciduous forest of variable composition. Rather large areas of the deciduous forest are self-sown, and some of these areas are protected research areas. The two largest research areas, section 386 in the southwestern part of the forest, and section 370 in its northern part (see map p. 16) were selected for the surface pollen studies.



The vegetation of Draved is being studied intensively by dr. Johs. Iversen, Geological Survey of Denmark, and his collaborators, and only a few notes on the areas studied will be mentioned here.

Section 386 contains a mixed forest of *Tilia cordata*, *Fagus silvatica*, *Quercus robur*, *Alnus glutinosa*, and *Betula pubescens*. A few trees of *Fraxinus excelsior*, *Pyrus malus*, *Sorbus aucuparia* and *Populus tremula* occur too. The natural composition of the forest is preserved in a high degree (cp. IVERSEN 1958). The height of the trees is about 20 m. The soil mostly is mull with an area of mor in the eastern part of the section (IVERSEN 1964). The area studied is bordered by fields towards southwest, by young *Fraxinus* plantations towards west, northeast and south, and by a young *Picea* plantation to the east.



Draved forest with the sections 386 and 370

Section 370 contains in addition abundant *Fraxinus excelsior*. *Ulmus glabra*, *Pyrus malus*, *Sorbus aucuparia* and *Populus tremula* occur with a few specimens. The composition of the forest is influenced by former tree-cutting. The tree height is about 20 m. The soil mostly is mull with a mor area in the central part. The area studied is bordered by a field and a young *Alnus* plantation to the west, by young *Fraxinus* plantations towards northwest and southwest, by mixed forests towards north and south, and by a young *Betula* plantation to the east. There is a rather dense undergrowth of young trees in the two sections. *Corylus avellana* is important in section 370.

LONGELSE FOREST

The area studied, named "Longelse Bondegårds Skov", is situated north of Søvertorp forest 5 km southeast of Rudkøbing on the island Langeland, southern Denmark (see the map p. 15). The area, which is privately owned, has been protected since 1940 and is being studied by "Skovhistorisk Selskab" under the leadership of P. Chr. Nielsen, lecturer at the Danish Veterinary and Agricultural University. The forest is self-sown and mainly consists of *Quercus robur*, *Fagus silvatica*, *Ulmus glabra*, *Fraxinus excelsior*, and *Carpinus betulus* in varying quantities and a few *Alnus glutinosa*. Single trees of *Populus tremula*, *Acer campestre*, and introduced *A. pseudoplatanus*, *Populus canescens* and *Aesculus hippocastanum* occur too. The trees mostly are about 30 m high. *Carpinus* is somewhat lower, about 25 m. The soil is a fertile mull.

Tree-cutting has been slight, at least since 1955, but the forest was greatly affected by the violent storm in october 1967. The area is bordered by old *Fagus* forest to the southwest and by fields on the other sides.

IV. THE COMPOSITION OF THE FORESTS STUDIED

In von Post's original concept (von Post 1918) the tree pollen diagrams were supposed to express the areal composition of the forest canopy, which constitutes the main pollen producing surface of the forest. In comparisons of surface pollen spectra with vegetation, various quantities such as basal areas, tree frequencies, wood volumes or even composite data ("importance values" i.e. an average of basal area and frequency percentage) have been used. Basal area and tree numbers can be measured rather simply from the ground, and data on wood volume can be obtained from forestry inventories, however, such figures can only be considered as more or less necessary substitutes for the areal composition of the crown canopy.

Measurements of tree basal areas were used for a comparison with surface pollen spectra in Draved forest at a time when tree crown maps had not been established (cp. Andersen 1967), and only basal area data exist for Longelse forest, as the storm catastrophe made air photographing impossible. Hence it is of interest to compare the data on crown areas from Draved with data on basal areas. As tree frequency data have been used by other authors in similar studies, it is also of interest to see how well such data reflect the forest composition expressed by crown areas.

MEASUREMENT OF TREE CROWN AREAS

Air photographs of Draved forest were made by "Landinspektørernes Luftfotoopmåling A/S" in august 1968, and maps of the tree crown projections in the scale 1:500 were worked out for the sections 386 and 370 by stereooptical methods by the same company. The air photographs were adjusted according to ground signals located on ground maps. Only trees participating in the crown canopy were recorded. The crown projections of a few trees felled by storms since 1954 were drawn subjectively. The tree crown maps will be published together with the botanical investigation.

The surface samples used for pollen analysis (see p. 25) were located on the tree crown maps, and the tree crown areas within circular plots of 20 and 30 m radius around each surface sample were measured planimetrically. The areas of the segments of tree crowns projecting into the circles were measured too. Some of the sample plots project beyond the study areas into ajoining nonpollenproducing forest vegetation.

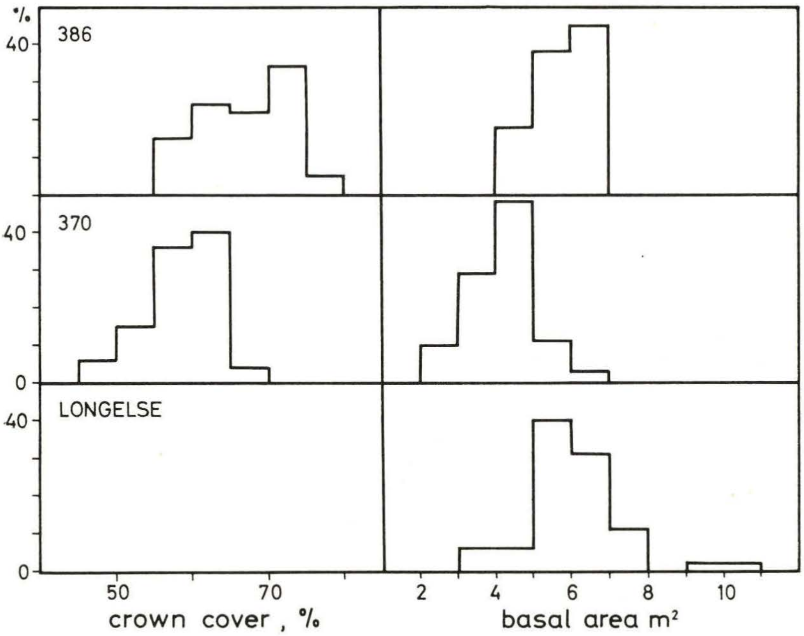
MEASUREMENT OF TREE BASAL AREAS

The basal areas of the trees were calculated with the help of tree maps. The maps from Draved forest were measured in 1954 on the scale 1:500, and Longelse forest was mapped in a similar way by "Dansk Skovhistorisk Selskab" in 1961. Tree diameters measured 1.3 m above the ground were inserted on the maps, and the basal areas of trees within plots similar to those used for the tree crown areas were worked out. Trees of *Quercus*, *Betula*, *Alnus*, *Fagus*, *Tilia* and *Fraxinus* 30 cm or more in diameter were included. *Ulmus* and *Carpinus* trees 25 cm or more in diameter were considered, as these trees flower at an early age. Trees at the limit of the sample plot were included, whereas trees just outside it were omitted.

FOREST STRUCTURE

The crown coverage was determined as the total tree crown area in percentage of the area of each 30 m sample plot. The distribution in coverage classes is shown below, and the average figures are shown in table 3. It may be seen that the tree crowns cover about 2/3 of the ground in section 386, and that the tree canopy is somewhat more open in section 370.

The crown sizes vary considerably. Their ranges are shown in table 4. *Quercus* has the largest and *Alnus* the smallest crowns.



Draved forest and Longelse forest. Percentage distribution of crown coverage and total tree basal areas in the 30 m sample plots

The variation in the total basal area per 30 m sample plot is shown on p. 19, and the average values are shown in table 5. The total basal area per sample plot is larger in section 386 than in section 370 in Draved forest. Longelse forest is similar to section 386 in this respect.

The largest basal areas of single trees are shown in table 6. The largest trees occur in Longelse, and *Quercus*, *Fagus* and *Fraxinus* have the largest trunks.

COMPARISON OF THE DATA ON FOREST COMPOSITION

The ratios of the total crown areas to the total basal areas measured in the 30 m sample plots are shown in table 7. The figures from section 386 are very uniform, only *Alnus* deviates slightly from the other trees. The figures from section 370 vary more. The ratios for *Betula*, *Alnus*, *Fagus* and *Fraxinus* are distinctly higher than the figures from section 386. These trees generally have larger crowns in relation to the trunk areas in section 370 than in section 386, probably because of the smaller tree density.

As Longelse forest resembles section 386 from Draved in respect to total basal area per sample plot, one may expect that there is no great variation in the relation of the tree crown areas to the basal areas.

Table 3. Draved forest. Average crown cover in the 30 m sample plots.
N = Sample number

	N	average crown cover	standard deviation	range
Draved 386	41	66.6 %	±5.7 %	56–76 %
Draved 370	67	57.9 %	±4.5 %	46–68 %

Table 4. Draved forest. Ranges of the tree crown areas, m^2

	Quercus	*Betula*	*Alnus*	*Fagus*	*Tilia*	*Fraxinus*
Draved 386	8–158	10–105	5–63	8–118	8–95	–
Draved 370	10–173	8– 90	8–53	5–103	10–68	8–113

Table 5. Average basal area per 30 m sample plot

	N	average basal area	standard deviation
Draved 386	40	5.77 m^2	±0.70 m^2
Draved 370	63	4.19 m^2	±0.83 m^2
Longelse	35	6.18 m^2	±1.33 m^2

Table 6. Largest basal areas of single trees, m^2

	Quercus	*Betula*	*Alnus*	*Carpinus*	*Ulmus*	*Fagus*	*Tilia*	*Fraxinus*
Draved 386.	0.866	0.159	0.238	–	–	0.332	0.442	–
Draved 370.	0.709	0.238	0.159	–	–	0.332	0.159	0.238
Longelse . . .	1.127	–	0.212	0.432	0.714	1.159	–	1.117

Table 7. Draved forest. Ratios of the total crown areas to the total basal areas in the 30 m sample plots

	N	*Quercus*	*Betula*	*Alnus*	*Fagus*	*Tilia*	*Fraxinus*
Draved 386. . . .	48	333	337	288	335	338	–
Draved 370. . . .	88	295	524	434	391	307	406

The area percentages of the tree species in Draved and in Longelse forest in the 30 m sample plots are shown in table 8. Figures for tree frequency calculated in the same way are shown too.

The deviations of the basal area and the tree frequency percentages from the crown area percentages and the deviations of the tree frequency percentages from the basal area percentages are shown in table 9.

The differences in the percentage figures found by these methods are not very large. The basal area figures from section 386 in Draved deviate the least

Table 8. Crown area, basal area and tree frequency in percentage of the total crown area, basal area and tree number

Draved 386	*Quercus*	*Betula*	*Alnus*	*Fagus*	*Tilia*	
Crown area.	20.8	12.4	18.7	20.0	28.1	
basal area	20.4	12.0	21.2	19.4	27.1	
tree frequency . .	14.8	13.6	25.7	16.7	29.1	

Draved 370	*Quercus*	*Betula*	*Alnus*	*Fagus*	*Tilia*	*Fraxinus*
Crown area.	23.5	20.7	16.7	14.6	2.9	21.7
basal area	30.9	15.3	14.9	14.5	3.6	20.7
tree frequency . .	18.4	18.2	20.1	15.2	4.2	23.9

Longelse	*Quercus*	*Betula*	*Carpinus*	*Ulmus*	*Fagus*	*Fraxinus*
basal area	26.8	1.1	14.1	19.3	20.4	18.3
tree frequency . .	15.6	2.1	22.3	26.1	17.9	16.1

Table 9. Deviations of basal area and tree frequency percentages

Deviations of basal area percentages from crown area percentages

	Quercus	*Betula*	*Alnus*	*Fagus*	*Tilia*	*Fraxinus*
Draved 386.	−0.4	−0.4	+2.4	−0.6	−1.0	
Draved 370.	+7.5	−5.4	−1.8	−0.1	+0.8	−1.0

Deviations of tree frequency percentages from crown area percentages

	Quercus	*Betula*	*Alnus*	*Fagus*	*Tilia*	*Fraxinus*
Draved 386.	−6.0	+1.3	+7.0	−3.3	+1.0	
Draved 370.	−5.0	−2.5	+3.3	+0.6	+1.3	+2.3

Deviations of tree frequency percentages from basal area percentages

	Quercus	*Betula*	*Alnus*	*Carpinus*	*Ulmus*	*Fagus*	*Tilia*	*Fraxinus*
Draved 386.	− 5.6	+1.7	+4.6	–	–	−2.7	+2.0	–
Draved 370.	−12.5	+2.9	+5.1	–	–	+0.7	+0.6	+3.2
Longelse . . .	−11.2	–	+0.9	+8.2	+6.7	−2.5		−2.2

from the crown area figures, but the deviations in section 370 are rather slight too, being largest in *Quercus*. The figures for tree frequencies resemble the figures for crown areas better than they resemble the basal area figures.

It may be concluded that forest composition may be estimated by basal area data with some confidence in the case of a rather dense forest vegetation and with some caution for more open forests too. Frequency data may be used with some caution too.

MEASUREMENT OF THE COVERAGE OF SHRUBS AND HERBACEOUS PLANTS

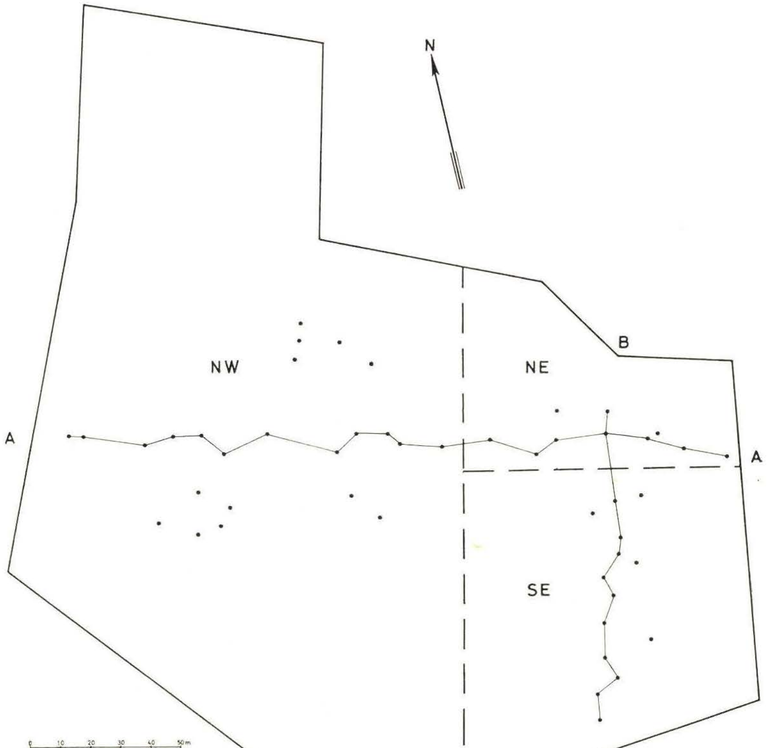
Shrubs are quite scarce in the forests studied except for *Corylus* in section 370 in Draved. The coverage of *Corylus* was estimated from the ground in circular sample plots of 10 m radius around each surface sample in 3 transects. The total *Corylus* crown area in each plot was calculated as a percentage of the area of the plot.

Data on the coverage of the herbaceous plants in Draved were taken from the vegetation analyses carried out by Johs. Iversen and his collaborators. Coverage was estimated by the point method of Cockayne and Levy in a modified form in circles of 50 cm radius around each main point of a 10 × 10 m coordinate system, and the analyses were carried out in may and in june in 1955 (section 386) and 1958 (section 370). The results are indicated as coverage in percentage of the area of the sample plots. Figures are shown for 2 transects from section 386 and 3 transects from section 370, which correspond to surface sample transects (p. 25).

V. THE SURFACE SAMPLES

ORIGIN AND DISTRIBUTION OF THE SAMPLES

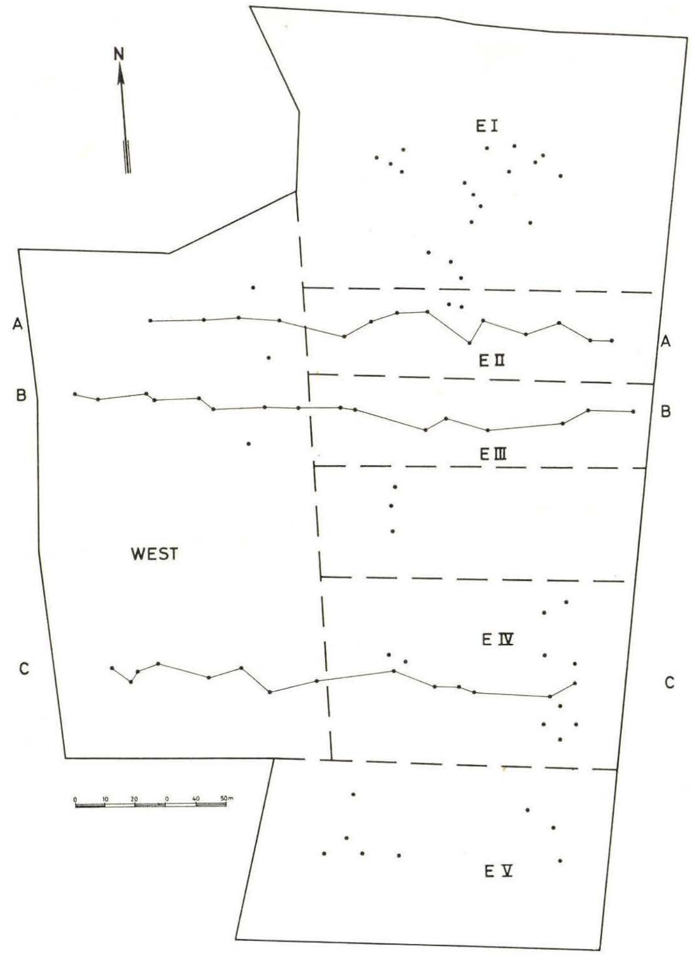
The deposition of pollen in the forest may be studied by means of pollen collectors or by analyzing the pollen content of surface samples. Pollen collectors may allow a determination of the annual deposition of the various kinds of pollen per area unit, however, only a limited number of collectors can be applied, and the collecting must be extended over a sequence of years in order to eliminate the annual variations in the flowering intensity of the various plants, and in the meteorological conditions. Pollen collectors of a type de-



Draved forest, section 386. The location of the moss samples and the transects A and B. The subdivisions NW, NE and SE are mentioned in chapter VIII scribed by Tauber (1967) have been set up in Draved forest since 1967, but the results are preliminary at present and only a few will be mentioned here.

Pollen preservation is bad in circumneutral soil (pH higher than 6, Dimbleby 1962), except in very dry climates (e. g. Potter and Rowley 1960, Wright et al. 1967), wereas acid soil, mor e. g., contains well-preserved pollen grains. The time interval comprized by surface mor samples may, however, be so long that the forest may have changed during that time.

Humus from moss polsters on tree stumps and fallen trees or branches were used in the present study. The debris collected here is isolated from the ground and the mixing activities of the soil fauna, and a humus layer with well-preserved pollen may develop even in forests with circumneutral soils. The samples were collected in 1964–66 in Draved and in 1968 in Longelse. The age of the tree-

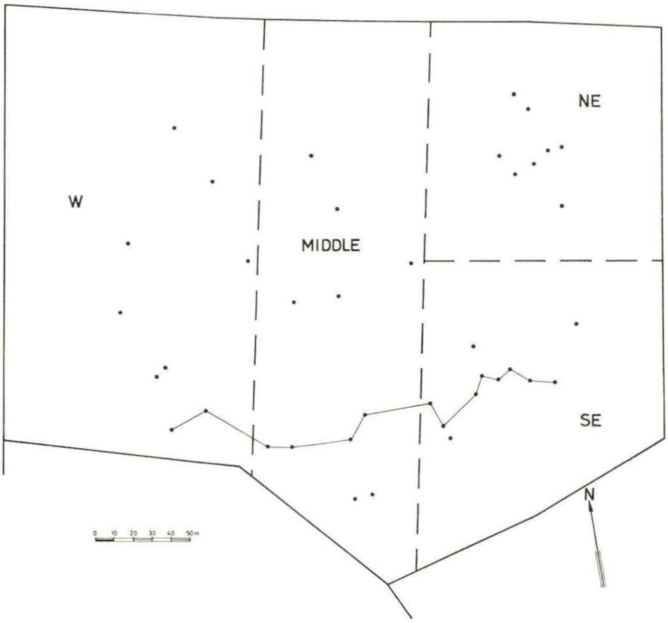


Draved forest, section 370. The location of the moss samples and the transects A, B and C. The subdivisions West and East I–V are mentioned in chapter VIII stumps and the other materials from which the samples were collected cannot be determined, however, tree cutting has been moderate and was eliminated since 1950 in Draved and 1955 in Longelse, and the forest composition cannot have changed greatly during the accumulation of the moss humus. In Longelse forest mosses were in some cases absent from the stumps probably due to strong shade, but accumulations of loose strongly decayed wood with well-preserved pollen could be found.

The moss samples were collected during the autumn or in early spring before the tree flowering. The forest bottom was searched systematically and one sample from each 10×10 m^2 was collected if possible. About 5×5 cm^2 were collected. The level of the samples varied between 5 and 35 cm above the ground. The distance of the nearest trees was measured for each sample and the samples were located on the tree maps.

In Draved forest the samples from 2 transects in section 386 and 3 transects in section 370 were analyzed for pollen content. Besides the transects a number of additional samples were selected within the areas of highest concentration of the tree species. 48 samples from section 386 and 88 samples from section 370 were analyzed. Their distribution is shown in the maps on p. 23 and 24.

39 moss samples were collected in Longelse forest and all the samples were used for pollen analysis. Their distribution, is shown in the map below. 14 samples are arranged in a transect.



Longelse forest. The location of the moss samples and the transect. The subdivisions W, Middle, NE and SE are mentioned in chapter VIII

PREPARATION AND ANALYSIS OF THE SAMPLES

The fresh moss samples were dried, and a small sub-sample was used for preparation. All green moss parts were removed, as otherwise the fresh pollen from the last flowering season might predominate in samples with badly preserved pollen and give a false impression of a good pollen preservation.

The sub-samples were boiled in KOH for a few minutes, seaved and washed repeatedly in a perforated porcelain crucible, treated with acetolysis mixture as described by FÆGRI and IVERSEN (1964), and mounted in silicone oil according to the method described by ANDERSEN (1960).

The pollen concentration varied greatly. A low pollen concentration could be increased by the use of a smaller sub-sample.

The recording of pollen was continued until about 100 "exotic" pollen grains (p. 42) had been counted. Only entire slides or exactly one half of a slide were counted. The samples published in ANDERSEN (1967) are included, however, most of them were re-counted, as the original counts were lower than the standard amount chosen for this study.

VI. POLLEN PRESERVATION IN THE SURFACE SAMPLES

Of the many preservation-classes distinguished by CUSHING (1967) corroded, crumpled and broken grains occurred. Only corrosion is considered important in the present cases, as crumpling and breakage do not remove the pollen grains from the samples and did not reduce their identifiability.

A type of corrosion where perforations of the exine occur and may unite to remove a greater part of it may be well-known to most pollen analysts (the perforation-type of HAVINGA 1964, 1967, cp. ELSIK 1966, Cushing 1967). As pointed out by ELSIK (l.c.) and HAVINGA (1967) this type of corrosion may be connected with the activities of phycomycetes and seems to occur in soils of a high biological activity (HAVINGA l.c.). HAVINGA (1964, 1967) described another type of corrosion in which the pollen exine is gradually thinned. He observed this type particularly in sandy soils and in artificially oxidised samples and pointed out that the two types of corrosion become indistinguishable in severe cases.

HAVINGA (1964) published a list of the experiences of various authors as to the relative corrosion susceptibility of various genera. This list is self-contradictory as the susceptibility of *Corylus* e.g. is considered slight or great by various authors. These discrepancies and a difference of opinion between HAVINGA (l.c.) and the present author (ANDERSEN 1967) are eliminated by the experiences from experiments made by HAVINGA (1967). HAVINGA (l.c.) showed that the sequence of taxa arranged according to corrosion susceptibility by artificial oxidation corresponds to the sequence reached from experiences made during the pollen analysis of sandy soil. The common tree genera occur in this list in the following sequence of increasing corrosion susceptibility.

> *Tilia*, *Alnus*, *Corylus*, *Betula*, *Carpinus*, *Ulmus*, *Quercus*,
> *Fagus*, *Fraxinus*.

The thinning-type of corrosion occurs in these cases.

A different sequence was shown by HAVINGA (l.c.) to exist in experiments where pollen grains were exposed to destruction in biologycally active soils (arranged as above),

> *Quercus*, *Fraxinus*, *Tilia*, *Betula*, *Fagus*, *Carpinus*, *Ulmus*,
> *Alnus*, *Corylus*.

The perforation-type of corrosion prevailed in these cases (HAVINGA l.c.).

The sequence corresponds to the sequence mentioned by ANDERSEN (1967).

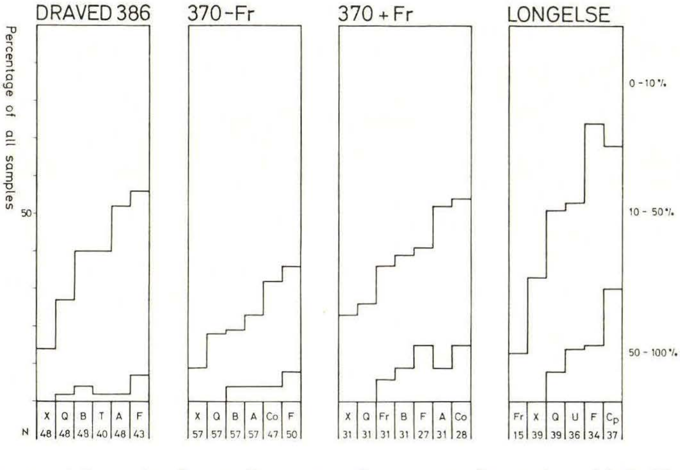
The state of preservation of the pollen grains found in the moss humus was good in most cases, but some of the samples contained many corroded grains with the perforation-type of corrosion. These samples particularly came from the areas with the soil of highest pH. Rain splashing may have added mineral soil matter to these moss polsters and made conditions favourable for pollen corrosion. Samples with very little pollen corrosion occurred in the same areas.

To obtain an idea of the intensity and the distribution of the corrosion the number of corroded pollen grains of each taxon was counted and the frequency of the corroded grains was calculated in percentage of the number of grains of the taxon in each sample. All pollen grains with the least signs of corrosion were considered corroded.

The figure below shows the degree of corrosion for the tree species, *Corylus*, and the "exotic" pollen (p. 42). The diagrams show the percentage distribution of the samples in 3 corrosion-classes for each taxon (only samples with more than 10 grains of the taxon were included). The samples from section 370 from Draved were divided into two groups, one group with *Fraxinus* pollen and the other without. The corrosion degree is highest in the first group, because these samples came from the best soils (cp. above).

The diagrams below show that the pollen preservation is best in the samples from Draved, and less good in the samples from Longelse. The diagrams also show that the frequencies of corroded grains vary in the various plants.

The plants are arranged in the 4 diagrams below according to increasing



Draved forest and Longelse forest. Percentage frequency of samples with 0–10, 10–50 and 50–100 % corroded pollen grains.

+ Fr = samples with *Fraxinus* pollen. – Fr = samples without *Fraxinus* pollen. x = exotic plants (see chapter VIII), Q = *Quercus*, Fr = *Fraxinus*, T = *Tilia*, B = *Betula*, U = *Ulmus*, A = *Alnus*, F = *Fagus*, Cp = *Carpinus*, Co = *Corylus*. N = number of samples percentages of corroded grains. These 4 sequences are nearly the same. The positions of the various taxa within the 4 sequences are indicated in table 10. This generalized sequence is almost identical to the sequence found by HAVINGA (1967) from experiments in biologically active soils. It does not give a quite unbiassed picture of corrosion resistance, but it does suggest that certain pollen grains are less readily attacked than others, and that the pollen analyses from samples with many corroded pollen grains may be distorted.

Table 10. Draved forest and Longelse forest. Positions in 4 sequences of increasing corrosion frequency

exotic plants	1, 1, 1, 2
Quercus	2, 2, 2, 3
Fraxinus	1, 3
Tilia	3
Betula	3, 4, 4
Ulmus	4
Alnus	4, 5, 6
Fagus	5, 5, 6, 6
Carpinus	6
Corylus	7

The pollen spectra of 2 samples from section 370 in Draved taken 3.5 m apart are shown in table 11. The percentages of corroded pollen grains are much higher in sample b than in sample a, but the pollen spectra only differ essentially with respect to *Corylus*. Sample a contained many lumps of *Corylus* pollen grains, and the difference in the *Corylus* frequencies is due to overrepresentation rather than corrosion. Hence corrosion may not change the pollen spectra severely in all cases.

Table 11. Draved forest, section 370. Pollen spectra and frequencies of corroded grains (in brackets) in 2 samples

	a % of AP		b % of AP	
Quercus	23	(15)	30	(48)
Betula	22	(27)	20	(71)
Alnus	23	(20)	23	(86)
Fagus	8	(55)	8	(93)
Tilia	0.4		2	
Fraxinus	24	(17)	16	(67)
Corylus	71	(17)	15	(82)
exotic plants	40	(5)	34	(43)

A great number of samples were available from the areas studied in Draved, and the counts with more than 50% corroded pollen grains could be excluded without diminishing the data seriously. Such a procedure would, however, reduce the material from Longelse greatly, and hence all data from this forest were considered. The results do not appear to be affected greatly (p.60).

VII. POLLEN DISPERSAL IN THE FOREST

Pollen grains may be deposited on the forest ground by wind dispersal (dry deposition), washing from the vegetation by rain (rain deposition), and falling to the ground with catkins or flowers (macroscopic deposition).

WIND CONDITIONS

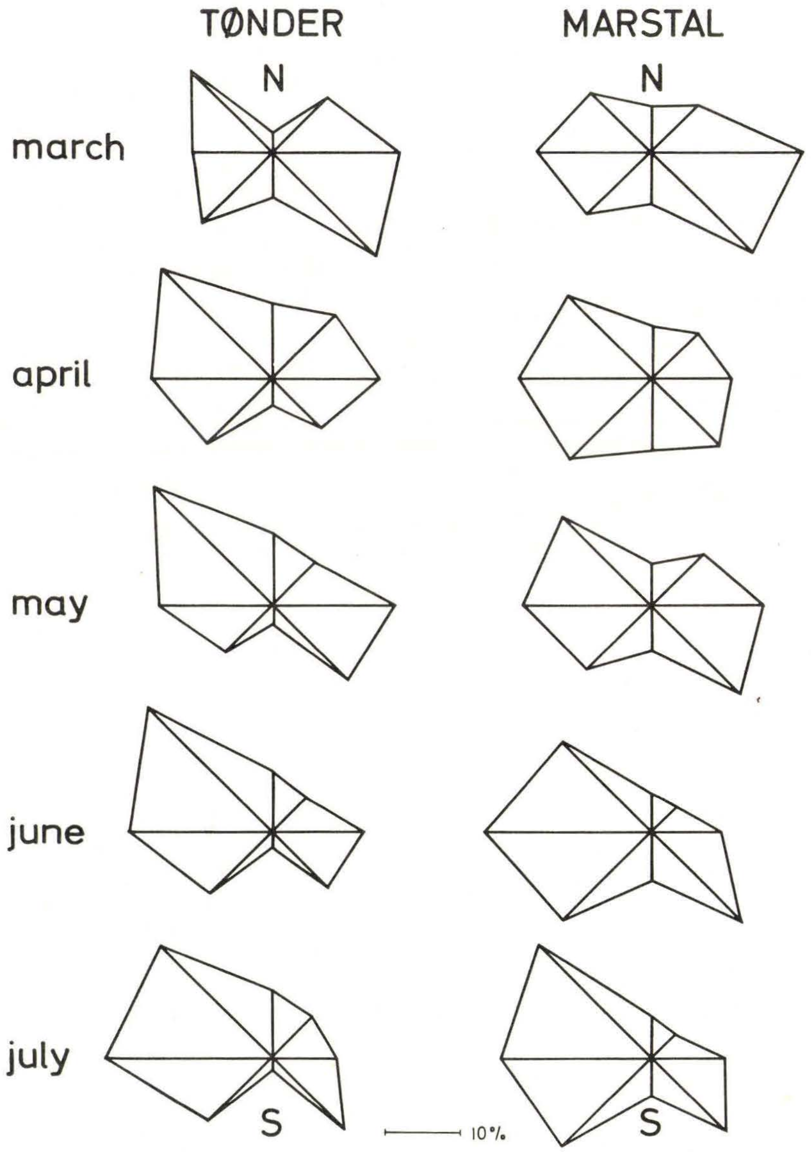
Wind recorders were operated in Draved during the flowering seasons of 1968 and 1969. One recorder was placed on a tower outside the forest and one inside the forest, in section 386. The elevation of the recorder outside the forest is 8.2 m and the one in the forest is 6.6 m. Undergrowth occurs irregularly around the recorder in the forest, which is placed about 140 m northeast of the forest edge. The air flows somewhat more easily through the forest southwest-northeast than southeast-northwest. The period of measurement is too short for a statement of general wind conditions, however, a few preliminary indications are mentioned below.

Wind directions

The observations of wind directions from the forest wind recorder suggest that the wind through the forest follows the outside wind directions quite faithfully, but there may be a tendency for the wind to turn into the direction of easiest flow. The wind passing through the crown space probably is even more similar to the outside wind in this respect.

As the observations of wind directions obtained from the recorders in Draved cover a very short period, a better picture may be obtained from the general meteorological observations. Average distributions in march-july 1950–1959 at the station Tønder East about 10 km southwest of Draved and at Marstal 20 km from Longelse are shown on p. 32. They were calculated from the figures published by the DANISH METEOROLOGICAL INSTITUTE (1951–1965).

The wind directions in march, april and may are almost equally distributed with some deficit for northern and southern winds, whereas northwest and west winds are prominent in june and july. A similar distribution occurred in Løgumkloster 4 km north of Draved in 1930–1939. Most of the trees flower during march, april and may, and their pollen may become rather uniformly dispersed.



Percentage distribution of the wind directions at Tønder East and at Marstal 1950-59

Wind velocity

Average wind velocities at Skrydstrup airfield 30 km northeast of Draved calculated from data published by STATENS LUFTFARTSVÆSEN (1963) and at Draved are shown in table 12. The wind velocities from Skrydstrup are 24 hour averages, which are lower than the wind velocity by day. They were multiplied by 1.35 to show the wind velocity at 1300 hours (the figures in brackets). The wind velocities at Skrydstrup are similar to those measured at Draved. The wind velocities at the middle of the day, where pollen emission is highest, are rather high in the flowering period (averages 6–10 m/sec). They are somewhat lower by night (averages 3–7 m/sec).

Table 12. Wind velocity at Skrydstrup airfield and at Draved, m/sec.

	Skrydstrup (20 m)		Draved (8.2 m)			
hour	000–2400	(1300)	1300		0100	
year	1954–1958		1968	1969	1968	1969
march	6.2	(8.4)	9.1	10.6	6.8	7.2
april	5.1	(6.9)	7.3	7.8	4.3	4.4
may	5.3	(7.2)	7.3	7.8	3.1	4.4
june	4.6	(6.2)	7.1	5.9	3.0	2.8
july	5.4	(7.3)	6.2	5.8	3.1	3.4

Table 13. Wind speed frequencies at Draved (%)

hour	1300				0100			
	<5 m/sec.		≧10 m/sec.		<5 m/sec.		≧10 m/sec.	
year	1968	1969	1968	1969	1968	1969	1968	1969
march	7	14	46	41	32	45	25	21
april	23	14	17	25	67	64	10	7
may	23	23	32	36	87	65	–	6
june	23	43	13	3	90	83	3	–
july	41	23	11	–	78	84	–	3

Table 13 shows the wind speed frequencies at Draved by day and by night. Winds speeds at 5 m/sec or more predominate by day and at less than 5 m/sec by night.

Measurements of wind velocities in forests are mentioned in Geiger (1966), however, the periods of measurement are very short, and the forests may differ from those studied here.

Average wind velocities measured in section 386 in Draved forest are shown in table 14. The average wind speed in the forest was highest in march and april before the leafing of the trees (about 2 m/sec) intermediate in may during leafing, and lowest in june and july, when the forest was in full leaf (about 1 m/sec). Similar observations on the effect of leafing are mentioned in Geiger (l.c.). The wind velocities by night were somewhat lower than those found by day.

Table 15 shows the wind speed frequencies in the forest by day and by night. Wind speeds at 2 m/sec or more predominate by day before leafing and at less

Table 14. Average wind velocity in section 386 in Draved forest, m/sec.

hour	1300		0100	
year	1968	1969	1968	1969
march	2.7	2.3	2.1	1.5
april	2.1	2.1	1.4	1.3
may	1.4	1.5	0.7	0.9
june	1.1	0.9	0.7	0.6
july	0.9	0.9	0.5	0.5

Table 15. Wind speed frequencies in section 386 in Draved forest, %

hour	1300				0100			
	<1 m/sec.		≧2 m/sec.		<1 m/sec.		≧2 m/sec.	
year	1968	1969	1968	1969	1968	1969	1968	1969
march	4	3	82	72	25	28	64	24
april	–	–	42	43	30	32	17	18
may	16	19	13	19	84	58	3	6
june	20	53	–	–	73	83	–	–
july	52	61	–	–	93	94	–	3

than 1 m/sec after leafing. Wind speeds at more than 1 m/sec predominate by night before leafing and at less than 1 m/sec after leafing.

The wind velocity increases in the crown layer and is in the tree tops nearly that above the trees, before leafing. After leafing the wind speed increases near the tree tops (Geiger 1966). The wind velocity decreases with about 50% near the ground according to profiles measured in Draved (cp. Geiger l.c.).

Longelse forest is very similar to Draved forest, and the wind speeds there are presumably similar to those measured in Draved.

DISPERSAL OF TREE POLLEN

Dry deposition

The pollen grains released during the anther dehiscence are in anemophilous trees with hanging catkins such as *Alnus*, *Betula* and *Quercus* deposited on the scales of the flowers beneath, whereas the pollen in trees with erect stamens such as *Fraxinus*, *Ulmus* (and *Tilia*) collect in the cup formed by the opened anther. In both cases the pollen is blown away when the wind velocity reaches a certain level (Gregory 1961).

Observations of Rempe (1937), Persson (1955), Grosse-Brauckmann and Stix (1969) and others indicate that the pollen release is highest about noon, at which time the wind speeds are highest.

The trajectories of the tree pollen grains are likely to be influenced by air turbulence in the crown layer, whereas they may fall freely through the trunk space due to a low turbulence there.

It is characteristic of the pollen of anemophilous trees that the single grains part easily, whereas the pollen of entomophilous species may stick together (POHL 1930). POHL (1933) and REMPE (1937) investigated the tendency of the pollen of various trees to form lumps. POHL (l.c.) collected pollen on slides placed on the ground under a large *Quercus robur*, and found that the pollen contained in lumps with more than 1 grain made out 24%, and the grains contained in lumps with more than 2 grains 10% of the total pollen count. REMPE (l.c.) caught the pollen of various tree species on vertical cylinders hung in the crowns of single trees during a flowering season. REMPE (l.c.) indicated the frequencies of lumps larger than 1 grain in percentages of the number of 'pollination entities', and the average number of pollen grains contained in the 'pollination entities'. The frequencies of the pollen grains contained in lumps, and the average lump sizes calculated from REMPE's figures are shown in table 16.

Table 16. Frequency of pollen grains contained in lumps and lump size (calculated from REMPE 1937) and terminal velocity of single grains (from GREGORY 1961)

	Pollen grains in lumps % of all pollen grains	average lump size number of grains	Terminal velocity cm/sec.
Quercus sp.	50	2.7	2.9
Betula verrucosa	34	2.9	2.4
Alnus glutinosa	34	3.2	(1.7)
Carpinus betulus	–	–	6.8
Ulmus montana	58	3.1	3.2
Fagus silvatica	24	2.4	5.5
Tilia cordata	85	9.0	3.2
Corylus avellana	37	3.9	2.5

POHL's figures quoted above are probably more realistic than the figures from REMPE's study, as the collection efficiencies of cylinders such as those employed by REMPE (l.c.) varies with the wind velocity and the particle size (GREGORY 1961, TAUBER 1965). REMPE did not measure the wind velocities. They may have varied in the various experiments, and the frequencies of the pollen lumps presumably are too large because of a higher collection efficiency. The frequency of pollen contained in lumps in table 16 for *Quercus* thus is twice the figure found by POHL (l.c.). It may be concluded that pollen grains contained in large lumps are rather scarce in most cases, but *Tilia* pollen may be somewhat lumpy.

Terminal velocities of single pollen grains also are shown in table 16. They vary from about 2 cm/sec for small grains to about 7 cm/sec for heavy grains. The terminal velocity for pollen lumps is larger as it increases with the square of the particle radius, according to Stoke's law. Their average terminal velocity probably is about 4 times the terminal velocity of single grains, and somewhat larger in the case of *Tilia*.

At the wind velocities prevailing in April (table 14), single pollen grains would travel 600–2000 m and the pollen contained in lumps about 100–500 m before reaching the ground, if turbulence is disregarded. Turbulence would cause a decrease in these distances (cp. Tauber 1965). *Tilia* pollen is likely to travel somewhat shorter distances.

Measuring ground deposition downwind from single sources Rempe (1937) and Colwell (1951) found distributions according with Chamberlain's theory i.e. no deposition at the source, increasing deposition some distance from the source untill a maximum is reached, and then decreasing deposition. Maximum deposition under or near the source has been observed in other cases. Pohl (1933) exposed slides under a single flowering *Quercus robur* for 2 hours and found 772 pollination entities (single grains or lumps) 3 m from the trunk (under the crown's edge), and 657 entities 11 m from the trunk, i.e. highest concentration under the tree crown. Wright (1952) exposed slides at a 45° angle near the ground under single trees or tree rows. The numbers of pollen grains found at increasing distances are shown in table 17.

Table 17. Decrease of pollen deposition with distance (from Wright 1952). Height of trees in brackets

	8 m	17 m	50 m	133 m	
Fraxinus ssp. (13–17 m)	2502	1110	110	2	
	17 m	33 m	167 m	300 m	
Populus nigra (13 m).......	202	8	110	38	
	8 m	50 m			
Pseudotsuga (8 m)	235	18			
	3 m	25 m	50 m	75 m	100 m
Pinus cembroides (8 m).....	8480	438	141	13	46
	0 m	55 m	110 m		
Malus pumila	132	1.2	2.0		

It may be seen that considerable amounts of pollen may be deposited beneath single trees and that the pollen deposition decreases strongly at distances equal to 1 or 2 times the tree altitude. The trees occurred in open areas, where at least moderate wind speeds and turbulence must have prevailed. GREGORY (1961) found the highest deposition of *Lycopodium* spores at 2.5 m from a source at 1 m altitude. In GREGORY's own comment (l.c. p. 83) "the unexpectedly large deposition on the ground near the source as shown in table XII, is evidence of factors near the source of a diffusing cloud which still remain to be elucidated".

Thus it appears that although the pollen would be expected to be carried far from the trees by the wind before they reach the ground in the forest, a high pollen deposition may occur under or very near the source trees in some cases due to conditions, which are not yet fully understood.

Rain deposition

Pollen grains dispersed by the wind may be caught on twigs or leaves in the crown layer during the flowering (DENGLER 1955, GREGORY 1961, TAUBER 1965, 1967) and washed to the ground by rain. Leaves are inefficient pollen collectors at wind speeds above 3 m/sec (GREGORY l.c.) and may be less important in this respect.

About 50% of the raindrops falling under deciduous trees are larger than 1 mm in diameter and most of the rain falls directly under the tree crowns (GEIGER 1966).

The pollen collected 1967 in Draved forest in open collectors (p. 24) was divided into a fraction collected in the spring and the summer, and a fraction collected during the autumn and the winter. The average frequencies of pollen collected during the autumn and winter in percentage of the whole year's count are shown in table 18.

The pollen collected during the autumn and the winter must have been washed by the rain from the tree crowns. A similar phenomenon was observed by

Table 18. Draved forest. Pollen deposition in autumn and winter in percentage of a whole year's count (1967). Averages of 6 collectors

	Averages of 6 collectors
Quercus	9%
Betula	13
Alnus	12
Fagus	7 (2 collectors)
Tilia	22 (1 collector)
Fraxinus	20
Corylus	10
exotic plants	17

TAUBER (1967). Further experiments are needed to see how much pollen is brought down by rain during the summer, however, it can be assumed that a considerable amount of the pollen is deposited on the forest floor in this manner.

The amount of pollen collected on twigs depends on the pollen concentration in the air and on the collection efficiency of the twigs (GREGORY 1961).

The highest concentrations of pollen in the air in the forest occur in the crown space (TAUBER 1965). The downwind concentration of a spore or pollen cloud emitted from a linear source decreases almost with the square of the distance (GREGORY 1961). The air concentration decreases further due to loss by filtration.

Dispersal distances of pollen in the crown layer of forests have been determined in a few cases, by measurement or indirectly. LANGNER (1962) collected the pollen emitted from a single *Betula* in a *Pinus* forest on spheres hung in the crown layer. The amount of *Betula* pollen caught decreased with 50% one *Pinus* tree crown away and to only a few per cent further away. GULDAGER (1967) exposed vertical pollen collectors in the crown layer of a *Larix* forest. The amount of stained *Larix* pollen and *Lycopodium* spores emitted from a source in the crown layer decreased logarithmically at increasing distances, and only 5% of the amount occurring near the source was captured 25–40 m away. LANGNER (1963) determined the proportion of *aurea*-seedlings of *Picea abies* at varying distances from a group of *aurea*-trees in a *Picea abies* plantation The pollen emitted from the *aurea*-trees produce 50% *aurea*-seedlings, when crossed with normal trees. LANGNER (l.c.) found 10–20% *aurea*-seedlings under normal trees 25 m from the *aurea*-source, and mostly less than 5% aberrant seedlings under trees 40–70 m from the *aurea*-trees.

The amount of pollen dispersed from a tree apparently decreases to insignificant values at distances of a few tens of m from the source tree.

The concentration of pollen grains near an elevated source decreases independently of their fall rate. However, the collection efficiencies of the twigs may not be the same for pollen grains of various sizes. Cylinders of 8 mm diameter, which is similar to the average thickness of branches, collect *Fagus* pollen grains 5 times more efficiently than *Betula* grains at wind velocities of 1 m/sec, but the difference in collection efficiency decreases strongly with increasing wind velocity (TAUBER 1965). At wind speeds of 6 m/sec the difference in collection efficiency is about 1.5 times. It is difficult to estimate the collection efficiences in the crown layer because the wind velocities are not known exactly and because the twig diameters are variable. The wind speeds in the tree tops, where flowering is most intensive, are likely to approximate the wind speeds above the tree crowns, particularly in the spring (p. 34), and the collection efficiencies for large and small pollen grains may not differ greatly. Twigs examined by TAUBER (1967) showed no increase in the frequency of *Fagus* pollen relative to the frequency of *Betula* pollen.

Macroscopic deposition

The inflorescences of the trees may in some cases be torn off by strong winds before the opening of the anthers and fall to the ground. Such inflorescences contain masses of pollen grains. The pollen grains released in the hanging catkins are likely to be blown away by the wind, but the inflorescences may act as pollen traps and collect pollen dispersed through the air from other flowers. This pollen may fall to the ground with the inflorescences, which mainly fall beneath or near the trees from which they derive. REMPE (1937) found that the catkins fallen to the ground under a large richly flowering *Alnus glutinosa* during the flowering season contained 111.000 pollen grains/cm^2, but it is not stated whether this pollen occurred in unopened anthers or adhering to old catkins. The pollen adhering to catkins may form a significant proportion of the pollen deposited on the ground, but the fact that 10–20% of a year's deposition is deposited in the autumn and the winter a long time after the catkins have fallen (table 18) suggest that this factor should not be overestimated.

Cases of overrepresentation where the pollen of a particular species occur with abruptly high frequencies are mentioned in chapter X. Such cases obviously are due to the incorporation of unopened anthers in the surface sample. They are, however, few in number.

DISPERSAL OF POLLEN FROM SHRUBS AND HERBACEOUS FOREST PLANTS

Corylus is the only important shrub in the forests investigated. Its pollen presumably is dispersed in a manner similar to the tree pollen. 10% of the *Corylus* pollen was deposited in the autumn in 1967 (table 18). The average wind speed in the trunk space is about 2 m/sec at its flowering time (p. 33), and its pollen presumably is dispersed shorter distances than the tree pollen.

The wind speed decreases rapidly below 1 m above the forest floor. 10 cm above the ground it is about 1 m/sec in april and less than 0.3–0.4 m/sec in july, according to wind profiles measured in Draved. Hence the pollen of low herbs have very little chance of dispersal beyond a few m. The pollen of taller herbs such as *Filipendula* or *Crepis* may have a somewhat better chance of dispersal by wind.

FOREIGN POLLEN

Pollen grains coming from outside the forest may be carried into the forest between the trees or they may be carried over the tree canopy and become mixed into the crown layer and the trunk space by turbulent wind.

Observations on the penetration of foreign pollen into the trunk space of forests were made by OGDEN et al. (1964), RAYNOR et al. (1966), and by BASTIN (1964). OGDEN et al. (l. c.) observed a drop in the air concentration of *Ambrosia* pollen to about 50% of the outside value a few m inside the forest edge. At 50 m from the forest edge the air concentration was about 25% and at 80 m nearly 0. RAYNOR et al. (l. c.) noticed a drop in pollen transport (dosage) from artificial *Ambrosia* pollen sources just outside a *Pinus*-forest to about 10% of the source strength at 40–50 m from the forest edge. BASTIN (l. c.) found in moss samples from a *Fagus* forest a decrease of NAP pollen (mostly foreign plants) from 100% (of tree pollen) at the forest edge to 58% at 25 m, 52% at 50 m, 45% at 100 m and 39% at 200 m from the edge, that is a drop within the first 25 m, whereafter the values remain almost constant. The forest investigated by RAYNOR et al. had an open trunk space. The structure of the forests investigated by the other authors mentioned is not stated, but it may be assumed that they also are more open than the Draved and Longelse forests, which have dense undergrowth. Hence it may be assumed that foreign pollen penetrates only a very short distance into these forests through the trunk space.

The NAP pollen found by BASTIN (l. c.) at distances more than 25 m from the forest edge presumably was carried over the tree tops. The wind velocity increases rapidly in this layer and the turbulence is particularly high due to the roughness of the vegetation and convection (GEIGER 1966). The pollen transported over the tree tops may be caught on the twigs or leaves when the wind currents pass down through the crown canopy. TAUBER (1967) thus found considerable amounts of pollen from exotic plants on twigs and leaves. In the pollen collectors mentioned on p. 37 17% of a year's deposition of pollen from exotic plants was washed down during the autumn and the winter, and a considerable proportion of the foreign pollen deposited on the forest floor probably is derived in this manner. Air streams passing down through the crown canopy may also carry foreign pollen into the trunk space, from where it settles on the forest floor.

SUMMARY OF CHAPTER VII

It appears that pollen is deposited on the forest bottom in a complex manner, but few facts are known about the mechanisms involved.

(1) Pollen grains falling through the air from the trees may be carried several hundred metres away before they reach the ground. However, substantial amounts may be deposited beneath or very near the source.

(2) Pollen lumps falling through the air may be deposited up to a few hundred m away or near the source.

(3) Pollen collected in the crown layer by filtration is washed to the ground by rain. The tree pollen deposited in this manner mainly derives from trees standing up to a few tens of m away. The rain drops fall nearly vertically to the ground.

(4) Pollen found in immature inflorescences and pollen collected on catkins may fall to the ground with these.

(5) The pollen of herbaceous forest plants are diffused a few metres only.

(6) Foreign pollen grains carried by the wind into the forest are deposited a few tens of metres from the forest edge. Foreign pollen carried over the tree tops may be mixed into the tree tops by air turbulence, caught by filtration, and washed to the ground. A considerable proportion of the foreign pollen is likely to be transported in this manner.

VIII. THE COMPOSITION OF THE EXOTIC POLLEN IN DRAVED AND LONGELSE FOREST

If foreign pollen is deposited evenly in the forest areas studied it may be used as a calculation basis for the deposition of other pollen. Nearly all the samples analyzed for pollen were taken more than 25 m from the forest edge, and the influence of foreign pollen carried horizontally into the trunk space is assumed to be low (p. 40), whereas it is likely that most of the foreign pollen found in the samples was carried over the tree tops.

A strong mixing of pollen takes place in the air because of turbulence or convection. REMPE (1937) thus collected pollen from an aeroplane. He found high pollen concentration up to 500–1000 m altitude, and heavy pollen grains were carried aloft as effectively as light pollen grains. The pollen transported over the forests derives from a vast area (TAUBER 1965), and the pollen concentration may not decrease significantly over short distances, as losses of pollen in the tree tops may be eliminated by the vertical mixing. In an experiment mentioned by GEIGER (1961) the dust content of the air was nearly the same at the lee side of a forest 1 km wide as at the windward side. A rather uniform addition of foreign pollen thus may be assumed for the small forest areas studied (diameters maximally 200 m).

The deposition of foreign pollen in the forests can be studied by means of pollen collectors. Preliminary results from Draved (from 1967) suggest a homogeneous deposition. The uniformity of the deposition of foreign pollen also can be studied by an examination of the composition of the foreign pollen in the moss humus samples. Losses of pollen from the air due to ground deposition or filtration in the vegetation are largest for heavy or large pollen grains. The relative frequencies of these pollen grains will accordingly be expected to decrease in the downwind directions if the air concentration and the deposition of foreign pollen decreases significantly within the areas studied.

The foreign pollen cannot be determined exactly in the moss humus samples, and only exotic pollen, i.e. pollen from plants known not to occur in the forests can be distinguished. The Gramineae are here considered exotic. Their pollen constitutes a major part of the foreign pollen, and the addition of pollen from grasses from the forest presumably is insignificant, as the forest grasses are rare and produce small amounts of pollen. Some non-arboreal pollen grains of more uncertain origin (Compositae, Cruciferae, Rubiaceae, Umbelliferae, *Lysimachia*, *Lotus*, *Potentilla*) were not included in the exotic pollen.

The frequencies of the most common exotic pollen types in percentages of

Table 19. Draved forest and Longelse forest. Composition of the exotic pollen. Frequencies in percentage of total exotic pollen

	Draved	Longelse
Pinus	7.6	10.9
Betula	–	4.8
Calluna	8.2	0.3
Gramineae	54.7	48.4
Cerealia	9.5	11.9
Rumex acetosella	7.3	1.8
Plantago lanceolata	2.1	0.8
Chenopodiaceae	1.9	17.6
Artemisia	0.9	2.4
Leguminosae	4.8	0.4
Sphagnum	1.4	0.2
others	1.6	0.6
Total	15 159	4 719

the total of pollen from exotic plants in Draved and Longelse forest are shown in tables 19–20 and 31–33 (pp. 92–93).

The exotic pollen from Draved and Longelse forest differs somewhat in composition (table 19). The more conspicuous differences are due to differences in the vegetation of the two regions such as the occurrence of boggy and sandy areas around Draved (*Calluna*, *Rumex acetosella*, *Sphagnum*) and beach vegetation at the shores of Langeland (Chenopodiaceae, *Artemisia*) or cultivation practice (grazing near Draved, Leguminosae, mainly *Trifolium* spp.). The group "others" comprises plants represented with a few pollen grains such as trees foreign to the forests, heath plants, weeds, and swamp plants and aquatics. Curiously enough, a few colonies of *Pediastrum*, a fresh water alga, occurred in Draved too.

The tables 20 and 31–33 show the composition of the exotic pollen in the sections 386 and 370 in Draved forest and in sample groups within the 2 sections. The pollen grains of the Leguminosae are omitted from these pollen totals (see below). Homogeneity was tested by the χ^2-method according to the procedure described by MOSIMANN (1965). A + in the row marked "total" indicates that the probability that the two samples are alike is less than 5% and a + in the rows for the various taxa indicates that the probability that the samples are alike with respect to that taxon is less than 5%.

Most plants listed in the tables flower in the summer, at which time northwestern and western winds predominate (p. 32). Section 386 is rather sheltered from such winds, whereas section 370 is near open fields towards north and west (see the map on p. 16).

The columns for the sections 386 and 370 in table 20 show that the exotic pollen is not the same in the two areas, however, within the 11 components it

Table 20. Draved forest, sections 386 and 370. Composition of the exotic pollen. Frequencies in percentage of total exotic pollen excluding the Leguminosae. Significance tests according to the χ^2-method

	386	370	Significance P 0.05
Gramineae	57.6	57.3	+
Pinus	7.4	8.3	
Calluna	8.9	8.5	
Cerealia	9.6	10.2	
Rumex acetosella	7.2	7.9	
Chenopodiaceae	2.1	1.9	
Plantago lanceolata	2.4	2.1	
Artemisia	0.9	1.0	
Sphagnum	2.2	1.1	+
others	1.8	1.7	
Total	5 315	9 114	+
Leguminosae	2.2	6.7	+

only differs with respect to 3, *Pinus*, *Sphagnum* and Leguminosae. The differences in the frequencies of *Pinus* pollen and *Sphagnum* spores only amount to about 1% and are unimportant, whereas the Leguminosae pollen is distinctly more frequent in section 370 than in the other area.

The variations in the exotic pollen frequencies within the sections 386 and 370 are shown in tables 31–32. Individual samples are not compared, as statistical significance only can be proved for very large differences due to the limited number of exotic pollen counted in each sample (about 100). Sample groups are compared instead.

The samples from section 386 were divided into 3 groups, northwest, northeast, and southeast (see the map on p. 23). The 3 groups differ with respect to the composition of the exotic pollen, but the difference is limited to 2 taxa, *Calluna* and Cerealia. *Calluna* pollen is somewhat more common in the northeastern area, and there is a slight increase in the Cerealia pollen frequencies in the direction northwest-southeast. Hence there is no distinct decrease in the frequency of heavy pollen in downwind direction.

The samples from section 370 were divided into a western and an eastern group (see the map on p. 24). The samples in these 2 groups only differ with respect to the frequencies of *Calluna* and Leguminosae. The *Calluna* pollen grains are slightly more frequent in the eastern area, and the Leguminosae pollen grains are somewhat more frequent in the western area. The Leguminosae pollen thus decreases somewhat in downwind direction. The samples from the eastern part of the section were divided into 5 groups, I–V, among which I is the northernmost, and V the southernmost. The composition of the exotic pollen in these 5 areas differs in particular with respect to Gramineae, *Pinus*, *Calluna*, Cerealia and Leguminosae. The Gramineae increase slightly and *Pinus* and *Calluna* decrease somewhat from north to south, in the downwind direction, but the heavy Cerealia pollen do not decrease.

It appears that the exotic pollen is deposited somewhat irregularly in Draved forest, but there is no distinct concentration of large pollen grains in the upwind parts of the 2 sections. The frequency of the Leguminosae pollen in section 370, decreases clearly in the downwind directions. In the pollen collectors exposed in 1967 23 % of the Leguminosae pollen was deposited during the autumn and winter, a figure which suggests that the grains were blown over the tree tops and washed to the ground from twigs and leaves in the same way as the other grains. The Leguminosae are the only insect-pollinators among the exotic plants listed in table 20. Such plants have sticky pollen grains which keep together in lumps (Pohl 1930), and the large fall-out of Leguminosae pollen in section 370 suggests that it was dispersed in heavy lumps which were quickly removed during their passage over the tree tops. The frequency of the Leguminosae pollen in the southeasternmost and most sheltered part of section 370 (2.3 %) is the same as the frequency in section 386 (2.2 %), which is also sheltered relative to the predominating winds.

Table 33 shows the composition of the exotic pollen in Longelse forest with the samples arranged in 4 groups according to their distribution within the area (see the map on p. 25). This part of the forest is bordered by fields towards west, north, east and southeast, and only is sheltered from wind by forest towards southwest.

The exotic pollen differs in composition, particularly with respect to Gramineae, *Pinus* and *Betula*. The Gramineae pollen is slightly more common in the western than in the eastern part, and *Pinus* and *Betula* pollen is slightly more common in the eastern than in the western part, but there are no differences in the frequencies of the heavy Cerealia pollen. Leguminosae pollen is very scarce in Longelse (table 19).

It appears that the data on the exotic pollen composition in Draved and Longelse forest give no clear evidence of differential filtering. Hence it is suggested that losses of pollen from the air mass over the forest are eliminated by downmixing from above, and that there are no large differences in the deposition of exotic pollen within the forest areas studied. One exception is the Leguminosae pollen in Draved, which presumably is dispersed in lumps and is rather quickly removed when the wind passes over the forest. Hence the Leguminosae pollen was excluded from the exotic pollen totals. The deposition of exotic pollen may of course vary somewhat in the individual samples, but such a variation cannot be determined.

IX. THE RELATIONSHIP BETWEEN FOREST COMPOSITION AND TREE POLLEN DEPOSITION

POLLEN PRODUCTIVITY (P- AND P_{rel}-VALUES)

The absolute pollen productivity of the trees is best defined as the number of pollen grains produced per unit crown area per time unit. This size may not always be the same in a tree species, as the flowering intensity of the trees may vary with exposure and from year to year. Single trees flower more richly and more frequently than trees in a closed stand, and the frequency of flowering years may vary with climate. We may consider the typical pollen productivity of a tree species as the pollen productivity of trees growing in closed stands.

The ratio of the absolute pollen productivity of a species to that of another species may be termed its relative pollen productivity.

The absolute pollen productivity of trees is difficult to determine. The method of POHL (1937) mentioned on p. 12 involves extrapolations of such dimensions that the results must remain uncertain. The relative pollen productivity may be determined by the method used by REMPE (1937, see p. 12), but the procedure requires corrections for wind velocities and long observation series. Hence comparisons from surface samples may be more useful.

The pollen deposited on the forest floor consists of a mixture of pollen brought down in various manners, however, it is likely that the tree pollen deposited at a certain point mainly derives from the trees within a short distance (see chapter VII).

If we assume that all the pollen of a tree species deposited on a sample point on the ground came from trees within a given distance (d) the amount of pollen deposited on a unit area per year (p) increases with the crown area of the trees (a) in a simple manner, assuming a linear relationship,

$$p = P \times a \tag{1}$$

The factor P expresses the degree with which the pollen deposition increases with the area of the species. It is high in tree species with a high pollen deposition and low in species with a low pollen deposition. As the pollen grains are deposited very near the sources, P depends greatly on the pollen productivity of the species and may be termed pollen productivity factor. P can be determined from formula (1) as

$$P = \frac{p}{a} \tag{2}$$

If the pollen of the trees is dispersed beyond the distance (d), pollen grains from trees outside this distance also will be deposited at the sample point. Formula (1) then becomes modified into the regression equation

$$p = P \times a + p_o \tag{3}$$

p_o here denotes the amount of pollen deposited on a unit area per year from trees standing at distances larger than d. If the species in question does not occur inside d, then a is 0 and $p = p_o$. Hence p_o can be determined as the amount of pollen deposited, when the tree species does not occur near the sample point.

From formula (3) P can be determined as

$$P = \frac{p - p_o}{a} \tag{4}$$

P and p_o can be determined in (3) by regression analysis, if a sufficient number of values of p and a are known. P and p_o can be determined for various values of d, which equals the sample plot radius. p_o is independent of the sample plot size if this is not too small. The P-value increases in a smaller sample plot.

The P-ratio of 2 species equals the relative pollen productivity and indicates how much more pollen is produced (or deposited) by one species than by the other. The relative pollen productivity of a species is indicated as its P_{rel}-value. The P_{rel}-values are independent of the sample plot size if the pollen of the various tree species is dispersed equally well but may vary with the sample plot size if the various species have different pollen dispersal distances. They may become somewhat modified if the collection efficiency in the crown layer differs greatly for small and large pollen grains (cp. p. 38).

The crown areas and the basal areas (in m^2) of the tree species within circles of 20 and 30 m radius are used as area values in the present investigation.

The absolute pollen deposition at a sample point can be determined with the help of pollen collectors. Such data have not been used here as the period of collection is too short. Hence, the tree pollen deposition was determined by means of the moss humus samples.

It is assumed that the deposition of exotic pollen is nearly constant in the forest areas studied (see chapter VIII). Hence, the relative pollen deposition of a tree species in a moss sample (p_r) can be determined as

$$p_r = \frac{\text{number of pollen grains deposited per cm}^2\text{ per year}}{\text{number of exotic pollen grains deposited per cm}^2\text{ per year}} = \frac{\text{number of pollen grains counted}}{\text{number of exotic pollen grains counted}}$$

Equation (3) then becomes modified into

$$p_r = P \times a + p_{r(0)} \tag{5}$$

Regression equations and determinations of the pollen productivity factors (P) of the various tree species are mentioned in chapter X. The relative pollen productivity (P_{rel}-value) of the various tree species is determined in relation to the P-value of *Fagus*.

POLLEN REPRESENTATION (R- AND R_{rel}-VALUES)

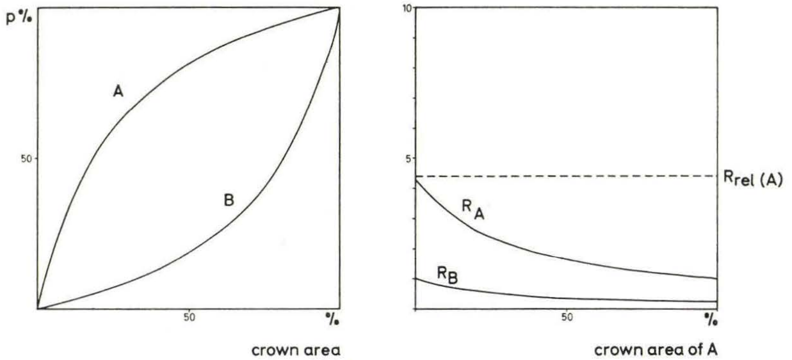
The relation of the pollen spectra to the vegetational composition may be expressed by R-values. The R-value for a species is (DAVIS 1963)

$$R = \frac{\text{pollen percentage}}{\text{area percentage}}$$

The R-values express the over- or underrepresentation of the species. R is > 1 if the species is overrepresented and < 1 if the species is underrepresented.

DAVIS (l.c.) pointed out that the R-values of a species are not constant, as they depend on the species combination. Some authors have not realized this point, and may still state that such or such species characteristically have low or high R-values.

Another point which has been overlooked, is the fact that the R-values vary with the areal frequency of the species even in cases where the species combination is the same. This point may be illustrated by a simple case where two species, A and B, occur together with varying frequencies (the figure below). If species A is 4.4 times better represented than B, their pollen and area percentages will vary as shown in the first diagram below, which is similar to diagrams shown by FÆGRI and IVERSEN (1960) and by LIVINGSTONE (1968). The second diagram illustrates the variation of the R-values of the two species (R_A and R_B) with the increasing areal percentages of species A. R_A decreases from 4.3 at 1% to 1.0 at 100% areal frequency of A, and R_B is 1.0 at 0% and 0.2 at 99% areal frequency of A. It appears that the R-values are variable and uncharacteristic even in this simple case.



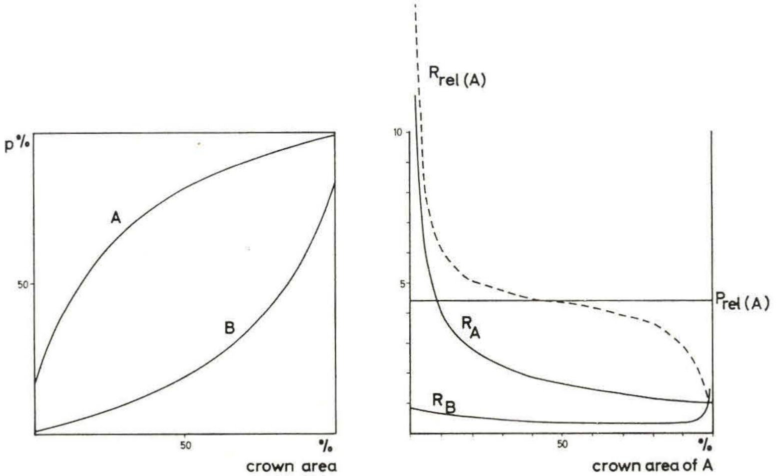
Left: pollen percentages (p%) and areal percentages (a%) of 2 species, A and B. Species A deposits 4.4 times more pollen than species B per crown area unit.
Right: R-values (pollen%: area%) for the species A and B (R_A and R_B) and R_{rel}-values for species A in relation to species B (R_A:R_B)

Davis (l. c.) also pointed out that the R-ratios of species occurring in various combinations are constant. The second diagram on p. 48 also shows the relative R-values of species A ($R_{rel(A)} = R_A : R_B$), which are constantly 4.4.

The calculations of the relation of pollen percentages to area percentages mentioned above assume that the pollen percentages of a species is 0 when its area percentage is 0, and 100 when its area percentage is 100. In that case formula (1) on p. 46 ($p = P \times a$) applies, and it can be shown rather simply that the relative pollen productivity of a tree species as here defined equals its relative pollen representation ($P_{rel} = R_{rel}$).

As mentioned above, formula (3) on p. 47 is more likely to be true in the case of the moss humus pollen spectra studied in the present work. The variations in the pollen percentages, area percentages, and the R- and R_{rel}-values of two species, A and B, according to this formula are shown in the figure below. The figures were calculated from the regression equations for *Betula* (species A) and for *Fagus* (species B) determined in section 386 in Draved forest (p. 54). P_{rel} for species A is 4.4.

The pollen percentage/area percentage curves in the first diagram below resemble those show on p. 48, however, the pollen frequency of species A now is 17% at 0 and 99% at 100% areal frequency, and the pollen frequency of species B is 1% at 0%, and 83% at 100% areal frequency. The second diagram below shows that the R-values of species A (R_A) vary from infinite to about



Left: pollen percentages (p %) and areal percentages (a %) of 2 species, A and B, the pollen deposition of which is in accordance with equation (3) on p. 47. The regression equations calculated for *Betula* and *Fagus* in section 386 in Draved forest (chapter X) were used.

The relative pollen productivity (P_{rel}) of species A (in relation to species B) is 4.4

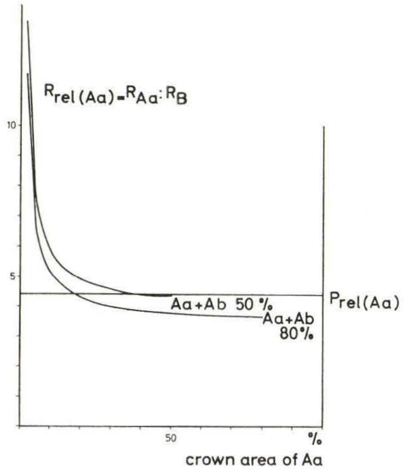
Right: R-values for the species A and B (R_A and R_B), and R_{rel}-values for species A in relation to species B. The R_{rel}-values of species A equal its P_{rel} values at areal frequencies 20–70 %

1, whereas the R-values of species B (R_B) are nearly constant in a large range of areal variation. The R_{rel}-values of species A vary greatly, from infinite at 0% to 1.2 at 98% areal value of species A. The R_{rel}-values of species A in this case approach the P_{rel}-value when its areal frequencies range from about 20 to 70%.

The variations of the R- and the R_{rel}-values become quite complicated when several species contribute to the pollen deposition. The figure below shows the variations of R_{rel} of a species, Aa, in cases where 3 species, Aa, Ab and B are present. Species Aa and Ab have the same P- and p_0-values as species A, and species B the same values as species B in the first example. The curves for R_{rel} of species Aa are calculated for 2 cases where the crown areas of species Aa + Ab constitute respectively 50% and 80% of the total tree crown area in the sample plots. The R_{rel} of species Aa approaches its P_{rel}-value at 15–50% areal frequency, in the case when the high pollen producers, species Aa and Ab, together constitute 50% of the total tree crown area in the sample plots, and at 10–30% areal frequency when Aa and Ab together constitute 80% of the total crown area.

As the R-values of species with a low pollen productivity are nearly constant in a large range of areal variation, their R_{rel}-values also are rather constant.

Whereas the P_{rel}-values are independent of frequency, the R_{rel}-values thus only are characteristic under certain conditions.



R_{rel}-values for a species, Aa (in relation to species B), which occurs together with the species Ab and B in 2 cases where species Aa and Ab together constitute 50%, respectively 80%, of the crown area. Aa and Ab both have the same regression equation for pollen deposition as species A on p. 49, and species B the same one as species B on p. 49. The R_{rel}-values of species Aa equal its P_{rel}-values at areal frequencies of 15–50%, respectively 10–30%

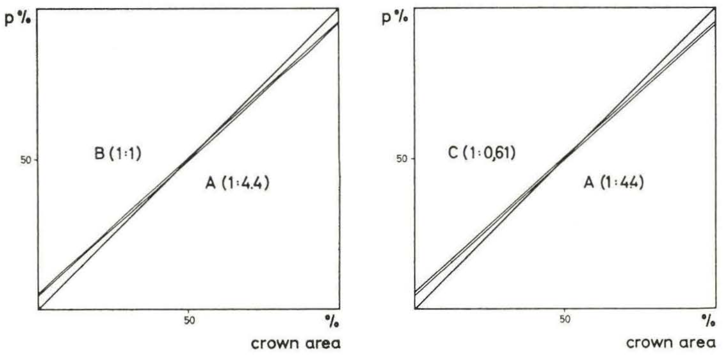
CORRECTION OF THE TREE POLLEN SPECTRA

The aim of the present investigation is to find methods by which the pollen spectra of the moss humus samples can be corrected in such a manner that the pollen percentages equal the areal percentages of the trees. The correction of a pollen spectrum thus requires a correction of the pollen counts for the various species prior to the calculation of the percentage spectrum.

In the simple case mentioned above where the pollen deposition of a species increases directly with its area ($p = P \times a$) the area of the species can be found from p if P is known ($a = \frac{p}{P}$), and the areal percentages can be calculated. A correction of the pollen counts with the P_{rel}-values will give the same result. The areal percentages can also be calculated from the pollen counts after a correction with the R-values. The R-values can, however, only be used in specific species combinations. The R_{rel}-values, on the other hand, equal the P_{rel}-values in these cases and can be used as correction factors in all cases.

In the more complicated case where pollen derived from outside the area considered is present too ($p = P \times a + p_0$) this value (p_0) should be subtracted from the pollen count prior to a correction. Such a procedure is not possible in pollen spectra from fossil humus samples, where p_0 is unknown.

In such cases p_0 may be disregarded and the pollen spectra may be corrected with the P_{rel}-values. This was done for the case shown on p. 49. The pollen values of species A were divided by 4.4 and those of species B were not changed.



Left: Corrected pollen percentages (p %) and areal percentages of the species A and B from the example on p. 49. The pollen frequencies of species A were divided by 4.4 before the percentage calculation

Right: Corrected pollen percentages (p %) and areal percentages of the species A and C. The regression equation for the pollen deposition of species A is the same as on p. 49. For species C the regression equation calculated for *Tilia* in section 386 in Draved forest chapter X) was used. P_{rel} for species C (in relation to species B) is 0.61. The pollen frequencies of species A were divided by 4.4 and those of species B by 0.61 before the percentage calculation

The area percentages and the corresponding corrected pollen percentages are shown in the first diagram on p. 51. The pollen percentages of the two species deviate slightly from their area percentages. They are too high (+ 5%) at the low areal frequencies and too low (÷ 5%) at the high areal frequencies of the two species.

A similar experiment was done for a case where species A occurs together with a species with a low P_{rel}, species C ($P_{rel} = 0.61$), and the result is shown in the second diagram on p. 51. The corrected pollen percentages deviate slightly from the areal percentages in this case too. The corrected pollen frequencies of species C deviate slightly more than those of species A at the high areal frequencies.

The examples in the figures on p. 51 show that the P_{rel}-values may be used for a correction of the humus pollen spectra without causing great errors. The R_{rel}-values equal the P_{rel}-values if they are calculated for areal frequencies of about 10–70% (p. 51), and can in these cases substitute the P_{rel}-values as correction factors.

The P_{rel}- and the R_{rel}-values thus are independent estimates of the same thing, the over- or underrepresentation in the various species. Both P_{rel}-values and R_{rel}-values were calculated from the data from Draved and Longelse forest and used as a common basis for correction factors. *Fagus silvatica* was chosen as a reference species for the P_{rel}- and the R_{rel}-values for the following reasons (1) its P-value is intermediate and hence likely to vary least, (2) the R-values of such a low pollen producer vary least within a large range of areal frequency, (3) the genus is monotypic in northern Europa and its pollen grains accordingly easily identifiable, (4) the species is the commonest tree in a large region, (5) the species flowers richly both on basic and moderately acid soils.

X. DETERMINATION OF THE POLLEN PRODUCTVITY FACTORS (P-VALUES) AND THE RELATIVE POLLEN PRODUCTIVITY (P_{rel}-VALUES) OF THE TREES IN DRAVED AND LONGELSE FOREST

P-VALUES AND TREE CROWN AREAS IN DRAVED FOREST

30 m sample plots

The pollen frequencies of the various tree species in the moss humus samples were determined as the relative pollen deposition (p_r) in relation to the exotic pollen totals (p. 42) and compared with the crown areas of the trees in the corresponding 30 m sample plots.

The variation in the relative pollen deposition values and the crown areas in 2 transects from section 386 and 3 transects from section 370 is shown on plates I-II. The transects from section 386 are orientated west-east (A) and north-south (B), and the transects from section 370 west-east (see the maps pp. 23 and 24).

Samples with more than 50% corroded pollen grains are marked with a +. As the exotic pollen is less corroded than the tree pollen (p. 29), one might expect the tree pollen frequencies to be too low in the samples with many corroded grains. Such samples, however, do not deviate from the other samples in the transects in a conspicuous way, and differential pollen destruction apparently does not affect the results greatly. The samples were, however, omitted from the calculations (cp. p. 30).

As the exotic pollen deposition can be assumed to be rather constant (p. 45), the tree pollen curves should give a true picture of the variations in the tree pollen deposition. The pollen curves follow the area curves in the transects quite faithfully, with some exceptions. The pollen curves of *Quercus* are somewhat irregular, the pollen curves of *Betula*, *Alnus* and *Tilia* have a few irregular peaks, and the pollen frequencies of *Fagus* are particularly low in the eastern part of transect C from section 370. The pollen frequencies of *Quercus*, *Betula* and *Alnus* are comparatively high, and those of *Fagus*, *Tilia* and *Fraxinus* particularly low in relation to the crown area curves.

The correlation of the relative pollen deposition values with the crown areas in the 30 m sample plots is shown in the diagrams on plates III–IV. The points are scattered a good deal. Nevertheless, the pollen frequencies tend to increase with the crown areas. A few samples (marked with a +) obviously differ from the others by having abruptly high pollen frequencies. Such cases particularly occur in *Betula*, *Alnus* and *Tilia*, and it is assumed that the pollen 'overrepresentation' is due to catkins or flowers with unopened anthers incorporated in the moss humus. The samples in question were omitted from the calculations.

Correlation coefficients (r) and the numbers of samples (N) are indicated on the diagrams on plates III–IV. No correlation coefficient was calculated for *Tilia* in section 370 due to its low areal frequencies. The correlation coefficients are highly significant except the one for *Fagus* in section 370 which only is half as large as the other ones. It appears that the *Fagus* pollen frequencies here fail to increase with the crown area. Samples deriving from the southeastern part of section 370 are indicated with circles on the *Fagus* diagram. They comprise all the high areal values, but their pollen frequencies are conspicuously low, and the correlation coefficient becomes considerably higher if they are omitted (0.50 instead of 0.31).

Regression equations were calculated according to equation (5) on p. 47 ($p_r = P \times a + p_{r(0)}$). The regression of *Fagus* in section 370 was calculated from the samples from outside the southeastern part of the section. It is somewhat uncertain as only low areal values are represented.

The standard error of p_r was calculated as $S_{(p_r)} = \sigma_{(p_r)} \sqrt{1 - r^2}$, where $\sigma_{(p_r)}$ is the standard deviation of the average p_r.

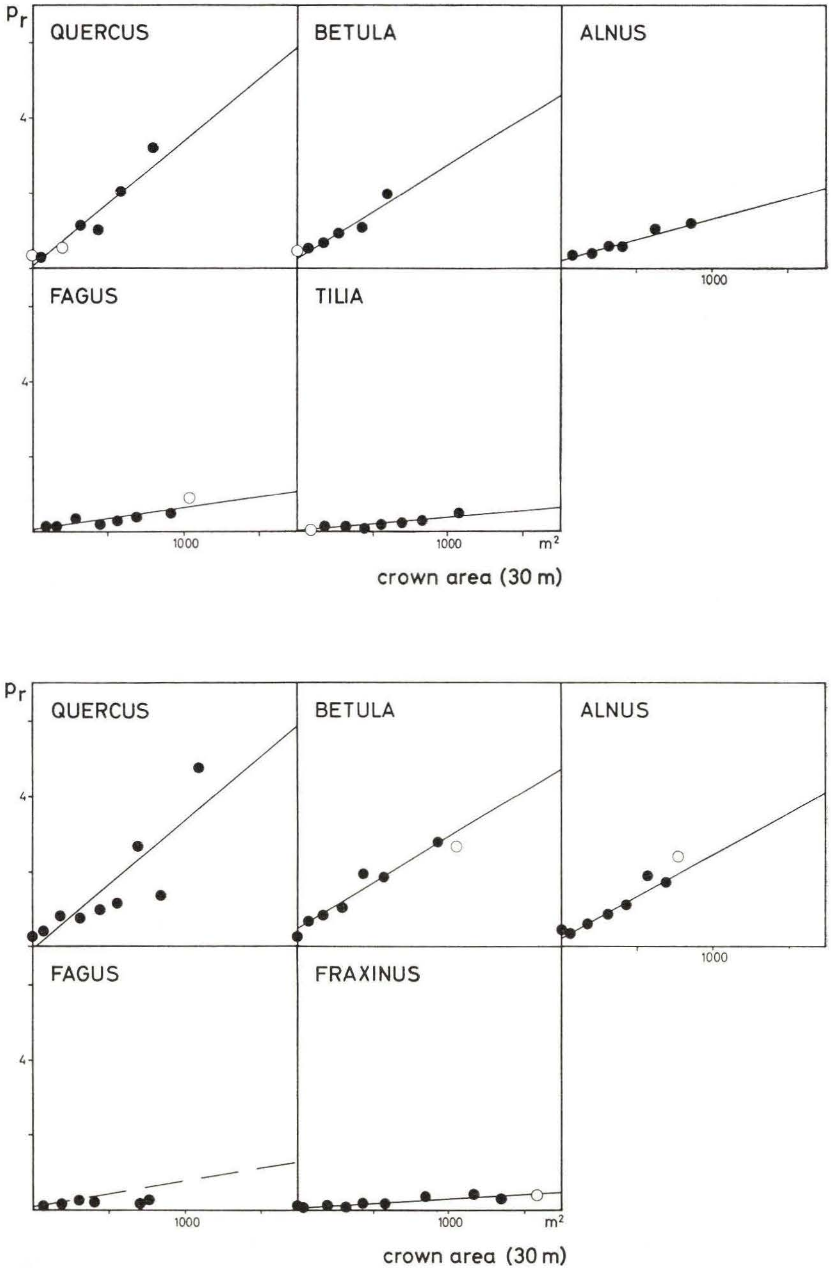
The regression lines with two standard errors of p_r are inserted on the correlation diagrams on plates III–IV. It may be seen that the points are fairly evenly distributed around the regression lines and that only a few points fall outside the 2 standard error limits.

The trends of the regression lines indicate that only a small proportion of the tree pollen is spread beyond 30 m, and that there is a direct relationship between the pollen deposition and the crown areas of the trees within 30 m from the sample points. The scattering of the p_r-values may be due to statistical sampling error and to irregularities in the pollen deposition. The sampling error presumably is quite large, but scattering due to irregular tree pollen deposition and irregularities in the deposition of exotic pollen probably is large too.

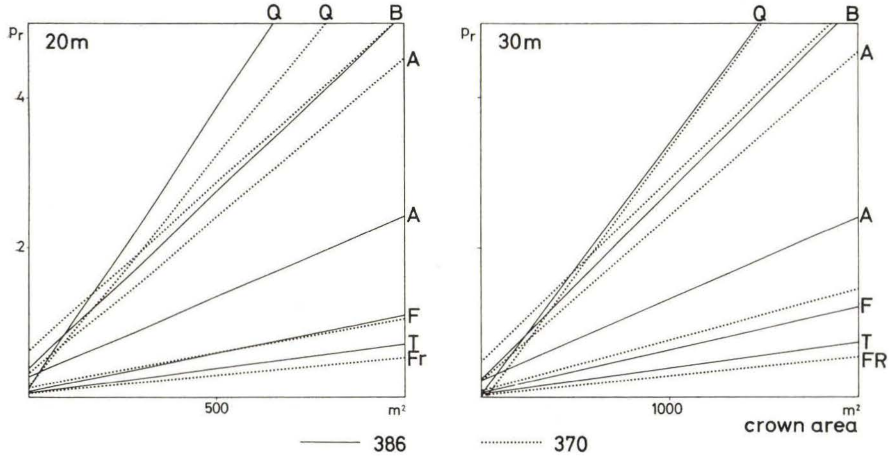
The high correlation coefficients suggest that the scatter of the p_r-values is random. The regression equations only are valid, however, if the regressions of the pollen frequencies on the crown area values are linear. Linearity can be tested by computing averages of the p_r-values in arrays of the crown area values. They should fall at or very near the regression lines. Such averages are shown in the diagrams on p. 55. The variation in the p_r-values now is greatly reduced. The midpoints fall very near the regression lines in most cases, and suggest a linear increase in the pollen production with increasing crown area. The midpoints for *Quercus*, however, suggest some kind of overrepresentation in the plots with high areal values. As a result the regression line for *Quercus* is somewhat too steep. The regression line indicated for *Fagus* in section 370 is higher than the pollen frequencies in the crown area arrays with high values from the southeastern part of the section.

The steepness of the regression lines reflects the pollen productivity of the trees. The lines for *Quercus*, *Betula* and *Alnus* are steepest, and *Fagus*, *Tilia* and *Fraxinus* have the flattest ones.

The regression lines from the 2 sections are shown on p. 56 at right, and table 34 (p. 93) shows the values of N, r, P, $p_{r(0)}$ and $S_{(p_r)}$. The results from the 2 areas are very much alike. The regression lines mainly are distributed in 2



Draved forest, section 386 (above) and section 370 (below). Averages of the relative pollen deposition values in tree crown area arrays and the calculated regression lines. p_r = relative pollen deposition. Filled circles: more than 2 samples. Open circles: 1 or 2 samples groups, one with the high pollen producers such as *Quercus*, *Betula* and *Alnus*, and the other with the low pollen producers such as *Fagus*, *Tilia* and *Fraxinus*. The regression lines for *Quercus* presumably are too steep, as mentioned above, and the P-values must be assumed to be somewhat too high. The regression line for *Alnus* from section 386 is intermediate and the P-value from section 386 only one half of the figure found in section 370 (0,109 and 0,220 × 10^{-2}).



Draved forest. Regression lines for the relative pollen deposition in relation to the tree crown areas in the 20 m and 30 m sample plots.
p_r = relative pollen deposition. Q = *Quercus*, B = *Betula*, A = *Alnus*, F = *Fagus*, T = *Tilia*, Fr = *Fraxinus*

It has not been attempted to evaluate the statistical significance of the P-values. Clearly, their determination is influenced by such sources of error that a statistical evaluation is rather meaningless. Their general similarity in the 2 sections supports the assumption that the deposition of the exotic pollen on which they are based is the same in the 2 areas. It may accordingly be assumed that the difference in the P-values of *Alnus* is due to a variation in its pollen productivity. The P-values found for *Fagus* are similar in the 2 sections and suggest that *Fagus* has a uniform pollen productivity except for the south-eastern part of section 370. Its low pollen frequencies there must be due to a reduced pollen productivity.

The regression lines intersect the vertical 0-axis at low positive p_r-values. These values indicate the relative pollen deposition at zero crown area ($p_{r(0)}$) and represent the pollen dispersed from trees outside the sample plots. The $p_{r(0)}$-values calculated for *Quercus* are too low because the regression lines are too steep. The other values are more accurate. They are high in *Betula* and *Alnus*, and low in *Fagus*, *Tilia* and *Fraxinus*.

20 m sample plots

Regression lines calculated for the relative pollen deposition values in relation to crown areas in the sample plots of 20 m radius also are shown on p. 56.

Figures for r, P, $p_{r(0)}$, and $S_{(p_r)}$ are shown in table 35. They are similar to those in table 34 except for the P-values, which are larger due to the smaller sample plot size.

P_{rel}-VALUES AND TREE CROWN AREAS IN DRAVED FOREST

Table 21 shows the P_{rel}-values for the 20 m and the 30 m sample plots. The P-values calculated for *Fagus* in section 386 were used for reference factors, because the P-values for *Fagus* in section 370 are somewhat uncertain (p. 54). P_{rel}-values based on the P-value for *Fagus* in section 370 are shown in brackets.

The P_{rel}-values should be independent of the sample plot size, however, they differ in sample plots of different sizes if the dispersal distances vary (p. 47). The P_{rel}-value for a species with a small dispersal distance should increase in a smaller sample plot.

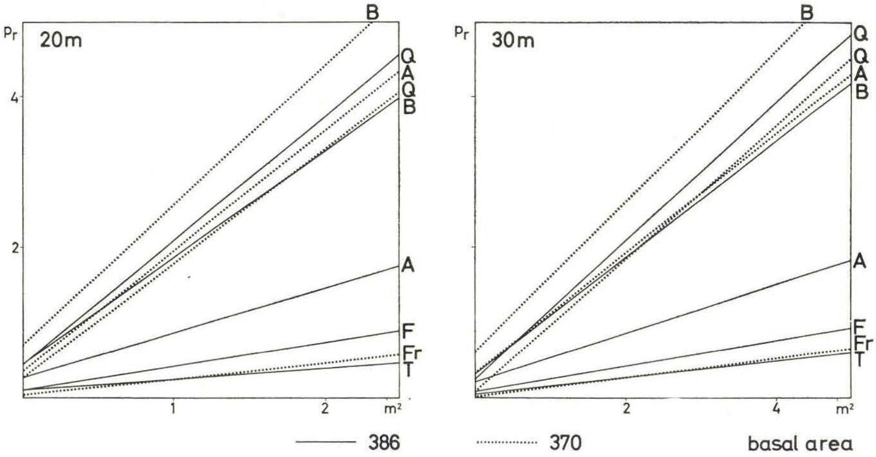
The P_{rel}-values shown in table 21 are almost independent of the sample plot size. Only the values for *Quercus* may be slightly larger in the 20 m sample plots than in the 30 m sample plots.

Table 21. Draved forest, sections 386 and 370. Relative pollen productivity (P_{rel}) based on tree crown areas in the 20 m and 30 m sample plots

	20 m		30 m	
	386	370	386	370
Quercus	7.5	6.2 (6.9)	5.8	6.0 (5.0)
Betula	4.7	4.5 (5.0)	4.4	4.2 (3.6)
Alnus	2.1	4.2 (4.7)	1.9	3.9 (3.2)
Fagus	1.0	(1.0)	1.0	(1.0)
Tilia	0.6		0.6	
Fraxinus		0.5 (0.5)		0.4 (0.4)

The P_{rel}-values for *Quercus* are likely to be too high, and the conspicuous difference in the P-values and hence the P_{rel}-values of *Alnus* in the two sections suggests a low flowering intensity in this tree in section 386. During the flowering it may be seen that the *Alnus* trees in section 370 are richly covered with catkins in contrast to the trees in section 386, where the flowers are much scarcer. A possible explanation is increased root competition from *Tilia* due to a desiccation of the soil in section 386 by the establishment of drainage ditches (Johs. Iversen, personal communication).

It is more difficult to explain the low *Fagus* pollen frequencies in the southeastern part of section 370. The trees there are rather young, and a low tree age may be a reason for the low flowering intensity.



Draved forest, section 386 and 370. Regression lines for the relative pollen deposition in relation to the tree basal areas in the 20 m and the 30 m sample plots. p_r = relative pollen deposition.

P-VALUES AND TREE BASAL AREAS IN DRAVED FOREST

It was mentioned in chapter IV that it is easier to estimate tree composition by means of tree basal areas than by means of tree crown areas, which must be measured from maps based on air photographs. Hence, it is of interest to compare the P-values calculated for the tree basal areas with those calculated for the crown areas.

Regression equations were calculated for the 20 m and the 30 m sample plots in Draved. Figures for N, r, P, $p_{r(0)}$ and $S_{(p_r)}$ in the 30 m sample plots are shown in table 36. The figures for *Fagus* in section 370 (in brackets) were calculated for samples outside the south-eastern part (cp. p. 54). The figures for the 20 m sample plots do not differ greatly from the figures for the 30 m sample plots, except for the P-values. The regression lines are shown above.

Table 22. Draved forest, sections 386 and 370. Relative pollen productivity (P_{rel}) based on the tree basal areas in the 20 m and 30 m sample plots

	20 m		30 m	
	386	370	386	370
Quercus	5.2	4.8 (6.0)	5.5	5.3 (4.4)
Betula	4.5	5.9 (7.3)	4.6	6.1 (5.0)
Alnus	1.9	5.0 (6.3)	2.0	4.8 (4.0)
Fagus	1.0	– (1.0)	1.0	– (1.0)
Tilia	0.5		0.7	
Fraxinus		0.7 (0.8)		0.8 (0.6)

P_{rel}-VALUES AND TREE BASAL AREAS IN DRAVED FOREST

P_{rel}-values based on the tree basal areas in the 20 m and the 30 m sample plots are shown in table 22. They are based on the P-value for *Fagus* from section 386. The figures in brackets show P_{rel}-values in section 370 based on the P-value for *Fagus* from this section.

The P_{rel}-values are rather similar in the sample plots of different size. They also are rather similar in the 2 sections with the exception of *Betula* and *Alnus*, which have higher P_{rel}-values in section 370 than in section 386.

The P_{rel}-values based on the basal areas in the 30 m sample plots are compared with the P_{rel}-values for the crown areas in table 23. These figures are rather similar in section 386, but differ in section 370, particularly with respect to *Betula*.

Table 23. Draved forest, sections 386 and 370.
P_{rel}-values for the 30 m sample plots

	386			370		
	Basal areas	Basal areas, corrected	Crown areas	Basal areas	Basal areas, corrected	Crown areas
Quercus..	5.5	5.6	5.8	5.3	6.1	6.0
Betula ...	4.6	4.6	4.4	6.1	3.9	4.2
Alnus	2.0	2.3	1.9	4.8	3.7	3.9
Fagus....	1.0	1.0	1.0	–	–	–
Tilia.....	0.7	0.7	0.6			
Fraxinus .				0.8	0.6	0.4

The P-values based on the basal areas can be re-calculated by means of the crown area: basal area ratios (table 7, p. 21). The corresponding P_{rel}-values also are shown in table 23. The values from section 386 have not changed greatly, but the corrected P_{rel}-values from section 370 now resemble the P_{rel}-values based on the crown areas better.

P-VALUES AND TREE BASAL AREAS IN LONGELSE FOREST

Crown areas could not be measured in Longelse forest (p. 18). Relative pollen deposition-values (p_r) and tree basal area values in the 30 m sample plots are shown for the west-east transect on plate V (cp. the map on p. 25), and the correlation of the p_r-values with the basal areas is shown on plate VI.

The pollen frequency curves and the basal area curves in the transect follow each other pretty well. A few irregularities may be noticed. *Ulmus* e.g. has an irregular peak of pollen deposition in one sample, and the *Fraxinus* pollen deposition is conspicuously low in the western part of the transect.

There also is a good deal of scattering in the p_r-values shown in the diagrams on plate VI, but increases in the pollen frequencies with increases in the crown areas are suggested. A few samples marked with crosses differ due to 'over-representation' and were omitted from the calculations. Samples with more than 50% corroded grains are indicated by circles on the scatter diagrams. The pollen frequencies might be expected to be too low in these samples (cp. p. 53). This does not appear to be the case, however, as the frequencies for the corroded samples are fairly evenly distributed within the range of scattering, and their inclusion can hardly affect the results.

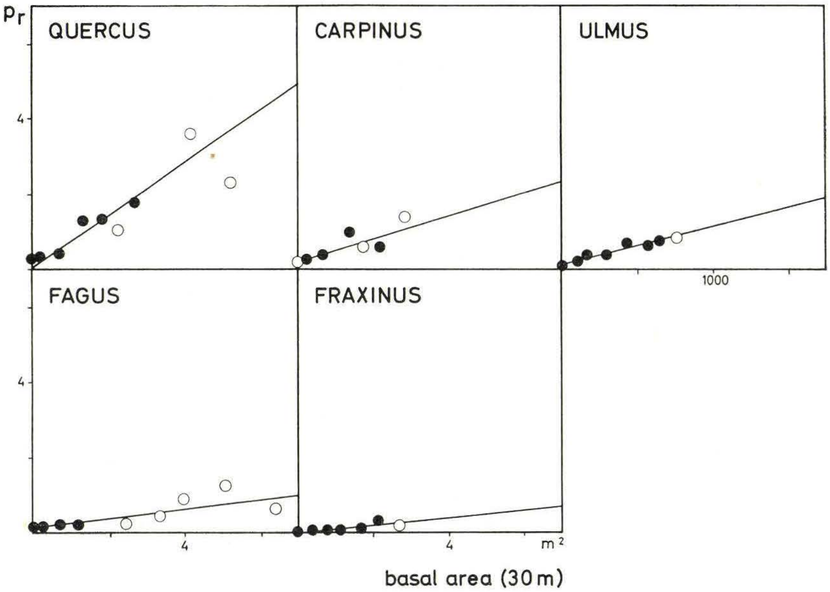
Correlation coefficients (r) and sample numbers (N) are indicated on the diagrams. The correlation coefficients are highly significant. The rather low figure for *Fraxinus* suggests a somewhat heterogenous pollen productivity.

Regression equations were calculated and regression lines with 2 standard error limits of p_r are indicated on the diagrams on plate VI. The pollen frequencies are fairly evenly distributed within these.

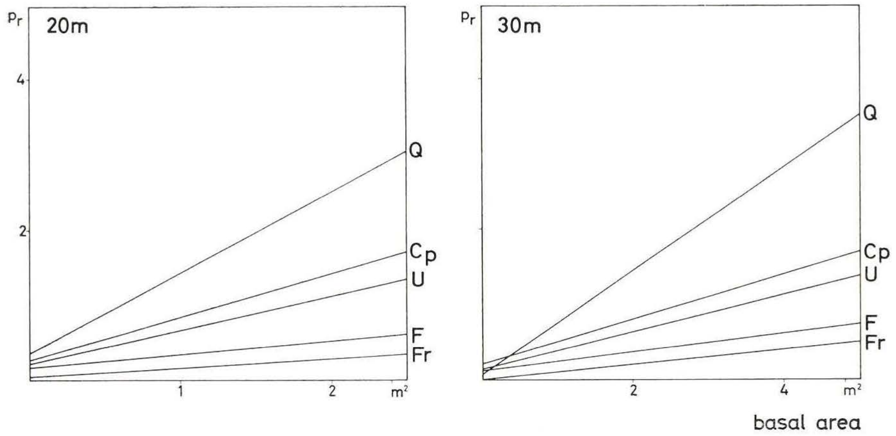
Average pollen deposition-values in crown area arrays are shown below together with the regression lines. They suggest linear regression.

The regression lines are shown on p. 61 together with regression lines for sample plots of 20 m radius and table 37 summarizes the values of N, r, P, $p_{r(0)}$ and $S_{(p_r)}$ in the 20 m and the 30 m sample plots.

The regression lines for the 2 sample plot sizes are similar. *Quercus* has the



Longelse forest. Averages of the relative pollen deposition values in tree basal area arrays, and the calculated regression lines.
p_r = relative pollen deposition. Filled circles: more than 2 samples.
Open circles: 1 or 2 samples



Longelse forest. Regression lines for the relative pollen deposition in relation to the tree basal areas in the 20 m and the 30 m sample plots.
p_r relative pollen deposition. Q = *Quercus*, Cp = *Carpinus*, U = *Ulmus*, F = *Fagus*, Fr = *Fraxinus*.

steepest line and *Fagus* and *Fraxinus* the flattest ones. The $p_{r(0)}$-values are fairly similar in the various sample plot sizes.

P_{rel}-VALUES AND TREE BASAL AREAS IN LONGELSE FOREST

The relative pollen productivity factors (P_{rel}) in Longelse forest are shown in table 24 together with the figures from Draved. The figures calculated for the 2 sample plot sizes in Longelse are rather similar.

THE RELATIVE POLLEN PROCUCTIVITY (P_{rel}-VALUES) OF THE TREES IN DRAVED AND LONGELSE FOREST COMPARED

The relative pollen productivity factors of the various trees in Draved and Longelse forest can be compared in table 24. They respectively refer to tree crown areas and tree basal areas, but the figures presumably are comparable, as there is reason to believe that there is a uniform relation between the crown areas and the basal areas in Longelse (p. 20). The similarity of the P_{rel}-values suggests that they may be of some validity. They indicate a high pollen productivity in *Quercus*, *Betula* and *Alnus*, intermediate in *Carpinus* and *Ulmus*, and a low one in *Fagus*, *Tilia* and *Fraxinus*.

The figures for *Quercus* presumably are somewhat too large (p. 56), and the actual pollen productivity of the trees with small pollen grains such as *Quercus*, *Betula* and *Alnus* may be somewhat larger than indicated by the P_{rel}-values (p. 47). The difference noticed in the pollen productivity of *Alnus* in the areas

Table 24. Draved forest and Longelse forest. Relative pollen productivity (P_{rel}) in the 20 m and 30 m sample plots based on crown areas (Draved) and basal areas (Longelse)

	20 m			30 m		
	Draved		Longelse	Draved		Longelse
	386	370		386	370	
Quercus	7.5	6.2	6.0	5.8	6.0	5.5
Betula	4.7	4.5	–	4.4	4.2	–
Alnus	2.1	4.2	–	1.9	3.9	–
Carpinus	–	–	3.2	–	–	2.4
Ulmus	–	–	2.5	–	–	2.0
Fagus	1.0	(1.0)	1.0	1.0	(1.0)	1.0
Tilia	0.6	–	–	0.6	–	–
Fraxinus	–	0.5	0.7	–	0.4	0.8

studied in Draved suggests that the pollen productivity of a species may vary according to the environment. The *Alnus* trees in section 386 in Draved grow under disadvantageous conditions, which are somewhat unnatural and have caused a decreased pollen productivity (p. 57). Hence we may consider the pollen productivity found for *Alnus* in section 370 to be typical for the species when it grows under natural conditions.

XI. THE TREE POLLEN SPECTRA AND DETERMINATION OF THE RELATIVE POLLEN REPRESENTATION (R_{rel}-VALUES) OF THE TREES IN DRAVED AND LONGELSE FOREST. CORRECTION FACTORS

POLLEN AND AREA PERCENTAGES

The tree pollen frequencies in the moss humus samples were calculated as percentages of the tree pollen sums, as the tree crowns constitute a rather closed canopy in the present cases. The areal frequencies of the tree species were calculated as percentages of the total area (crown area or basal area) of the trees within the 30 m sample plots.

The horizontal variation of the tree pollen percentages and the tree area percentages is shown on plate VII–IX. The transects from Draved show crown area percentages and the transect from Longelse shows basal area percentages.

The pollen curves in the transects follow the area curves in a general way. The pollen curves for *Quercus*, *Betula*, *Alnus*, *Carpinus* and *Ulmus* are as a rule too high and those for *Fagus*, *Tilia* and *Fraxinus* are too low. There are, however, many deviations and irregularities. Such variations may be due to irregularities in the pollen deposition of the species and to variations in the total pollen deposition due to differences in species dominance.

Diagrams showing the scattering of the pollen percentages in relation to the area percentages are shown on plates X–XI. *Quercus*, *Betula*, *Alnus*, *Carpinus* and *Ulmus* have in most cases high, and *Fagus*, *Tilia* and *Fraxinus* in most cases low pollen percentages compared with the area values. The points are distributed in a manner, which resembles the theoretical curves of species A and species B on p. 49.

R- AND R_{rel}-VALUES

The pollen representation (R-value) of a species is calculated as the ratio of its pollen percentage to its area percentage (p. 48) and its relative pollen representation (R_{rel}-value) as the ratio of its R-value to the R-value of *Fagus* (p. 52).

The R- and the R_{rel}-values in the individual moss humus samples vary greatly, as one might expect. Average values are more useful and can be found from composite areal and pollen spectra for all samples within an area studied. This, of course is a very coarse estimate which only is justified as a linear increase in the pollen deposition with area can be shown (chapter X). Figures were calculated for the 2 sections in Draved forest and for Longelse forest for the 20 m and the 30 m sample plots. The areal and the pollen percentages are shown in table 38 with the R-values, and the R_{rel}-values are shown in table

Table 25. Draved forest and Longelse forest. Relative pollen productivity (P_{rel}) and pollen representation (R_{rel}) in the 20 m and the 30 m sample plots and suggested correction factors

	P_{rel}						R_{rel}						Correction factors
	20 m			30 m			20 m			30 m			
	Draved		Longelse	Draved		Longelse	Draved		Longelse	Draved		Longelse	
	386	370		386	370		386	370		386	370		
Quercus	(7.5)	(6.2)	(6.0)	(5.8)	(6.0)	(5.5)	5.6	3.6	3.4	4.6	3.8	3.3	1:4
Betula	4.7	4.5	–	4.4	4.2	–	(6.0)	4.6	–	(4.8)	4.6	–	1:4
Alnus	2.1	4.2	–	1.9	3.9	–	2.7	3.5	(5.4)	2.3	3.6	(3.6)	1:4 (1:2)
Carpinus	–	–	3.2	–	–	2.4	–	–	(3.0)	–	–	(2.5)	1:3
Ulmus	–	–	2.5	–	–	2.0	–	–	2.0	–	–	1.7	1:2
Fagus	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1×1
Tilia	0.6	–	–	0.6	–	–	0.6	(0.7)	–	0.6	(0.8)	–	1×2
Fraxinus	–	0.5	0.7	–	0.4	0.8	–	0.4	0.5	–	0.4	0.5	1×2

25. The statistical significance has not been evaluated, but the error presumably is large.

The R-values differ somewhat in the 3 areas investigated, as one might expect because of the different species combinations. The R_{rel}-values, on the other hand, do not differ greatly. One exception is *Alnus*, as the R_{rel}-value of this tree is distinctly lower in section 386 than in section 370 in Draved, which is in accordance with the observations made earlier of a low flowering intensity of this tree in section 386 (p.57).

THE P_{rel}- AND R_{rel}-VALUES COMPARED. CORRECTION FACTORS

The high pollen producers (*Quercus*, *Betula*, *Alnus*, *Carpinus*) together constitute about 50% of the total tree area in the 3 areas studied (see table 38). Hence their R_{rel}-values should be similar to the P_{rel}-values at least when their areal frequencies are about 15–50% (p. 50). The R_{rel}-values of the low pollen producers should resemble the P_{rel}-values in all cases.

The R_{rel}-values for trees with less than 15% areal frequency are shown in brackets in table 25.

Most of the R_{rel}-values resemble the P_{rel}-values. One exception is *Quercus*. As mentioned on p. 57, the P_{rel}-values for this tree presumably are too high. The R_{rel}-values are lower and presumably more true. The difference is due to the fact that the regression lines, from which the P_{rel}-values were calculated, take more notice of the very high pollen frequencies at the high areal values than the average percentages, from which the R_{rel}-values were computed. The R_{rel}-values for *Alnus* from the 2 sections in Draved forest differ in the same way as the P_{rel}-values.

Correction factors for the pollen analyses suggested by means of the P_{rel}- and the R_{rel}-values are indicated in table 25 too. The correction factor for *Quercus* mainly is based on the R_{rel}-values. The pollen productivity of *Alnus* in section 370 presumably is characteristic (p. 57) and suggests a correction factor of 1:4. A lower correction factor is suggested for this tree in section 386 because of its low pollen productivity there.

XII. CORRECTED TREE POLLEN SPECTRA FROM DRAVED AND LONGELSE FOREST

The correction factors can be tested preliminarily by a comparison of corrected pollen percentages in the composite spectra with the area percentages. The result is shown in table 26. It is quite satisfactory as the pollen percentages deviate less than 5% from the area percentages.

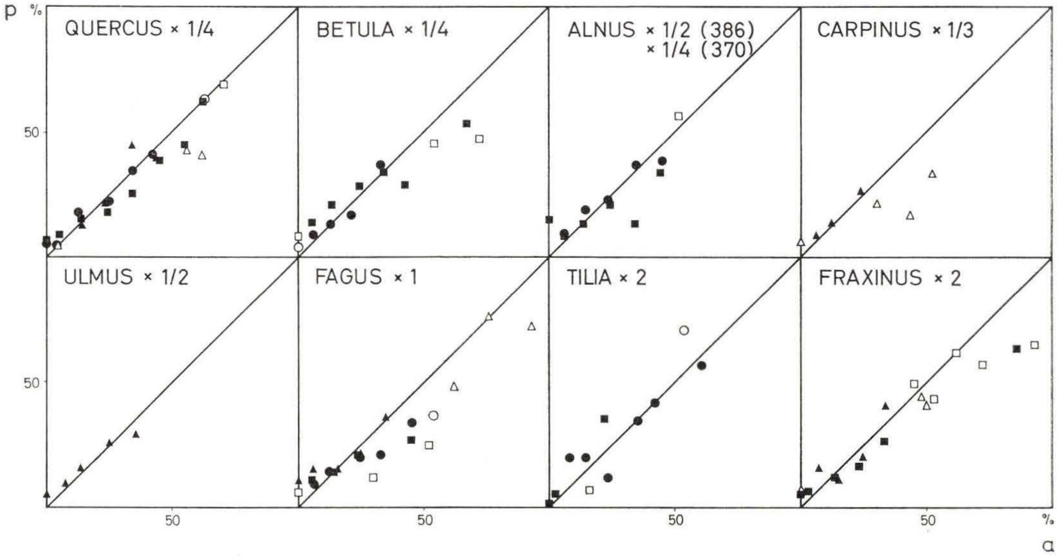
Table 26. Draved forest and Longelse forest. Area percentages in the 30 m sample plots and corrected pollen percentages

	Correction factors	Draved				Longelse	
		386		370			
		crown area %	pollen %	crown area %	pollen %	basal area %	pollen %
Quercus . .	1:4	21.0	21.4	23.9	22.7	26.8	23.4
Betula . . .	1:4	12.5	13.3	20.4	23.4	–	–
Alnus	1:4 (1:2)	18.9	19.4	17.1	15.4	1.1	1.1
Carpinus .	1:3	–	–	–		14.0	18.6
Ulmus . . .	1:2	–	–	–		19.3	17.2
Fagus	1 × 1	19.6	17.4	15.3	15.3	20.4	21.9
Tilia	1 × 2	28.0	28.5	2.9	4.7	–	–
Fraxinus .	1 × 2	–		20.4	18.2	18.3	17.8

The corrected pollen percentages are compared with the area percentages in the transects on plates XII–XIV. It may be seen that the pollen percentages now are randomly scattered around the area values. A few peaks in the pollen percentages presumably are due to overrepresentation by admixture of pollen from unopened catkins. The *Fagus* pollen frequencies are too low in the eastern part of transect C from section 370 in Draved, and the *Fraxinus* pollen frequencies are too low in the western part of the Longelse transect presumably due to a particularly low pollen productivity there.

The scatter of the corrected pollen percentages in the individual samples are shown on plates XV–XVI. Confidence limits for deviations of ±10% from the area percentages are indicated on the diagrams. The scatter of the individual points is not reduced by the correction, but the pollen percentage values now are rather regularly distributed around the area percentage values. One conspicuous exception is *Fagus* in section 370 in Draved, where the pollen percentages in the southeastern area are too low.

The average values of the corrected pollen percentages in 10% arrays of the area percentages are shown in the figure below. The scatter of the points now is reduced, and the variation in the pollen percentages resembles the theoretical lines shown on p. 51, where the corrected pollen percentages are somewhat too high at very low and somewhat too low at very high area percentages.



Draved forest and Longelse forest. Averages of the corrected pollen percentages in area-percentage arrays.

p = corrected pollen frequency in percentage of the corrected tree pollen sum. a = areal frequency in percentage of the total crown area (Draved) or basal area (Longelse) per sample plot.

● = Draved forest, 386. ■ = Draved forest, 370. ▲ = Longelse forest. Filled symbols: more than 2 samples. Open symbols: 1 or 2 samples.

XIII. THE REPRESENTATION OF THE RARE TREES, THE SHRUBS AND THE HERBACEOUS FOREST PLANTS IN THE POLLEN SPECTRA FROM DRAVED AND LONGELSE FOREST

RARE TREES

Some tree species are so scarce that they were omitted in the calculations discussed above. Their pollen frequencies mentioned below were calculated as percentages of the corrected tree pollen sum, which is assumed to provide a rather constant calculation basis.

Fraxinus excelsior, *Populus tremula* and *Sorbus aucuparia* are represented in the samples from section 386 in Draved with a few scattered pollen grains.

A few young trees of *Ulmus glabra* occur in section 370. Beneath them and at a distance up to 40 m, samples with 4–6% and in a single case 15% *Ulmus* pollen occurred. Outside this area only a few *Ulmus* pollen grains were found. *Sorbus aucuparia* is scattered in the area. A few pollen grains were found in most of the samples, and frequencies of 5–20% occurred in a few samples suggesting a rather irregular scattering of the grains. A few trees of *Populus tremula* are represented in the pollen samples with a few grains only.

The few scattered trees of *Populus* and *Acer* in Longelse forest are represented with a few grains. *Aesculus* pollen was not noticed.

CORYLUS

Corylus avellana is scarce in section 386 in Draved, and in Longelse forest, and its pollen only occurs with low frequencies (1–10% of the corrected tree pollen sum) in these areas.

Corylus pollen is rather frequent in the samples from section 370 in Draved. The tree canopy there is rather open (about 58% crown coverage, p. 20), but the flowering intensity of *Corylus* is low. The *Corylus* pollen presumably is dispersed in a manner similar to that of the tree pollen (p. 39). Crown cover percentages (p. 22) and pollen frequencies in the 3 west-east transects are shown on plate XVI. It may be seen that the *Corylus* pollen frequencies resemble the area frequencies, particularly in the western part of the area, where the soil is best. As the tree pollen total was corrected in such a manner that it equals that of a pure *Fagus* forest, it may be concluded that the pollen productivity of *Corylus* is similar to that of *Fagus*, when it grows under the conditions mentioned above.

Corylus produces more pollen when it grows without a tree canopy (JONASSEN 1950). In such cases the *Corylus* pollen probably should be corrected and included in the pollen total.

OTHER SHRUBS

Shrubs other than *Corylus* are rare in the forest areas studied. *Crataegus oxyacantha, Frangula alnus, Ilex aquifolium* and *Viburnum opulus* are represented in the pollen analyses from Draved with a few scattered grains, *Frangula* in a single case with a frequency of 36%. *Hedera helix* and *Lonicera periclymenum* are represented with a few grains too, *Hedera* in a single case with 10%.

Scattered pollen grains of *Salix* and *Sambucus nigra* presumably are due to long-distance transport.

HERBACEOUS FOREST PLANTS

The moss humus samples are not ideal for a study of the pollen representation of the forest herbs as the samples were collected on tree stumps elevated 5–35 cm from the ground. The tall herbs thus have a better chance of a fair representation than the low herbs, which do not reach that level.

Data on coverage and pollen frequencies of the herbaceous plants in the transects from Draved are shown on plates XVII–XVIII. The data for coverage were derived from the vegetationel analyses from the two 10 m-lines (p. 22) nearest to the transects as averages of the vegetational analyses at each pair of 10 m-points. The pollen frequencies are indicated as percentages of the corrected tree pollen totals.

Anemone nemorosa. Anemone pollen occurs with frequencies up to 14% in the areas where the species is common, but they are notably low in the eastern part of the transects from section 370. Mor prevails there, and a decreased pollen productivity on the poor soil is suggested. The pollen is not dispersed outside of the areas where the plant is frequent.

Crepis paludosa. Liguliflorae pollen is quite abundant (up to 33%) in the western part of section 370 and undoubtedly represents *Credis paludosa* which is common there. The Liguliflorae pollen found outside that area probably derives from plants outside the forest.

Filipendula ulmaria. The pollen of this tall herb is quite abundant with frequencies up to 22% in the areas where the species is common, and it is apparently quite well dispersed in the forest.

Carex. The pollen productivity of the *Carex* species (*C. silvatica* and *C. remota*) is low. The pollen frequency is in one case 12% (section 386).

Ranunculus and *Ficaria.* The pollen of the species *Ranunculus repens* and *Ficaria verna* was not distinguished. The pollen frequencies are low (up to 4%) compared with the areal frequencies.

Sanicula europaea. Sanicula pollen is in some cases rather frequent in the western part of section 370 (up to 5%), where the species is common.

Stellaria holostea. The pollen is rather scarce compared with the areal frequencies of the species. It may locally obtain up to 3% of the pollen total.

Oxalis acetosella. The pollen is rather rare in section 386 (plate XVII). The pollen frequency reaches 10% in one case. Only a few grains occurred in section 370, where the species grows quite commonly too (the transects are not shown).

Rubus spp. mostly *R. fruticosus*). The pollen frequencies in section 386 are shown on plate XVII. The pollen may be frequent locally (up to 17%), but it is not dispersed very far. Only a few pollen grains occurred in section 370 (15% in one sample).

Dryopteris austriaca. Dryopteris spores may locally be abundant (up to 26 %), but they are not dispersed horizontally in great quantity.

Geum rivale is locally abundant in section 370, but only a few pollen grains occurred. Only 2 pollen grains can be referred to *Gagea spathacea*, which is quite common in some places, and spores of *Pteridium aquilinum* are rare too even in places where the species grows abundantly. These plants are not shown on the transects.

The data presented above indicate that herbaceous plants such as *Crepis, Filipendula, Rubus* and *Dryopteris* may be rather well represented in the pollen spectra. The pollen frequencies of *Anemone, Sanicula, Carex, Ranunculus, Stellaria holostea and Oxalis* are rather low compared with the areal frequencies, and *Geum rivale, Gagea* and *Pteridium* scarcely are represented.

Urtica dioica pollen occurred in most of the samples (up to 5 %) in spite of the fact that the species is rare. The pollen probably was derived from outside the forest in most cases. A few pollen grains of *Mercurialis perennis* definitely are due to long-distance transport, as the species does not grow in the forest.

No vegetational analyses from Longelse forest are available. *Anemone* pollen and *Dryopteris* spores were quite frequent (up to 22 %), and a few pollen grains of *Filipendula, Mercurialis* and *Oxalis* were noted. *Circaea* pollen occurred abundantly in one sample.

XIV. COMPARISON OF THE RESULTS FOR THE TREES IN DRAVED AND LONGELSE FOREST WITH SIMILAR INVESTIGATIONS. R_{rel}-VALUES AND CORRECTION FACTORS FOR PINUS, PICEA AND ABIES

Correction factors were determined from the relative pollen productivity and the relative pollen representation values for the tree species *Quercus robur*, *Betula pubescens*, *Alnus glutinosa*, *Carpinus betulus*, *Ulmus glabra*, *Fagus silvatica*, *Tilia cordata and Fraxinus excelsior*. *Carpinus*, *Fagus* and *Fraxinus* are monotypic in Northern Europe but figures for the species *Quercus petraea*, *Betula pendula*, *Alnus incana*, *Ulmus laevis*, *U. campestris* and *Tilia platyphyllos* must be calculated in other forests, if possible. Their pollen productivity may, however, not differ greatly from that found for the other species of the same genera. *Pinus silvestris*, *Picea abies* and *Abies alba*, which also occur in Northern Europe, are not represented in the present material. These trees do not grow naturally in Denmark, and their pollen productivity must be determined outside of Denmark.

It was shown in chapter X that R_{rel}-values which resemble the P_{rel}-values can be found by means of the ratios of the pollen percentages to the areal percentages. Data on areal composition occur in some of the investigations of surface pollen spectra from forests mentioned on p. 13. Figures based on composite spectra calculated from the investigations of BORSE (1939), KRIŽO (1963, 1964, 1966) and MULLENDERS (1962) are shown in table 27 together with the P_{rel}- and R_{rel}-values from Denmark. The figures based on areal frequencies less than 10% are considered unreliable and are shown in brackets.

The investigation of BORSE (l.c.) was mentioned briefly in ANDERSEN (1967). BORSE (l.c.) analyzed surface samples from forests in northern Poland and stated tree frequencies in percentages of the number of trees within 20 m from the samples. The degree of pollen destruction is indicated in a scale with 5 classes.

The forests consist of mixed stands of *Betula* sp., *Alnus glutinosa*, *Tilia cordata*, *Quercus robur*, *Carpinus betulus*, *Fagus silvatica*, *Pinus silvestris*, and *Picea abies*. *Pinus*, *Betula*, *Picea* and *Fagus* are most common in the sample plots, and *Quercus*, *Alnus*, *Carpinus* and *Tilia* are rather rare. Differential pollen destruction seems to influence the pollen spectra, as *Pinus* and *Picea* have particularly high pollen frequencies in the samples with a high degree of destruction, and only the samples with a good pollen preservation (degree of destruction 2 or less) were used. 2 sets of data were calculated, one for composite spectra from all samples and the other for samples where *Fagus* is present. The R_{rel}-values are based on Betula = 4.4 in the first case, as the *Fagus*-frequency is too low there. The R_{rel}-value for *Carpinus* is too low presumably because the samples with a good pollen preservation are limited to the acid soils, which are unfavourable for this tree.

KRIŽO (l.c.) analyzed the tree pollen content of humus and moss samples from forests in central Czechoslovakia and compared them with the tree composition in stands varying from about 3 to 27 ha. Each pollen spectrum is an average of 3–12 surface samples taken

Table 27. P_{rel}- and R_{rel}-values from Denmark (Draved and Longelse) and areal frequencies (a %), R- and R_{rel}-values for pollen spectra from forests calculated from published sources and suggested correction factors. N = number of samples

N	Denmark		Borse (1939)						Križo			Mullenders			Correction factor
			all samples			samples with Fagus			(1963–1966)			(1962)			
			35			6			46			5			
	P_{rel}	R_{rel}	a %	R	R_{rel}	a %	R	R_{rel}	a %	R	R_{rel}	a %	R	R_{rel}	
Pinus	–	–	18.7	1.82	4.3	16.8	2.04	3.6	(5.0)	(4.84)	(10.9)	–	–	–	1:4
Quercus	5.8	4.6	(6.4)	(0.59)	(1.4)	–	–	–	11.8	1.36	3.06	12.0	0.91	1.3	1:4
Betula	4.4	4.8	10.1	1.85	4.4	(8.0)	(1.88)	(3.4)	(2.4)	(3.62)	(8.2)	–	–	–	1:4
Alnus	3.9	3.6	(7.1)	(1.32)	(3.1)	(2.7)	(1.97)	(3.5)	–	–	–	–	–	–	1:4
Carpinus	2.4	2.5	(4.5)	(0.45)	(1.1)	12.8	0.21	0.4	(3.2)	(1.09)	(2.5)	14.9	3.30	4.6	1:3
Ulmus	2.0	1.7	–	–	–	–	–	–	–	–	–	(1.4)	(1.22)	(1.7)	1:2
Picea	–	–	44.9	0.66	1.6	33.4	0.92	1.6	18.4	1.30	2.9	–	–	–	1:2
Fagus	1.0	1.0	(3.7)	(0.55)	(1.3)	20.9	0.56	1.0	37.0	0.44	1.0	35.5	0.71	1.0	1×1
Abies	–	–	–	–	–	–	–	–	21.7	0.34	0.8	–	–	–	1×1
Tilia	0.6	0.6	(4.7)	(0.15)	(0.4)	(5.4)	(0.08)	(0.1)	–	–	–	(2.9)	(0.15)	(0.2)	1×2
Fraxinus	0.4	0.4	–	–	–	–	–	–	–	–	–	18.3	0.58	0.8	1×2
Acer	–	–	–	–	–	–	–	–	(0.65)	(0.32)	(0.7)	15.1	0.13	0.2	1×2 ?

within the stand. It is not stated in which way the tree composition was calculated. *Quercus robur*, *Picea abies*, *Fagus silvatica* and *Abies alba* are best represented in the forest stands, and *Pinus silvestris*, *Betula* sp., *Carpinus betulus* and *Acer* spp. (*A. platanoides*, *A. campestre*) are rather scarce. It may be assumed that the samples derive from acid soils, but the pollen preservation is not described. The high R_{rel}-values for *Pinus* and *Betula* are due to the influence of pollen transported from outside the stands.

MULLENDERS (l. c.) analyzed moss samples from a forest near Sedan, northern France. Samples from 2 forest stands were analyzed, and the average tree cover in each stand was stated. The state of pollen preservation is not described. The tree species are *Quercus robur* and *Q. petraea* (not distinguished), *Carpinus betulus*, *Ulmus glabra*, *Fagus silvatica*, *Tilia cordata* and *T. platyphyllos* (not distinguished), and *Acer campestre* and *A. pseudoplatanus* (not distinguished). The figures shown in table 27 are based on the samples from a *Carpineto-Fraxinetum*, as only 2 pollen spectra are available from the other forest stand. *Quercus* has a very low R_{rel}-value.

The material used for the calculation of the figures shown in table 27 is heterogenous. The pollen productivity of the trees may vary due to differences in climate, soil conditions and the structure of the forest stands studied. Still, the R_{rel}-values are in most cases not unlike the figures calculated in the material from Denmark.

Judging from the R_{rel}-values the pollen productivity of *Pinus* is similar to that of *Betula*, that of *Picea* about twice that of *Fagus*, and that of *Abies* similar to *Fagus*. *Acer* seems to have a low pollen productivity. The following correction factors are suggested from these data (cp. table 27)

Pinus 1:4 *Picea* 1:2 *Abies* 1×1 *Acer* 1×2 (?)

XV. TREE POLLEN SPECTRA FROM OPEN AREAS

The figures from JONASSEN (1950) shown on p. 13 indicate that the tree pollen spectrum from a glade in a forest differs from the forest pollen spectrum due to a much larger pollen source area. TAUBER (1965) pointed out that the pollen sedimentated on the surface in open areas in forests such as glades, lakes or bogs has 3 components, one carried through the trunk space, one carried over the tree tops, and a rainout component. TAUBER (l. c.) assumed the proportions of these 3 components to be about 8 : 1 : 1 in the pollen deposition in the middle of a small lake or bog (diameter 100–200 m) and 1 : 7 : 2 in a large lake or bog (diameter some km). In experiments from a small lake TAUBER (1967) found the rainout component to be about 15% of the total amount deposited in a sampler on the lake, which is similar to the expected figure. The lake sampler collected from 2 to 34 times more pollen of the various taxa, exotic and local, than a collector in the trunk space. This result suggests that the importance of the trunk space component was overestimated in TAUBER (1965) and that pollen transported over the tree tops is important in the pollen deposition even in rather small forest openings.

The results of REMPE (1937) mentioned on p. 42 indicate a strong vertical mixing, by means of which heavy pollen grains are carried up to high altitudes as effectively as light pollen grains. From REMPE's figures (l. c.) TAUBER (1965) estimated the pollen drift above a forest to be half as large as the pollen drift in the crown space. OGDEN et al. (1964) collected pollen in the air in and above a forest with a rotoslide sampler, which collects pollen independently of the wind speed. The numbers of pollen grains collected are shown in table 28. They indicate that the pollen concentration above the tree tops is half as large as in the crown space and similar to that in the trunk space. Due to the high wind speeds the pollen drift in the layer above the tree tops is similar to that of the crown layer in this case. Pollen spectra from the various levels calculated from the figures of OGDEN et al. (l. c.) also are shown in table 28. These spectra are very uniform and indicate a strong mixing by which even the heavy *Fagus* and *Tsuga* pollen grains are lifted into the air above the tree tops.

It appears that pollen from the forest is mixed uniformly into the air above the tree tops, and that pollen transported there constitutes an important fraction of the pollen deposition in lakes and bogs.

Based on the formulae of Sutton and Chamberlain, TAUBER (1965) calculated cumulative curves for the percentages of light pollen grains (*Betula*) and heavy

Table 28. Tree pollen collected at different levels during the pollination period (may 21–28). Forest in the Adirondacks, U.S.A. Calculated from Ogden et al. (1964)

	pollen grains/cm² (rotoslide sampler)	*Betula*	*Fagus*	*Fraxinus*	*Tsuga*	*Acer*	*Pinus*	others
open air (43 m).........	12 068	83	4.4	2.9	1.0	0.5	1.8	6.4%
Above tree crowns (30 m)	9 859	80	4.4	4.0	1.1	0.4	2.1	7.6%
crown space (15 m)	21 149	86	3.3	2.6	1.1	0.3	1.1	5.7%
trunk space (1.6 m)	13 031	90	2.3	1.6	0.7	0.3	1.5	3.2%

pollen grains (*Fagus*) arriving from various distances at a sampling point. At a point immediately above the tree canopy 20% of the light and 3% of the heavy pollen grains derive from outside 10 km. This difference is due to a greater loss of the heavy grains by ground deposition. If the sample point is 500 m from the forest edge 20% of the light and 3% of the heavy grains will be derived from outside 50 km. The pollen source area thus increases with the distance from the forest, and the tree pollen spectra from unforested areas must represent very large areas.

The difference in the dispersal effectivity of light and heavy pollen grains noticed by Tauber (l.c.) may be overestimated because losses from a pollen cloud passing over vegetation, and particularly a forest, are not due to ground deposition, but rather to filtration. The filtration efficiencies of various vegetation types are not known very well but it appears that over a forest, at least, the difference in the filtration efficiency for heavy and light pollen grains decreases with increasing wind speed (p. 38) and may be strongly reduced at the wind speeds prevailing in the tree tops. The calculations in the second example quoted from Tauber (l.c.) above also overlook the fact that no deposition is supposed to take place within the first 200 m from the forest edge, at least according to Tauber's own theory (l.c.). The figures for differential pollen transport calculated by Schmidt (1967) also assume loss of pollen by ground deposition and probably overestimate the differential losses of light and heavy pollen grains.

Light pollen grains deposited in open areas still may have somewhat larger source areas than heavy pollen grains due to differential filtration and the trees with light pollen grains are likely to be somewhat overrepresented in a pollen spectrum. Such an overrepresentation will be particularly strong if tree species with light pollen grains are rare near the sampling point and increase in areal frequencies with distance, and the very high R-values for *Quercus*, *Pinus* and *Betula* noticed by Davis (1963), Janssen (1967) and Livingstone (1968) are explained in this way.

It appears that comparisons of tree pollen spectra from open areas with forest composition require data for increasingly large forest areas, the larger the open area is. An example is given in the data from Steinberg on p. 13. The distance to forest here is 3–4 km, and the tree pollen spectrum from the surface sample has no relation to the forest composition stated for an area of 27.3 km^2.

Lakes or bogs surrounded by forests of large dimensions are scarce in Europe, and the data for the forest composition in large areas must be inaccurate. Only a few investigations exist. Areal frequencies and R- and R_{rel}-values calculated from the works of Müller (1937), Firbas (1949), Straka (1960) and Kral (1968) are shown in table 29.

Müller (1937) compared a pollen spectrum from a bog in Switzerland 300 × 100 m large and almost completely surrounded by forest with the forest composition within 4 km. The forest composition is stated in percentages of the trees larger than 8 cm in diameter. Only *Picea* and *Fagus* occur in the vegetation with appreciable frequencies.

Firbas (1949) stated a composite pollen spectrum from bogs in the Oberharz, Germany, and the forest composition in Kreis Zellerfeld (based on a forest inventory). Only *Picea* and *Fagus* are present with appreciable frequencies in this case too.

Straka (1960) stated a pollen spectrum from Hinkelsmaar in the Eifel mountains, Germany, 125 × 90 m large, which is compared with data for the forest composition within 1.5 km. *Pinus*, *Picea* and *Fagus* are the commonest trees.

Kral (1968) stated a pollen spectrum from a bog 0.66 ha large. It is compared with the forest composition within 100 m. *Pinus* and *Picea* are the only important trees, and the R_{rel}-values were calculated for a R_{rel}-value for Pinus = 4.0.

Table 29. Areal frequencies (a %), R- and R_{rel}-values for pollen spectra from lakes or bogs, calculated from published sources

	Müller 1937			Firbas 1949			Straka 1960			Kral 1968		
	a %	R	R_{rel}	a %	R	R_{rel}	a %	R	R_{rel}	a %	R	R_{rel}
Pinus . . .	(3)	(6.0)	(10.5)	–	–	–	23	2.0	4.0	70	1.06	4.0
Quercus .	(0.5)	(2.0)	(3.5)	(0.4)	(16.3)	(41)	(5)	(2.8)	(5.5)	(3)	(1.7)	(6.3)
Betula . .	(0.2)	(5.0)	(8.8)	–	–	–	–	–	–	–	–	–
Alnus . . .	(1.3)	(0.08)	(0.2)	–	–	–	–	–	–	–	–	–
Picea . . .	76	0.9	1.6	80	0.7	1.9	39	0.5	1.1	25	0.3	1.1
Fagus . . .	14	0.57	1.0	20	0.37	1.0	35	0.51	1.0	(2)	(0.5)	(1.9)
Abies . . .	(5)	(1.0)	(1.8)	–	–	–	–	–	–	–	–	–

The R_{rel}-values in table 29 contain many elements of uncertainty, and the figures are of course particularly uncertain if the trees occur with low areal frequencies. Figures based on areal frequencies smaller than 10 % are shown in brackets, and it may be noticed that trees with light pollen grains such as *Pinus*, *Quercus* and *Betula* may have particularly high R- and R_{rel}-values in these cases. Otherwise, the R_{rel}-values in table 29 are not unlike the R_{rel}-values calculated in the previous chapters by means of surface samples from forests.

To illustrate the applicability of comparisons of pollen spectra from open areas with forest composition, figures from North America are shown in table 30. The data for Brownington Pond, Vermont, are from Davis and Goodlett (1960) and from Livingstone (1968). Brownington Pond is about 900 × 700 m and is surrounded by partially forested country. Davis and Goodlett (l.c.) compared a surface pollen spectrum from the lake bottom with the forest composition within 3.2 km (calculated from tree-basal areas) and Livingstone (l.c.) compared the same pollen spectrum with the vegetational composition of the whole state of Vermont (based on land surveys). The figures in table 30 only refer to the tree pollen spectrum and the forest composition. Livingstone (l.c.) also calculated R-values for a number of lakes and bogs in Eastern North America, and stated average R-values. The R-value for *Fagus* happens to be nearly 1 (0.93) and these R-values are stated in table 30 without a re-calculation. Although other tree species are represented in these investigations, the R_{rel}-values in table 30 resemble the figures found for the corresponding European trees quite well. The figures with areal frequencies less than 10% are shown in brackets. The R_{rel}-values are in some of these cases much too high because the vegetational analysis comprises a too small area (cp. p. 75).

Table 30. Areal frequencies (a %), R- and R_{rel}-values for pollen spectra from lakes and bogs in North America calculated from published sources

	Brownington Pond						average
	Davis and Goodlett (1960)			Livingstone (1968)			Livingstone (1968)
	a %	R	R_{rel}	a %	R	R_{rel}	R
Pinus	(0.04)	(200)	(133)	(7)	(1.2)	(2.0)	(6.8)
Quercus	(0.01)	(240)	(160)	(2)	(1.0)	(1.6)	(146)
Betula	(9)	(5.6)	(3.7)	18	2.8	4.6	4.8
Ulmus	(2.7)	(1.1)	(0.7)	–	–	–	(26)
Picea	11	0.6	0.4	15	0.4	0.7	0.7
Fagus	(5)	(1.50)	(1.0)	11	0.61	1.0	(0.93)
Abies	12	0.14	0.1	(6)	(0.3)	(0.4)	0.3
Fraxinus	(3)	(0.48)	(0.3)	(1.3)	(1.1)	(1.8)	(0.5)
Acer	20	0.19	0.1	24	0.2	0.3	0.2
Tsuga	(6)	(1.2)	(0.8)	12	0.6	0.9	(4.6)

The possibilities for a calculation of correction factors by a comparison of pollen spectra from surface samples from open areas with forest composition are limited because of the lack of satisfactory material. The few results mentioned do, however, not contradict the results obtained from forests.

XVI. DISCUSSION OF THE RESULTS

The North European trees can be arranged in the following sequence of decreasing pollen productivity, according to the present investigation,

Pinus, Betula, Quercus, Alnus
Carpinus
Ulmus, Picea
Fagus, Abies
Tilia, Fraxinus, Acer.

Similar sequences have been estimated by various authors.

HESMER (1933) summarized the following sequence from experiences with surface samples,

Pinus, Betula, Alnus, Carpinus
Picea
Fagus, Quercus, Tilia.

This sequence mainly differs from the one mentioned above with respect to *Quercus*. HESMER (l.c.) investigated himself surface samples from bogs in Mark Brandenburg, Germany. The forests in this area are rich in *Pinus*, and *Pinus* pollen dominate the pollen spectra. HESMER (l.c.) found the percentages of *Fagus* pollen in bogs surrounded by *Fagus* forest to be similar to the frequencies of *Quercus* pollen in bogs surrounded by *Quercus*-forest, and concluded that *Fagus* and *Quercus* are equal pollen producers. However, it happens that the bogs in *Fagus* forest are rather small (the largest is 125 × 80) and the bogs in *Quercus* forest rather large (the smallest is 350 × 250). The pollen spectra from the large bogs are likely to reflect the forest in a larger area and to include more pollen from the *Pinus* forests than the spectra from the small bogs, which explains the low *Quercus* pollen frequencies found by HESMER.

POHL (1937) estimated the following sequence,

Alnus, Pinus, Tilia, Betula, Picea
Carpinus
Quercus, Fagus

The investigation of POHL (l.c.) is mentioned on p. 12. It is based on large extrapolations and may contain errors. It mainly differs from the present results with respect to *Tilia, Picea* and *Quercus*.

REMPE's investigation (1937) is mentioned on p. 12. It is based on collections during one season and the results are somewhat uncertain.

FIRBAS (1949) summarized the following sequence of decreasing pollen productivity,

Pinus, Alnus, Betula
Abies, Carpinus, Picea
Fagus, Quercus, Ulmus?, Tilia, Acer

This sequence is based mainly on the investigations mentioned above and differs from the present one mainly with respect to *Quercus*.

FÆGRI and IVERSEN (1950, 1964) summarized the following sequence,

Pinus, Betula, Alnus
Picea, Quercus, Fraxinus, Fagus
Tilia

This sequence also differs from the one on p. 78 with respect to *Quercus*. It is based mainly on the investigation of POHL (1937) and the works of MÜLLER (1937), STEINBERG (1944) and a pollen spectrum from a fossil forest (IVERSEN 1947). MÜLLER's figures actually suggest a rather high R_{rel}-value for *Quercus* (table 29), and the comparison made by STEINBERG (l.c.) is not reliable, as the forest area is too small (p. 13). The pollen spectrum from IVERSEN (1947) with a low *Quercus* pollen frequency probably is not representative, as single pollen spectra from forests vary greatly.

JONASSEN (1950) found the following sequence,

Pinus, Betula, Alnus, Quercus
Fagus
Picea

The pollen productivity of *Picea* probably is underestimated here because the investigation was based on *Picea* plantations in Denmark, where *Picea* seems to flower badly.

BASTIN (1964) estimated the relative pollen productivity of the trees as follows,

Pinus, Betula, Quercus
Fagus
Carpinus

It may be seen that previous estimates as to the pollen productivity of the various trees in Northern Europe differ as to the detailed sequence. There is some agreement with the present investigation, but differences also are apparent. The pollen productivity of *Quercus* in particular seems to have been underestimated by some authors.

The correction factors suggested for the North European trees from the relative pollen productivity values (P_{rel}-values) and the relative pollen representation-values (R_{rel}-values) in the present investigation can be summarized as follows,

Pinus, Betula, Quercus, Alnus	1:4
Carpinus	1:3
Ulmus, Picea	1:2
Fagus, Abies	1×1
Tilia, Fraxinus, (Acer)	1×2

Müller (1937) used the R-values (see table 29, p. 76) for a correction of pollen spectra. This procedure is misleading as R-values vary with the species combinations and only can be used in the specific cases, for which they were calculated (p.51).

Iversen (1947, cp. Fægri and Iversen 1964) suggested the following correction factors,

Pinus, Betula, Alnus	1:4
Picea, Quercus, Fraxinus, Fagus	1×1
Tilia	1×2

Although these figures were chosen arbitrarily, they are quite similar to the ones suggested in the present investigation with the exception that the correction factor for *Quercus* rather should be 1:4, for *Picea* 1:2, and for *Fraxinus* 1×2.

Jonassen (1950) suggested the following correction factors

Quercus	1:5
Betula, Alnus	1:4
Fagus	1×1

These figures are similar to those mentioned above. Jonassen (l.c.), however, found his material to be too limited with regard to *Quercus* and *Pinus*, and he did not believe his figures to be generally applicable.

Kral (1968) used the following correction factors,

Pinus	1:2
Fagus, "Quercetum mixtum"	1×1
Picea, Abies	1×2

These figures are not quite the same as found in the present investigation (cp. table 29).

Davis (1965), Livingstone (1968) and Tsukada (1958) used R-values for a correction of pollen spectra in North America and Japan, but such a procedure may lead to erroneous results (cp. Davis 1967 and above).

The present investigation of surface pollen samples thus has provided new information about the relative pollen productivity of the most important tree species in northern Europe, and new correction factors are suggested. The knowledge in these respects has been rather uncertain, and the new information may be an improvement.

The surface samples mainly derive from forest humus in status nascendi, and the correction factors may be applied in studies of pollen-containing material derived within forests with some confidence. Pollen diagrams from profiles derived within forests are becoming increasingly important in studies of vegetational history. In these cases the corrected pollen spectra are likely to resemble the true tree areal composition within 20–30 m from the sample point.

Tree pollen spectra from open areas in forests such as lakes or bogs reflect the vegetation of much larger areas. Trees with light pollen grains such as *Pinus*, *Betula*, *Quercus* and *Alnus* may be somewhat overrepresented in corrected tree pollen spectra from such places because they have larger source areas than the other trees, whereas trees with lumpy pollen such as *Tilia* may be somewhat underrepresented. Absolute pollen diagrams may be corrected in order to show the forest composition better.

The pollen productivity of the trees may depend somewhat on the climate and the soil conditions. The present investigation has not revealed differences due to climate within the regions studied, and it is not possible at present to distinguish such features, but it is suggested that the pollen productivity of the trees may decrease when they grow at disadvantageous soil conditions.

The corrected tree pollen sum is in forested areas likely to provide a relatively stable basis for a calculation of the percentages of the trees, the shrubs and the herbaceous plants. *Corylus* seems to be a low pollen producer in dense forest. Its pollen percentages are likely to equal its areal frequencies in a corrected pollen diagram from a forest, whereas forest herbs are more or less underrepresented in such cases. The pollen from shrubs and herbs in the forest is likely to be badly dispersed into lake or bog deposits. If the tree canopy is discontinuous, the pollen productivity of the shrubs and the herbs increases considerably. *Corylus* thus is considered a great pollen producer, when it grows in open areas (HESMER 1933, IVERSEN 1947, FIRBAS 1949, JONASSEN 1950). The pollen dispersal also improves and the shrubs and the herbs in vegetation with discontinuous forest or no forest should be included in the pollen total. Their pollen productivity and pollen representation is, however, difficult to determine, especially in cultivated areas. LIVINGSTONE (1968) calculated R-values for non-arboreal vegetation, but they may be difficult to apply in general, and correction factors for shrubs and herbs are badly known at present.

GLOSSARY

tree crown area = area of the horizontal projections of the tree crowns in the canopy layer, measured in m^2 (p.18).

tree basal area = area of the cross section of the tree trunks 1.3 m above the ground, measured in m^2 (p.19).

absolute pollen productivity of a tree species = number of pollen grains produced per unit crown area per year (p.46).

relative pollen productivity of a tree species = the ratio of the absolute pollen productivity of a species to that of another species (p.46, *Fagus silvatica* is used as a reference species in the present work).

p = amount of pollen of a tree species deposited at a sampling point per unit area per year (p.46).

P = pollen productivity factor (p.46)

p_o = amount of pollen of a tree species deposited at a sampling point per unit area per year from trees standing outside a given distance (outside the sample plot, p.47).

P_{rel} = ratio of the P-value of a species to that of another species (= relative pollen productivity, p.48, *Fagus silvatica* is used as a reference species in the present work).

p_r = relative pollen deposition of a tree species = the ratio of the pollen deposition of the tree species to the deposition of exotic pollen per cm^2 per year (p.47).

$p_{r(o)}$ = relative pollen deposition at zero area of a tree species = the relative pollen deposition of the species derived from trees standing outside a given distance (outside the sample plot, p.47).

R = pollen representation factor = the ratio of the pollen percentage of a species to the area percentage of the species (p.48).

R_{rel} = relative pollen representation = the ratio of the R-value of a species to that of another species (p.49, *Fagus silvatica* is used as a reference species in the present work).

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DANSK SAMMENDRAG

NORDEUROPÆISKE TRÆERS RELATIVE POLLENPRODUKTION OG POLLENREPRÆSENTATION SAMT KORREKTIONSFAKTORER FOR TRÆPOLLENSPEKTRE, BESTEMT VED POLLENANALYSE AF OVERFLADEPRØVER FRA SKOVE

I. INDLEDNING

Von Post påpegede allerede i 1916 at pollenspektrene ikke gengiver vegetationens sammensætning direkte men påvirkes af plantearternes, specielt træernes uensartede pollenproduktionsevne og pollenspredning. Den uensartede pollenrepræsentation kan også forårsage ændringer i pollendiagrammerne, som kun er tilsyneladende. Disse vanskeligheder kan overvindes, hvis man kan korrigere pollenanalyserne med omregningsfaktorer, således at vegetationens sammensætning gengives mere direkte. En anden mulighed er en beregning af absolutte pollendiagrammer, hvor der er taget hensyn til ændringer i sedimentationshastigheden, men også sådanne diagrammer må korrigeres, hvis man vil vide noget om vegetationens kvantitative forhold.

II. OVERFLADEPOLLENSPEKTRE OG VEGETATION

Pollenindholdet i talrige overfladeprøver er undersøgt i tidens løb og sammenlignet med den nuværende vegetation. Man kan sammenligne fossile pollenspektre med tilsvarende recente og deraf slutte sig til den daværende vegetationstype, men denne metode har sine begrænsninger. Det er derfor bedre, hvis man kan beregne omregningsfaktorer. Man har forsøgt at bestemme træernes pollenproduktion direkte, men disse undersøgelser støder på store vanskeligheder. Man har også forsøgt at beregne omregningsfaktorer ved at sammenligne pollenspektre fra overfladeprøver med vegetationens sammensætning. Ved undersøgelse af overfladeprøver må man være klar over, at det vegetationsareal der er repræsenteret varierer stærkt. I overfladeprøver fra åbne arealer stammer træpollenet fra et meget stort område, mens overfladeprøver taget inde i skoven er stærkt lokalbetonede.

III. DE UNDERSØGTE SKOVE

Nærværende forfatter har undersøgt pollenindholdet i overfladeprøver fra Draved skov i Sønderjylland og Longelse Bondegårds skov på Langeland. I Draved skov er to områder undersøgt, afdeling 386 og afdeling 370, der begge er fredet som forskningsområder. I afdeling 386 findes blandet skov af *Tilia cordata*, *Fagus silvatica*, *Quercus robur*, *Alnus glutinosa* og *Betula pubescens*, og i afdeling 370 er foruden de førnævnte træer også *Fraxinus excelsior* almindelig. Longelse Bondegård skov, her kaldet Longelse skov, er ligeledes fredet.

Den består af *Quercus robur*, *Fagus silvatica*, *Ulmus scabra*, *Fraxinus excelsior* og *Carpinus betulus*. De vigtigste danske træer er således repræsenteret i de undersøgte områder.

IV. DE UNDERSØGTE SKOVES SAMMENSÆTNING

Ved undersøgelser af træarternes pollenproduktion må man først og fremmest tage hensyn til arealet af deres pollenproducerende flade, d.v.s. arealet af deres kronprojektion. Man har dog også benyttet træernes stammeareal, d.v.s. arealet af stammetværsnittet i 1.3 m højde, eller træantallet. I Draved skov har det været muligt at fremstille nøjagtige kort over træarternes kronprojektioner ved hjælp af luftfotos. Træarternes kronarealer er målt planimetrisk i kredsrunde prøveflader med 20 m og 30 m radius omkring de enkelte overfladeprøver. Stammearealer er bestemt i de samme prøveflader ved hjælp af trækort opmålt af Danmarks Geologiske Undersøgelse. Det viser sig, at der er et ensartet forhold mellem kronarealer og stammearealer i afdeling 386, som har et sluttet krondække, mens dette forhold varierer noget i afdeling 370, som er mere åben (table 7). Kort over træernes kronprojektioner kunne ikke udarbejdes i Longelse skov på grund af et stormfald ved oktoberstormen i 1967. Heldigvis foreligger der et trækort udarbejdet af Skovhistorisk Selskab i 1961, og ved hjælp af dette har træernes grundfladearealer kunnet beregnes. Longelse skov ligner i struktur afdeling 386 i Draved mest, og man kan derfor her benytte de målte stammearealer som erstatning for kronarealer.

V. OVERFLADEPRØVERNE

Pollensedimentationen er undersøgt ved hjælp af mosprøver indsamlet på træstubbe etc. Under disse forhold dannes et surt humuslag, hvor pollen fra en længere årrække er bevaret. Der er analyseret 48 prøver fra afdeling 386 og 88 prøver fra afdeling 370 i Draved skov og 39 prøver fra Longelse skov. Nogle af disse er sammenstillet i linieprofiler igennem de undersøgte arealer.

VI. POLLENBEVARING I OVERFLADEPRØVERNE

Pollenet var velbevaret i de fleste prøver, men nogle prøver med megen pollenkorrosion fandtes også. Der er foretaget en undersøgelse af hyppigheden af korroderede pollenkorn hos de forskellige træer, og træerne er sammenstillet efter tiltagende hyppighed af korroderede korn (table 10). I Draved blev prøver med over 50% korroderede korn udelukket. I Longelse blev alle prøver benyttet, idet det viste sig, at der ikke var nogen forskel i resultaterne fra de forskellige prøver.

VII. POLLENSPREDNING I SKOVEN

Pollen kan aflejres på skovbunden ved vindspredning, ved nedskylning fra vegetationen ved regn og ved at falde til jorden i rakler eller blomster.

Vindforholdene er undersøgt med selvregistrerende vindmålere uden for og inde i skoven. Forsøgsperioden er lovlig kort endnu, og resultaterne fra målingerne uden for skoven er derfor sammenlignet med meteorologiske målinger over længere perioder. Resultaterne er vist i tables 12–15.

Pollen fra træerne skulle ved turbulens eller frit fald spredes flere hundrede m med vinden, før de når jorden, men målinger i praksis har vist ganske korte spredningsafstande på 20–40 m. Pollenindsamlinger i Draved har vist, at en betydelig del af årets pollensedimentation sker ved nedvaskning med regn. Man må formode, at pollenet opfanges på kviste i kronlaget under blomstringen og senere vaskes ned. Pollenkoncentrationen i luften aftager meget hurtigt med afstanden fra pollenkilden, og det må formodes, at det nedvaskede pollen stammer fra de nærmeste træer. Nedfaldne uåbnede rakler kan indeholde store pollenmængder, og tilfælde af en sådan overrepræsentation findes i de analyserede mosprøver.

Pollen fra urter i skoven spredes over meget korte afstande på grund af de lave vindhastigheder.

Fremmed pollen kan tilføres horisontalt gennem stammerummet eller over trækronerne. Eksperimenter har vist at pollenmængden tilført i stammerummet aftager til ubetydelige værdier kort inden for skovkanten. Pollen kan transporres over trækronerne langvejs fra på grund af stor vindhastighed og stærk turbulens. Når vinden passerer trækronerne kan pollenet frafiltreres på kviste og blade, og det har vist sig at en stor del af årets sedimentation af fremmed pollen nedvaskes fra disse med regn.

VIII. SAMMENSÆTNINGEN AF DET FREMMEDE POLLEN I DRAVED OG LONGELSE SKOV

Hvis det fremmede pollen aflejres ensartet i de undersøgte områder kan man bruge det som beregningsbasis for sedimentationen af andet pollen. Mængden af pollen transporteret horisontalt ind i stammerummet formodes at være ringe i mosprøverne, da disse er taget i en vis afstand fra skovkanten, og det er sandsynligt at det meste af det fremmede pollen er transporteret over kronlaget. Både lette og tunge pollenkorn transporteres effektivt højt op i luften, og tabet af pollenkorn til kronlaget under passagen hen over dette udlignes formodentlig på grund af turbulens. Hvis der sker et væsentligt fald i aflejringen af fremmed pollen i vindretningen må faldet være størst for tunge pollenkorn. En sådan ændring i sammensætningen af det fremmede (eller eksotiske) pollen kan ikke konstateres inden for de undersøgte områder. En undtagelse udgøres af pollen af Leguminosae, som i Draved skov tydeligt er hyppigere i de dele der er nærmest vindsiden. Dette skyldes sandsynligvis at Leguminosae pollenet spredes i klumper, som frafiltreres hurtigt under passagen over trætoppene. Leguminosae pollen er derfor ikke medtaget i beregningssummen.

IX. FORHOLDET MELLEM SKOVENS SAMMENSÆTNING OG SEDIMENTERINGEN AF TRÆPOLLEN

Pollenproduktivitet

Ved træarternes absolutte pollenproduktivitet forstås antallet af pollenkorn produceret pr. arealenhed af kronlaget pr. år. Den relative pollenproduktivitet er forholdet mellem to træarters absolutte pollenproduktivitet. Som nævnt i kapitel VII er det sandsynligt at det meste af det træpollen der aflejres på et punkt stammer fra de nærmeste træer. Hvis alt træpollenet aflejret på et punkt stammer fra træerne indenfor en given afstand vil mængden af pollen af en træart aflejret pr. arealenhed pr. år (p) under forudsætning af linearitet tiltage med træartens kronareal (a) indenfor denne afstand efter ligningen

$$p = P \times a \tag{1}$$

hvor vi kan kalde P for pollenproduktionsfaktoren. Hvis der også tilføres pollen fra træer udenfor den givne afstand vil formel (1) modificeres til en regressionsligning

$$p = P \times a + p_0 \tag{2}$$

hvor p_0 er det antal pollenkorn der tilføres pr. arealenhed pr. år fra træer udenfor den givne afstand.

Værdierne af P og p_0 i (2) kan bestemmes ved regressionsanalyse, hvis a og p kendes i tilstrækkeligt mange tilfælde.

Forholdet mellem 2 træarters P-værdier udgør deres relative pollenproduktivitet (P_{rel}).

En træarts relative pollensedimentation (p_r) i en mosprøve er bestemt som

$$p_r = \frac{\text{antal pollenkorn aflejret pr. cm}^2\text{ pr. år}}{\text{antal eksotiske pollenkorn aflejret pr. cm}^2\text{ pr. år}} = \frac{\text{antal pollenkorn talt}}{\text{antal eksotiske pollenkorn talt}}$$

Ligning (2) modificeres derfor til

$$p_r = P \times a + p_{r(0)} \tag{3}$$

Efter (3) kan P og $p_{r(0)}$ bestemmes i mosprøverne, når p_r og a er kendt i et antal prøver. a er bestemt som kronareal eller stammeareal i 20 m- og 30 m-prøveflader (kapitel IV).

Pollenrepræsentation

En træarts pollenrepræsentation (R-værdi) er bestemt ved forholdet

$$R = \frac{\text{pollenprocent}}{\text{arealprocent}}$$

R-værdierne er ikke artsspecifikke, de varierer i de enkelte tilfælde efter hyppigheden af de forskellige arter (figur s. 48) og efter artssammensætningen. Derimod er forholdet mellem to arters R-værdier, den relative pollenrepræsentation (R_{rel}), konstant. Disse betragtninger forudsætter at pollensedimentation og areal tiltager proportionalt efter ligning (1) ovenfor. Dette er ikke tilfældet i mosprøverne, hvor ligning (2) snarere gælder. Som vist på s. 49 varierer R-værdier og R_{rel}-værdier for en stor pollenproducent her efter en sigmakurve selv i simple tilfælde med kun 2 arter. R_{rel}-værdierne er lig med P_{rel}-værdierne i et ret snævert interval af træartens relative hyppighed (15–70 %). Forholdene er naturligvis mere komplicerede når flere arter er repræsenteret (se figur s. 50).

I den her foreliggende undersøgelse er P- og R-værdierne for *Fagus silvatica* brugt som beregningsbasis for P_{rel}- og R_{rel}-værdierne hos de andre træarter.

Korrektionsfaktorer

I det simple tilfælde illustreret ved ligning (1) ovenfor kan pollenprocenter omregnes til arealprocenter ved hjælp af P_{rel}- eller R_{rel}-værdierne. R-værdier kan derimod ikke bruges som korrektionsfaktorer. I tilfælde af ligning (2) ovenfor burde p_0 subtraheres først. Dette kan ikke gøres i fossile prøver, men fejlen ved at se bort fra p_0-værdien er uvæsentlig (figur s. 51).

X. BESTEMMELSE AF POLLENPRODUKTIONSFAKTOREN (P-VÆRDIEN) OG DEN RELATIVE POLLENPRODUKTIVITET (P_{rel}-VÆRDIEN) HOS TRÆERNE I DRAVED OG LONGELSE SKOV

Variationen i den relative pollensedimentation og kronarealerne i prøvefladerne med 30 m radius i linieprofiler i Draved skov er vist på plates I–II og korrelationen mellem pollenfrekvenserne og kronarealerne i de enkelte prøver er vist på plates III–IV. Der er en vis spredning af punkterne, men korrelationskoefficienterne (r) er i de fleste tilfælde tilstrækkelige til at vise en positiv korrelation. Regressionsligninger er beregnet efter formel (3) på side 87 og regressionslinier og linier for 2 × middelfejlen er vist på diagrammerne. Regressionsliniernes stejlhed udtrykker træernes pollenproduktivitet. Punkter for middelværdierne af pollenfrekvenserne i grupper af kronarealværdierne er vist på s. 55 sammen med regressionslinierne. De viser en tydelig lineær regression i de fleste tilfælde. Hos *Quercus* er der en tendens til overrepræsentation ved de højeste arealværdier, hvilket giver for stejle regressionslinier og hos *Alnus* er regressionslinierne i de to afdelinger noget forskellige. De beregnede talværdier i regressionsligningerne er vist i table 34. Regressionslinier er også beregnet for 20 m prøvefladerne. De er vist på s. 56 sammen med regressionslinierne for 30 m prøvefladerne.

Træernes relative pollenproduktivitet i forhold til *Fagus* (P_{rel}-værdier) er vist i table 21.

Den relative pollensedimentation i forhold til træernes stammearealer i 30 m prøveflader i Longelse skov er vist i et linieprofil på plate V og i korrelationsdiagrammer med beregnede regressionslinier på plate VI. Talværdierne er vist i table 37 og regressionslinier for 20 m og 30 m prøveflader i figuren på s. 61.

Den relative pollenproduktivitet (P_{rel}-værdier) hos træerne i Draved og Longelse skov er vist i table 24. Til trods for visse usikkerhedsmomenter, som er uundgåelige, er tallene ensartede. De viser den højeste pollenproduktion hos *Quercus*, *Betula* og *Alnus*, intermediær hos *Ulmus* og *Carpinus* og den laveste hos *Fagus*, *Tilia* og *Fraxinus*. *Alnus* har to forskellige værdier i Draved. Den lave værdi i afdeling 386 skyldes en nedsat blomstringsevne, sandsynligvis som en følge af større rodkonkurrence fra *Tilia* efter en udtørring ved grøftning.

XI. TRÆPOLLENSPEKTRE OG BESTEMMELSE AF TRÆERNES RELATIVE POLLENREPRÆSENTATION (R_{rel}-VÆRDI) I DRAVED OG LONGELSE SKOV. KORREKTIONSFAKTORER.

Træernes pollenprocenter i moshumusprøverne og træernes arealprocenter i 30 m prøvefladerne i linieprofilerne fra Draved og Longelse skov er vist på plate V, og spredningen af pollenprocenter og arealprocenter er vist på plate VI. R-værdierne og R_{rel}-værdierne i de enkelte prøver viser stor variation, men grove gennemsnitsværdier kan fås ved hjælp af pollen- og arealspektre for alle prøver i de undersøgte områder. Denne fremgangsmåde forudsætter den lineære tiltagen af pollensedimentationen som er påvist i kapitel X. Procentværdierne og R-værdierne er vist i table 38 og R_{rel}-værdierne er vist sammen med de tilsvarende P_{rel}-værdier i table 25. Disse svarer i de fleste tilfælde ganske godt til hinanden, kun er P_{rel}-værdierne for *Quercus* lovlig høje, hvilket skyldes at dens regressionslinier er noget for stejle. For *Alnus* må den høje pollenproduktion i afdeling 370 anses for typisk. Korrektionsfaktorer for pollenanalyserne baseret på P_{rel}- og R_{rel}-værdierne er vist nedenfor (sml. table 25, hos *Quercus* er der taget mest hensyn til R_{rel}-værdierne):

Quercus, Betula, Alnus	1:4
Carpinus	1:3
Ulmus	1:2
Fagus	1×1
Tilia, Fraxinus	1×2.

XII. KORRIGEREDE TRÆPOLLENSPEKTRE FRA DRAVED OG LONGELSE SKOV

Korrigerede træpollenprocenter er sammenlignet med arealprocenterne på plates XII–XVI og i figuren på s. 67. Overensstemmelsen mellem pollenværdier og arealværdier er ganske god i de fleste tilfælde, men den uundgåelige spredning i de enkelte prøver er naturligvis stadig stor.

XIII. FOREKOMSTEN AF POLLEN AF SJÆLDNE TRÆER, BUSKE OG SKOVURTER I DRAVED OG LONGELSE SKOV

Spredtstående træer af *Sorbus aucuparia*, *Populus tremula*, *Acer campestre* og *A. pseudoplatanus* er kun repræsenteret med få pollenkorn i pollenanalyserne. Pollen af *Sorbus aucuparia* kan dog lokalt være ret hyppigt.

Den korrigerede træpollensum udgør et nogenlunde ensartet beregningsgrundlag for hyppigheden af pollen af buske og urter. *Corylus avellana* er ret udbredt i afdeling 370 i Draved skov, men den blomstrer dårligt. Dens dækningsprocenter og pollenprocenter i 3 linieprofiler er vist på plate XVI. Pollenprocenterne svarer nogenlunde til dækningsprocenterne, hvilket viser at *Corylus* under disse forhold har en pollenproduktion omtrent som *Fagus*, der udgør beregningsgrundlaget for den korrigerede træpollensum.

Skovbundsurterne er dårligere repræsenteret i forhold til deres dækningsgrad. Dækningsprocenter og pollenprocenter for de mest almindelige i linieprofilerne i Draved skov er vist på plates XVII–XVIII. Bedst repræsenteret er de høje skovbundsurter, men pollenet er meget lokalt udbredt.

XIV. SAMMENLIGNING AF RESULTATERNE FOR TRÆERNE I DRAVED OG LONGELSE SKOV MED LIGNENDE UNDERSØGELSER. KORREKTIONSFAKTORER FOR PINUS, PICEA OG ABIES.

Korrektionsfaktorerne fra Draved og Longelse skov dækker de vigtigste nordeuropæiske løvtræslægter, men pollenproduktionen af andre arter af de samme slægter bør naturligvis undersøges andetsteds. Det er dog ikke sikkert at sådanne tal vil afvige væsentligt fra de allerede fundne. Korrektionsfaktorer for *Pinus silvestris*, *Picea abies* og *Abies alba* må bestemmes udenfor Danmark, hvor de forekommer naturligt. Korrektionsfaktorer for disse træarter er udregnet på grundlag af publicerede undersøgelser i Polen og Czekoslovakiet (table 27). *Acer* arterne synes at have en lav pollenproduktion. Følgende korrektionsfaktorer synes at være sandsynlige:

Pinus 1:4   *Picea* 1:2   *Abies* 1 × 1   *Acer* 1 × 2 (?)

XV. TRÆPOLLENSPEKTRE FRA ÅBNE OMRÅDER

Træpollenspektre fra åbne områder afviger fra pollenspektre fra den nærmeste skov fordi skoven i et langt større område er repræsenteret, hvilket må tages i betragtning ved sammenligninger mellem overfladepollenanalyser fra sådanne steder og skovsammensætningen. Under tilførslen af pollen henover trætoppene kan der muligvis ske en vis udvælgelse af de letteste pollenkorn fordi de tunge pollenkorn tilbageholdes noget bedre ved filtrering når vinden passerer trækronerne. Det er desværre vanskeligt at foretage sammenligninger mellem pollenspektre fra søer eller moser med skovsammensætningen fordi sådanne steder omgivet af tilstrækkeligt store nogenlunde naturlige skove er yderst sjældne i dag. Nogle få publicerede tilfælde er vist i table 29. I disse tilfælde bliver R_{rel}-værdierne beregnet for træer med lette pollenkorn let alt for høje når disse forekommer i vegetationsanalysen med lave værdier fordi pollen transporteret fra større afstande påvirker resultatet. I de tilfælde hvor træerne forekommer med arealværdier over 10 % ligner de fundne R_{rel}-værdier de ovenfor beregnede ganske godt.

XVI. DISKUSSION AF RESULTATERNE

De nordeuropæiske træer kan sammenstilles i den følgende rækkefølge efter aftagende pollenproduktion og med de viste korrektionsfaktorer:

Pinus, Betula, Quercus, Alnus	1:4
Carpinus	1:3
Ulmus, Picea	1:2
Fagus, Abies	1×1
Tilia, Fraxinus, Acer	1×2

Rækkefølgen afviger ikke væsentligt fra hvad man har fundet tidligere, dog ser det ud til at pollenproduktionen hos *Quercus* har været undervurderet. Korrektionsfaktorer har været dårligt kendt tidligere og der skulle med den nærværende undersøgelse være skabt et bedre grundlag for en bedømmelse af disse.

Klima- og jordbundsforskelle kan muligvis påvirke træernes pollenproduktion og dermed korrektionsfaktorernes anvendelighed, men det har ikke været muligt at påvise væsentlige forskelle af denne karakter.

De fundne korrektionsfaktorer må kunne anvendes til en omregning af træpollenværdierne i pollenanalyser fra skove. *Corylus* og de andre buske samt urterne har en nedsat pollenproduktion i disse tilfælde, og deres pollenfrekvenser kan udregnes i forhold til den korrigerede træpollensum. I pollendiagrammer fra søer og moser omgivet af skov vil buske og urter fra skoven være dårligt repræsenteret. Hvis træernes krondække ikke er sammenhængende kan disse planter få en stor pollenproduktion og mere effektiv spredning og bør medregnes i pollensummen; men desværre er deres pollenproduktion dårligt kendt, og det er vanskeligt at beregne korrektionsfaktorer.

TABLES 31-38

Table 31. Draved forest, section 386. Composition of the exotic pollen in various areas. Frequencies in percentage of total exotic pollen ÷ Leguminosae. Significance tests according to the χ^2-method

	NW	NE	SE	Significance P 0.05
Gramineae	59.0	56.2	56.1	
Pinus	7.2	8.0	7.3	
Calluna	8.5	11.0	8.1	+
Cerealia	8.3	9.4	11.8	+
Rumex acetosella	7.2	6.4	7.9	
Chenopodiaceae	2.4	1.5	2.0	
Plantago lanceolata	2.5	2.5	2.1	
Artemisia	0.8	1.4	0.8	
Sphagnum	2.4	1.9	2.2	
others	1.8	1.8	1.8	
Total	2740	1038	1537	+
Leguminosae	2.0	2.0	2.7	

Table 32. Draved forest, section 370. Composition of the exotic pollen in various areas. Frequencies in percentages of total exotic pollen ÷ Leguminosae. Significance tests according to the χ^2-method

	West	East	Significance P 0.05	East					Significance P 0.05
				I	II	III	IV	V	
Gramineae	56.7	57.2		57.4	52.7	55.9	60.8	59.7	+
Pinus	7.0	8.3		10.3	9.1	6.6	8.7	7.9	+
Calluna	7.9	9.4	+	8.7	11.9	9.6	7.8	5.9	+
Cerealia	11.4	11.9		8.9	11.0	11.5	8.4	10.5	+
Rumex acetosella	8.7	7.8		7.2	7.4	8.0	7.9	8.1	
Chenopodiaceae	1.9	2.0		1.8	2.6	2.0	1.6	2.0	
Plantago lanceolata	2.4	2.0		2.1	1.9	2.3	1.8	1.9	
Artemisia	1.0	0.8		1.2	1.3	0.7	0.6	1.1	
Sphagnum	1.3	1.0		1.0	1.1	0.9	1.1	0.6	
Others	1.7	1.7		1.4	1.1	2.5	1.5	2.3	
Total	2607	3815		1880	1138	910	1767	812	+
Leguminosae	7.0	5.6	+	10.4	9.4	4.7	3.6	2.3	+

Table 33. Longelse forest. Composition of the exotic pollen. Frequencies in percentage of total exotic pollen. Significance tests according to the χ^2-method

	W	Middle	NE	SE	Significance P 0.5
Gramineae	54.8	47.8	50.5	41.9	+
Pinus	7.8	10.2	13.2	12.7	+
Betula	1.9	5.3	4.0	7.3	+
Cerealia	12.2	10.7	11.3	13.1	
Chenopodiaceae	18.1	18.4	15.7	17.7	
Artemisia	1.5	2.6	2.4	2.9	
Rumex acetosella	1.5	1.9	1.3	2.2	
Plantago lanceolata	0.9	0.6	0.5	1.1	
Others	1.3	2.4	1.0	1.2	+
Total	1172	1293	918	1336	+

Table 34. Draved forest, 386 and 370. Sample number (N), correlation coefficient (r), pollen productivity factor (P), relative pollen deposition at zero crown area ($p_{r(0)}$) and standard error of the relative pollen deposition ($S_{(p_r)}$) for the relative pollen deposition in relation to the crown areas in the 30 m sample plots

	N		r		P($\times 10^2$)		$p_{r(0)}$		$S_{(p_r)}$	
	386	370	386	370	386	370	386	370	386	370
Quercus	47	87	0.73	0.77	0.333	0.339	(0.042)	(−0.077)	±0.803	±0.861
Betula	45	81	0.81	0.77	0.250	0.242	0.243	0.476	±0.303	±0.542
Alnus	46	82	0.72	0.74	0.109	0.220	0.217	0.223	±0.242	±0.418
Fagus	46	(65)	0.81	(0.50)	0.057	(0.068)	0.064	(0.093)	±0.113	(±0.106)
Tilia	46		0.66		0.035		0.042		±0.111	
Fraxinus		86		0.72		0.025		0.041		±0.094

Table 35. Draved forest, 386 and 370. r, P, $p_{r(0)}$ and $S_{(p_r)}$ for the relative pollen deposition in relation to the tree crown areas in the 20 m sample plots

	r		$P(\times 10^2)$		$p_{r(0)}$		$S_{(p_r)}$	
	386	370	386	370	386	370	386	370
Quercus.......	0.79	0.80	0.757	0.620	(0.092)	(0.117)	±0.714	±0.818
Betula	0.80	0.78	0.477	0.453	0.370	0.598	±0.366	±0.527
Alnus	0.79	0.77	0.215	0.422	0.272	0.298	±0.211	±0.398
Fagus.........	0.88	(0.42)	0.101	(0.090)	0.083	0.141	±0.094	(±0.111)
Tilia..........	0.69		0.064		0.061		±0.108	
Fraxinus		0.69		0.048		0.050		±0.097

Table 36. Draved forest, 386 and 370. N, r, P, $p_{r(0)}$ and $S_{(p_r)}$ for the relative pollen deposition in relation to the tree basal areas in the 30 m sample plots

	N		r		P		$p_{r(0)}$		$S_{(p_r)}$	
	386	370	386	370	386	370	386	370	386	370
Quercus..................	47	87	0.66	0.82	0.920	0.888	0.250	0.069	±0.896	±0.577
Betula	46	80	0.73	0.68	0.773	1.008	0.324	0.599	±0.406	±0.548
Alnus..................	46	82	0.74	0.78	0.327	0.798	0.205	0.322	±0.235	±0.388
Fagus.................	46	79 (65)	0.80	0.30 (0.53)	0.167	(0.202)	0.091	(0.121)	±0.118	(±0.104)
Tilia...................	46		0.76		0.111		0.097		±0.097	
Fraxinus		86		0.86		0.125		0.021		±0.069

Table 37. Longelse forest. N, r, P, $p_{r(0)}$ and $S_{(p_r)}$ for the relative pollen deposition in relation to the tree basal areas in the 20 m and the 30 m sample plots

	N	r		P		$p_{r(0)}$		$S_{(p_r)}$	
		20 m	30 m	20 m	30 m	20 m	30 m	20 m	30 m
Quercus . .	39	0.60	0.70	1.083	0.694	0.356	0.074	±0.837	±0.749
Carpinus .	38	0.62	0.64	0.580	0.302	0.268	0.214	±0.251	±0.248
Ulmus . . .	37	0.66	0.75	0.453	0.251	0.218	0.142	±0.220	±0.193
Fagus	39	0.61	0.67	0.181	0.127	0.165	0.121	±0.204	±0.190
Fraxinus .	39	0.43	0.58	0.118	0.103	0.051	−0.001	±0.104	±0.093

Table 38. Draved forest and Longelse forest. Area percentages, pollen percentages and R-values in the 20 m and the 30 m sample plots

Draved Section 386	crown area %		pollen %	R	
	20 m	30 m		20 m	30 m
Quercus	19.41	21.02	40.99	2.11	1.95
Betula	11.10	12.51	25.34	2.28	2.03
Alnus	17.94	18.90	18.53	1.03	0.98
Fagus	21.92	19.57	8.33	0.38	0.43
Tilia	29.63	28.00	6.81	0.23	0.24

Section 370					
Quercus	24.27	23.89	33.17	1.37	1.39
Betula	20.04	20.35	34.53	1.72	1.70
Alnus	17.05	17.11	22.52	1.32	1.32
Fagus	14.80	15.30	5.59	0.38	0.37
Tilia	3.33	2.92	0.86	(0.26)	(0.29)
Fraxinus	20.51	20.42	3.32	0.16	0.16

Longelse	basal area %				
	20 m	30 m			
Quercus	27.95	26.79	46.76	1.67	1.75
Alnus	0.83	1.14	2.21	(2.66)	(1.94)
Carpinus	12.53	14.01	18.53	1.48	1.32
Ulmus	17.24	19.31	17.13	0.99	0.89
Fagus	22.34	20.41	10.94	0.49	0.54
Fraxinus	19.11	18.34	4.44	0.23	0.24

LITERATURE

AARIO, L., 1940. Waldgrenzen und subrezente Pollenspektren in Petsamo, Lappland. Ann. Acad. Scient. Fenn., A, *54*.

ANDERSEN, S. T., 1960. Silicone oil as a mounting medium for pollen grains. Danmarks Geol. Unders., IV, *4*, *1*.

— 1967. Tree-pollen rain in a mixed deciduous forest in South Jutland, Denmark. Rev. Palaeobot. Palynol., *3*, 267–275.

BASTIN, B., 1964. Recherches sur les relations entre la végétation actuelle et le spectre pollinique récent dans la forêt de Soignes (Belgique). Agricultura, *12*, 341–373.

BENT, A. M. and WRIGHT, H. E., 1963. Pollen analyses of surface materials and lake sediments from the Chuska Mountains, New Mexico. Bull. Geol. Soc. America, *74*, 491–500.

BERTSCH, F., 1935. Das Pfrunger Ried und seine Bedeutung für die Florengeschichte Südwestdeutschlands. Beih. Bot. Centralbl., *54*, 185–243.

BOROWIK, M., 1963. The trapping of Scots pine and oak pollen in Białowieża National Park (Summary). Acta Soc. Bot. Pol., *32*, 655–676.

BORSE, C., 1939. Über die Frage der Pollenproduktion, Pollenzerstörung und Pollenverbreitung in ostpreussischen Waldgebieten. Schr. Psysik.-ökonom. Ges. Königsberg, *71*, 127–144.

CARROLL, G., 1943. The use of bryophytic polsters and mats in the study of recent pollen deposition. Amer. Journ. Bot., *30*, 361–366.

COLWELL, R. N., 1951. The use of radioactive isotopes in determining spore distribution patterns. Amer. Journ. Bot., *38*, 511–523.

CUSHING, E. J., 1967. Evidence for differential pollen preservation in late Quaternary sediments in Minnesota. Rev. Palaeobotan. Palynol., *4*, 87–101.

DANISH METEOROLOGICAL INSTITUTE 1951–1965. Meteorologisk Årbog, 1. Del. 1950–1959. Publikationer fra Det Danske Meteorol. Inst., Årbøger, 1950–1959.

DAVIS, M. B., 1963. On the theory of pollen analysis. Amer. Journ. Sc., *261*, 897–912.

— 1965. Phytogeography and palynology of northeastern United States. The Quaternary of the United States, (ed. H. E. Wright, Jr. and David G. Frey), 377–401. Princeton.

— 1967. Pollen accumulation rates at Rogers Lake, Connecticut during late- and postglacial time. Rev. Palaeobot. Palynol., *2*, 219–230.

DENGLER, A., 1955. Über den Pollenflug und seine Ausfilterung innerhalb von Waldbeständen. Zs. Forstgenetik, *4*, 110–113.

DIMBLEBY, G. W., 1962. The development of British heathlands and their soils. Oxford Forestry Mem., *23*.

ELSIK, W. C., 1966. Biologic degradation of fossil pollen grains and spores. Micropaleont., *12*, 515–518.

ERDTMANN, G., 1943. Pollenspektra från svenska växtsamhällen jämte pollen-analytiska markstudier i södra Lappland. Geol. Fören. Stockholm Förhandl., *65*, 37–66.

FÆGRI, K., 1947. Heterodokse tanker om pollenanalysen. Geol. Fören. Stockholm Förhandl., *69*, 55–66.

FÆGRI,.K and IVERSEN, J., 1950. Textbook of modern pollen analysis. Copenhagen.

FÆGRI, K. and IVERSEN, J., 1964. Textbook of pollen analysis. Copenhagen.

FAGERLIND, F., 1952. The real signification of pollen diagrams. Bot. notiser, 1952, 185–224.

FIRBAS, F., 1949. Waldgeschichte Mitteleuropas. 1. Band. Jena.

FIRBAS, F. und SAGROMSKY, H., 1947. Untersuchungen über die Grösse des jährlichen Pollenniederschlags vom Gesichtspunkt der Stoffproduktion. Biol. Zentralbl., *66*, 129–140.

GEIGER, R., 1966. The climate near the ground. Cambridge, Massachusetts.

GREGORY, P. H., 1961. The microbiology of the atmosphere. London and New York.

GROSSE-BRAUCKMANN, G. und STIX, E., 1968. Kontinuierliche Bestimmungen des Pollen- und Sporengehaltes der Luft. Ber. Deutsh. Bot. Ges., *81*, 528–534.

GULDAGER, P., 1967. Nogle undersøgelser af pollenspredning og blomstringsforhold i en lærkefrøhave. Licentiatafhandl., Kgl. Vet. og Landbohøjskole.

HANSEN, H. P., 1949. Pollen contents of moss polsters in relation to forest composition. American Midland Naturalist, *42*, 473–479.

HAVINGA, A. J., 1964. Investigation into the differential corrosion susceptibility of pollen and spores. Pollen Spores, *6*, 621–637.

— 1967. Palynology and pollen preservation. Rev. Palaeobot. Palynol., *2*, 81–98.

HEIM, J., 1963. Recherches sur les relations entre la végétation actuelle et le spectre pollinique récent dans les Ardennes Belges. Bull. Soc. Roy. Bot. Belg., *96*, 5–92.

HESMER, H., 1933. Die natürliche Bestockung und die Waldentwicklung auf verschiedenartigen märkischen Standorten. Zs. Forst- u. Jagdwesen, *65*, 515–651.

IVERSEN, J., 1947. Discussion in: Nordiskt kvartärgeologiskt möte den 5.–9. november 1945. Geol. Fören. Stockholm Förhandl., *69*, 205–206.

— 1949. The influence of prehistoric man on vegetation. Danm. Geol. Unders., IV, *3*, *6*.

— 1958. Pollenanalytischer Nachweis des Reliktencharakters eines jütischen Linden-Mischwaldes. Veröff. Geobot. Inst. Rübel, Zürich, *33*, 137–144.

— 1964. Retrogressive vegetational succession in the Post-Glacial. Journ. Ecol., *52*, (Suppl.), 59–70.

JANSSEN, C. R., 1966. Recent pollen spectra from the deciduous and coniferous-deciduous forests of northeastern Minnesota: A study in pollen dispersal. Ecology, *47*, 804–825.

— 1967. A comparison between the recent regional pollen rain and the sub-recent vegetation in four major vegetation types in Minnesota (U. S. A.). Rev. Palaeobot. Palynol., *2*, 331–342.

JESSEN, K., 1920. Moseundersøgelser i det nordøstlige Sjælland. Danm. Geol. Unders., II, *34*.

JØRGENSEN, S., 1954. A pollen analytical dating of Maglemose finds from the bog Aamosen, Zealand. Danm. Geol. Unders., II, *80*, 159–187.

JONASSEN, H., 1950. Recent pollen sedimentation and Jutland heath diagrams. Dansk Bot. Arkiv, *13*, *7*.

KING, J. E. and KAPP, R. O., 1963. Modern pollen rain studies in eastern Ontario. Can. Journ. Bot., *41*, 243–257.

KRAL, F., 1968. Pollenanalytische Untersuchungen zur jüngeren Waldgeschichte des Dunkelsteiner Waldes. Centralbl. Ges. Forstwesen, *85*, 206–222.

KRIŽO, M., 1963. Shedding of pollen and its transport in forest trees. I. Pollen shedding in the fir (*Abies alba*, Mill.). (Summary). Acta Univ. Agriculturae, Brno, C, 1963, 189–206.

— 1964. Shedding of pollen and its transport in forest trees. II. Pollen shedding in the spruce (*Picea excelsa* Link.), pine (*Pinus silvestris* L.), and beech (*Fagus silvatica* L.). (Summary). Acta Univ. Agriculturae, Brno, C, 1964, 277–288.

KRIŽO, M., 1966. Pollenniederschlag und Transport bei den Waldbäumen. III. Pollenniederschlag der Eiche (*Quercus* sp.), Birke (*Betula* sp.) und Hainbuche (*Carpinus betulus* L.). Acta Univ. Agricult. Brno, C, *35*, 325–337.

LANGNER, W., 1952. Die diagnostische Bedutung eines *aurea*-Faktors bei *Picea abies* für die genetisch wirksame Pollenverbreitung. Zs. Forstgenetik, *2*, 21–22.

LEIBUNDGUT, H. und MARCET, E. 1953. Pollenspektrum und Baumartenmischung. Beobachtungen über den Pollenniederschlag auf dem Ütliberg bei Zürich im Jahre 1950. Schweiz. Zs. Forstw., *104*, 594–611.

LICHTI-FEDEROVICH, S. and RITCHIE, J. C., 1965. Contemporary pollen spectra in central Canada, 2. The forest-grassland transition in Manitoba. Pollen Spores, *7*, 63-87.

LIVINGSTONE, D. A., 1968. Some interstadial and postglacial pollen diagrams from Eastern Canada. Ecolog. Monographs, *38*, 87–125.

MAHER, L. J., 1963. Pollen analyses of surface materials from the southern San Juan Mountains, Colorado. Bull. Geol. Soc. Amer., *74*, 1485-1504.

MIKKELSEN, V. M., 1949. Præstø Fjord. Dansk Bot. Arkiv, *13*.

MOSIMANN, J. E., 1965. Statistical methods for the pollen analyst: Multinomial and negative multinomial Techniques. Handbook of Paleontological Techniques (ed. B. Kummel and D. Raup). San Francisco and London.

MÜLLER, P., 1937. Das Hochmoor von Etzelwill. Ber. Geobot. Forschungsinst. Rübel, Zürich, 1936, 85–106.

MULLENDERS, W., 1962. Les relations entre la végétation et les spectres polliniques en Forêt du Mont-Dieu (Département des Ardennes, France). Bull. Soc. Roy. Bot. Belgique, *94*, 131–138.

OGDEN, E. C., RAYNOR, G. S. and VORMEVIK, J. M., 1964. Travels of airborne pollen. New York State Mus. and Sc. Serv. Progr. Rep. *5*.

PERSSON, A., 1955. Frequenzen von Kiefernpollen in Südschweden 1953 und 1954. Zs. Forstgenetik, *4*, 129-136.

POHL, F., 1930. Kittstofreste auf der Pollenoberfläche windblütiger Pflanzen. Bot. Centralbl., *46*.

— 1933. Freilandversuche zur Bestäubungsökologie der Stieleiche. Beih. Bot. Centralbl. *51*, *1*, 673–692.

— 1937. Die Pollenerzeugung der Windblütler. Beih. Bot. Centralbl. *56*, *1*, 365–470.

POP, E., 1967. Some aeropalynological remarks and conclusions in the south Carpathian mountains. Rev. Palaeobot. Palynol., *4*, 233–241.

VON POST, L., 1916. Skogsträdpollen i sydsvenska torfmosselagerföljder. Geol. Fören. Stockh., Förhandl., *38*, 384–394.

— 1918. Skogträdpollen i sydsvenska torvmosselagerföljder. Forh. 16. skand. naturforskermöte 1916, 433–465. Kristiania.

POTTER, L. D. and ROWLEY, J., 1960. Pollen rain and vegetation, San Augustin Plains, New Mexico. Bot. Gazette, *122*, 1–25.

RAYNOR, G. S., SMITH, M. E., SINGER, J. A., COHEN, L. A. and HAYES, J. V., 1966. The dispersion of ragweed pollen into a forest. 7th Nat. Conf. Agricult. Meteor. of Amer. Meteor. Soc. New Brunswick, New Jersey.

REMPE, H., 1937. Untersuchungen über die Verbreitung des Blütenstaubes durch die Luftströmungen. Planta, *27*, 93–147.

RITCHIE, J. C. and LICHTI-FEDEROVICH, S., 1963. Contemporary pollen spectra in central Canada. 1. Atmospheric samples at Winnipeg, Manitoba. Pollen Spores, *5*, 95–114.

SCHMIDT, F. H., 1967. Palynology and Meteorology. Rev. Palaeobot. Palynol. *3*, 27–45.

STATENS LUFTFARTSVÆSEN., 1963. Aeronautical Climatology of Denmark. 1949–1958. IV. Statens Luftfartsvæsen. Civil Aeronautical Meteorological Division. Copenhagen.

STEINBERG, K., 1944. Zur spät- und nacheiszeitlichen Vegetationsgeschichte des Untereichsfeldes. Hercynia, *3*, 529–587.

STRAKA, H., 1960. Zwei postglaziale Pollendiagramme aus dem Hinkelsmaar bei Manderscheid (Vulkaneifel). Decheniana, *112*, 219–241.

TAUBER, H., 1965. Differential pollen dispersion and the interpretation of pollen diagrams. Danm. Geol. Unders., II, *89*.

— 1967. Investigations of the mode of pollen transfer in forested areas. Rev. Palaeobot. Palynol., *3*, 277–286.

TROELS-SMITH, J., 1954. Pollenanalytische Untersuchungen zu einigen schweizerischen Pfahlbauproblemen. Das Pfahlbau-Problem, 11–64. Schaffhausen.

TSUKADA, M., 1958. Untersuchungen über das Verhältnis zwischen dem Pollengehalt der Oberflächenproben und der Vegetation des Hochlandes Shiga. Journ. Inst. Polytechn. Osaka City Univ., D, *9*, 217–234.

WRIGHT, H. E., MCANDREWS, J. H. and VAN ZEIST, W., 1967. Modern pollen rain in western Iran, and its relation to plant geography and Quaternary vegetational history. Journ. Ecol., *55*, 415–443.

WRIGHT, J. W., 1952. Pollen dispersion of some forest trees. Northeast Forest Explor. Sta., Paper *46*. Forest Serv. U.S. Dept. Agricult.

PLATE I

Draved forest, section 386. Transects A and B. Tree crown areas in the 30 m sample plots and pollen frequency as relative pollen deposition (in relation to the exotic pollen total). + = sample with more than 50 % corroded pollen grains

PLATE I

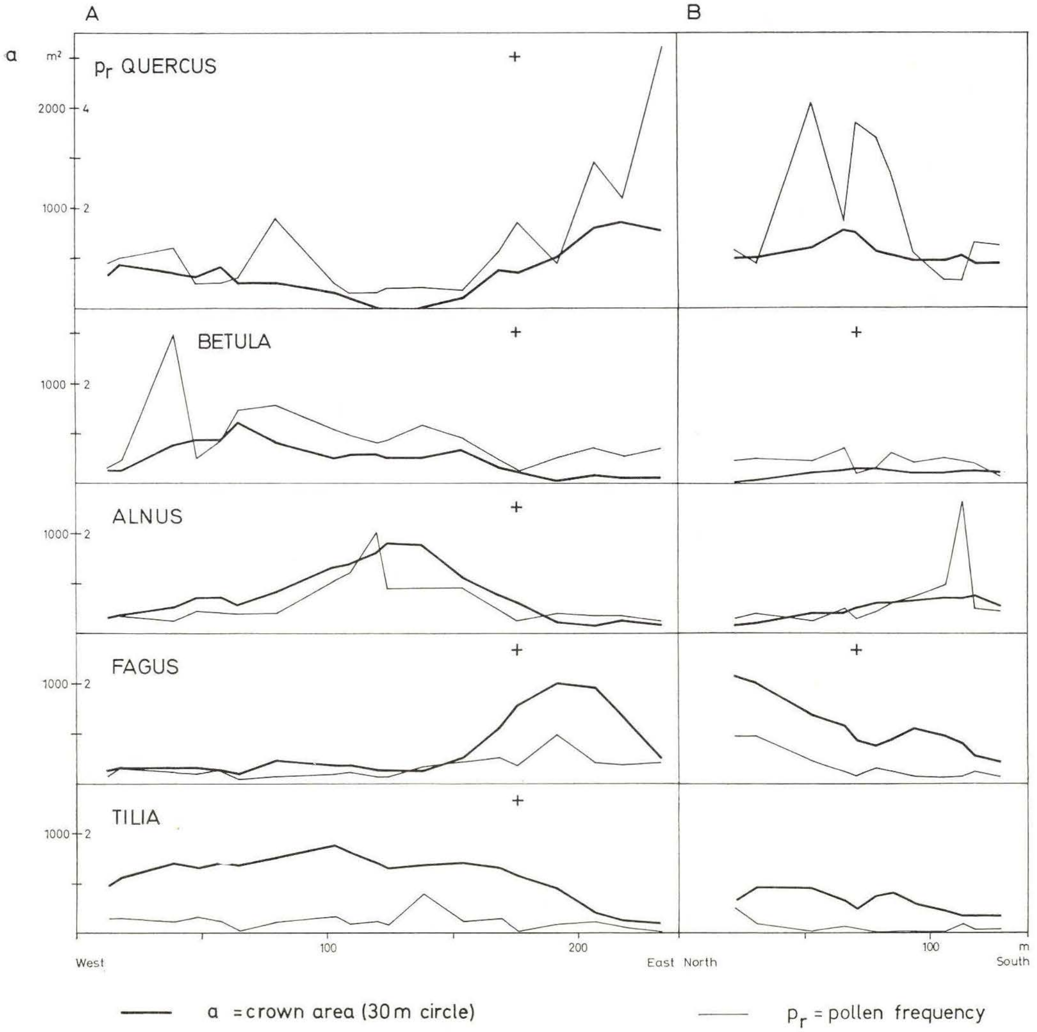

A
B
a
m²
2000 – 4
1000 – 2
p_r QUERCUS
BETULA
ALNUS
FAGUS
TILIA
+
100
200
West
East
North
South
m
a = crown area (30 m circle)
p_r = pollen frequency

PLATE II

Draved forest, section 370. Transects A, B and C. As PLATE I.

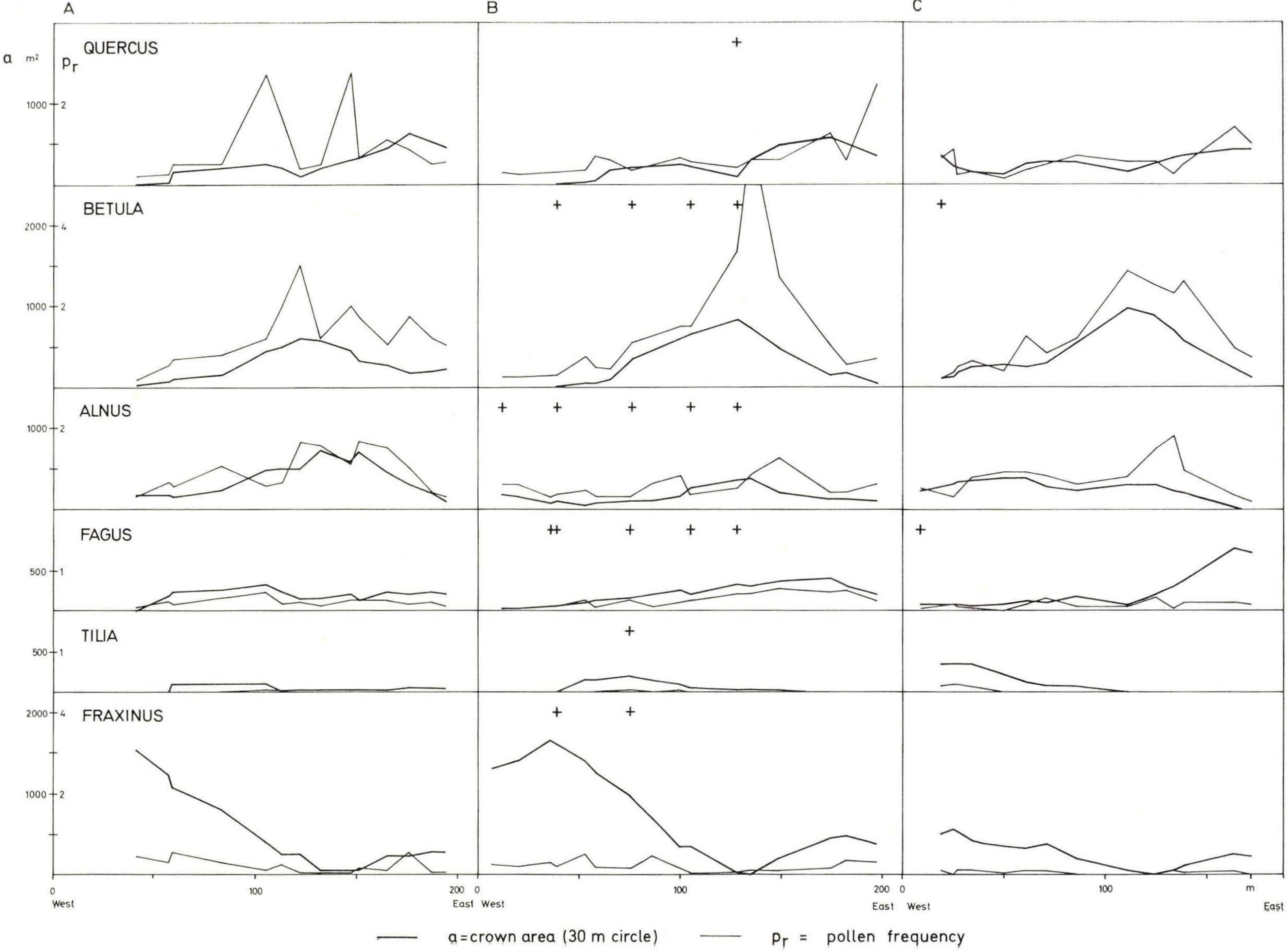

A
B
C
a m²
p_r
QUERCUS
1000 — 2
BETULA
2000 — 4
1000 — 2
ALNUS
1000 — 2
FAGUS
500 — 1
TILIA
500 — 1
FRAXINUS
2000 — 4
1000 — 2
0 West
100
200 East
0 West
100
200 East
0 West
100
m East
a = crown area (30 m circle)
p_r = pollen frequency

PLATE II

PLATE III

Draved forest, 386. Pollen frequencies and crown areas in the 30 m sample plots. Calculated regression lines with 2 standard error limits. p_r = relative pollen deposition. N = sample number. r = correlation coefficient. + = sample with "overrepresentation"

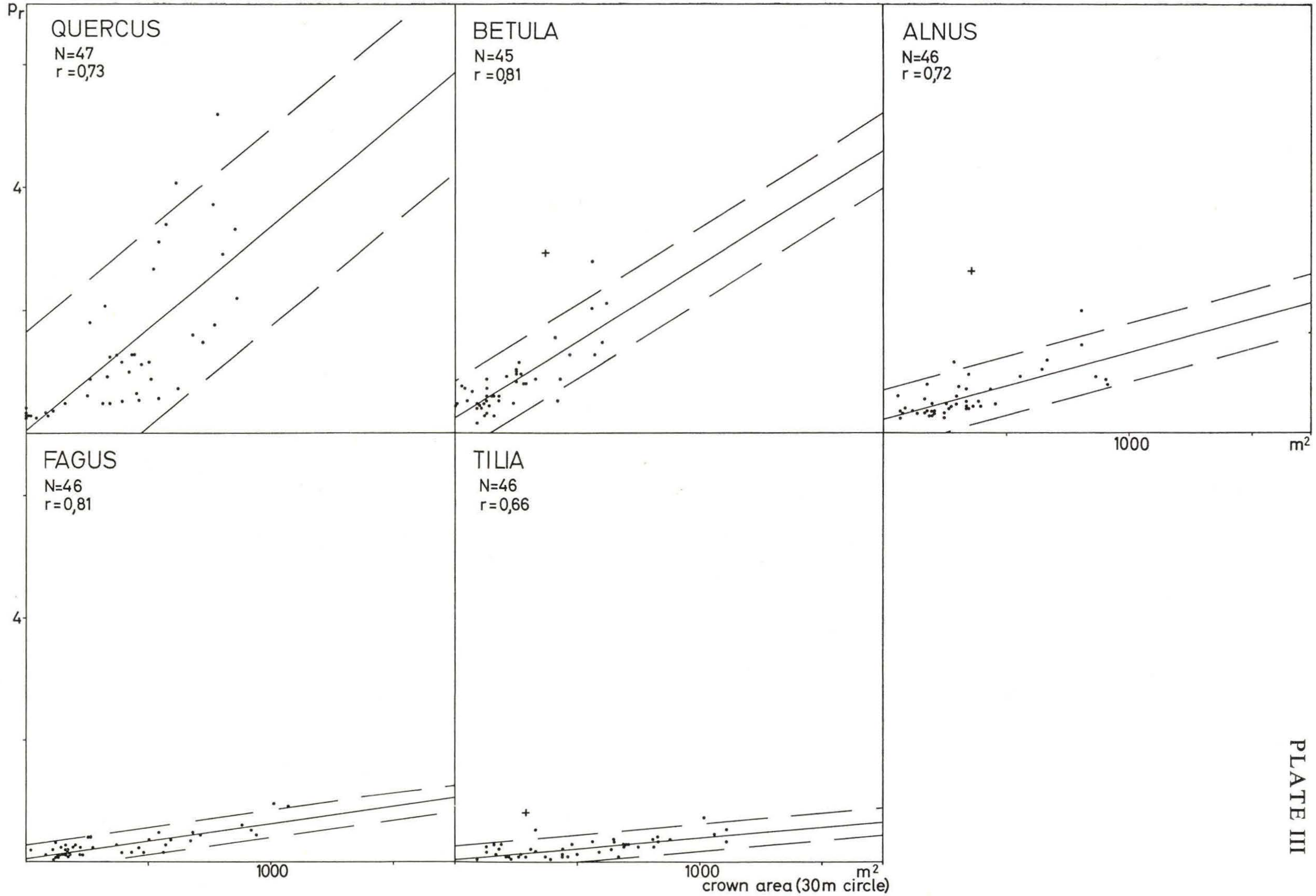

Pr
4
QUERCUS
N=47
r =0,73
BETULA
N=45
r =0,81
ALNUS
N=46
r =0,72
+
1000
m²
4
FAGUS
N=46
r=0,81
1000
TILIA
N=46
r=0,66
+
1000
m²
crown area (30m circle)

PLATE III

PLATE IV

Draved forest, 370. As PLATE III.

⊙ = sample from the southeastern part of the section

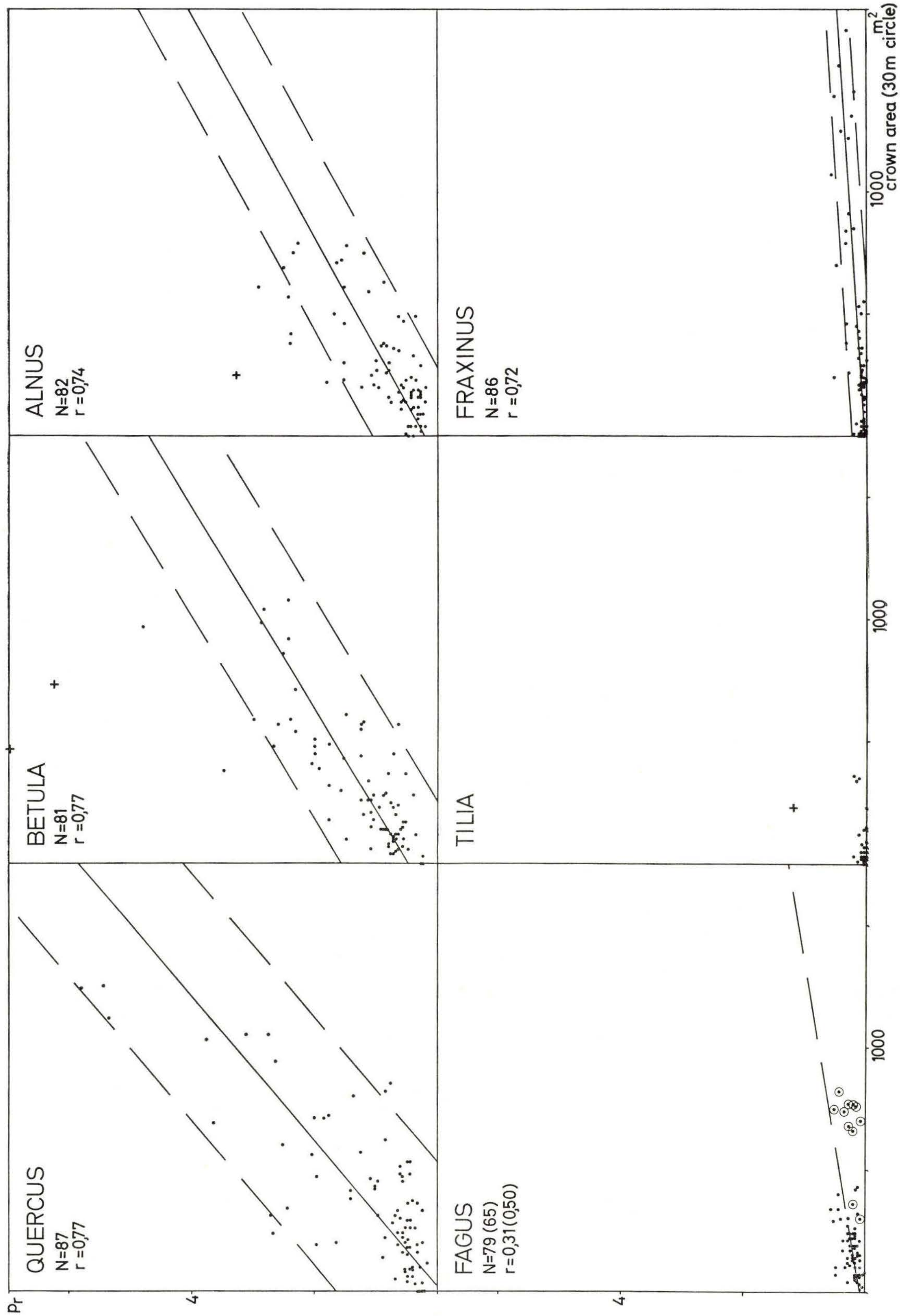

QUERCUS
N=87
r =0,77
BETULA
N=81
r =0,77
ALNUS
N=82
r =0,74
FAGUS
N=79 (65)
r=0,31(0,50)
TILIA
FRAXINUS
N=86
r =0,72
Pr
4
4
1000
1000
1000
m^2
crown area (30m circle)

PLATE V

Longelse forest. Transect. Tree basal areas in the 30 m sample plots and pollen frequency as relative pollen deposition. More than 50% corroded grains occurred in the sample at 173 m (in *Quercus*, *Ulmus* and *Fagus*)

PLATE V

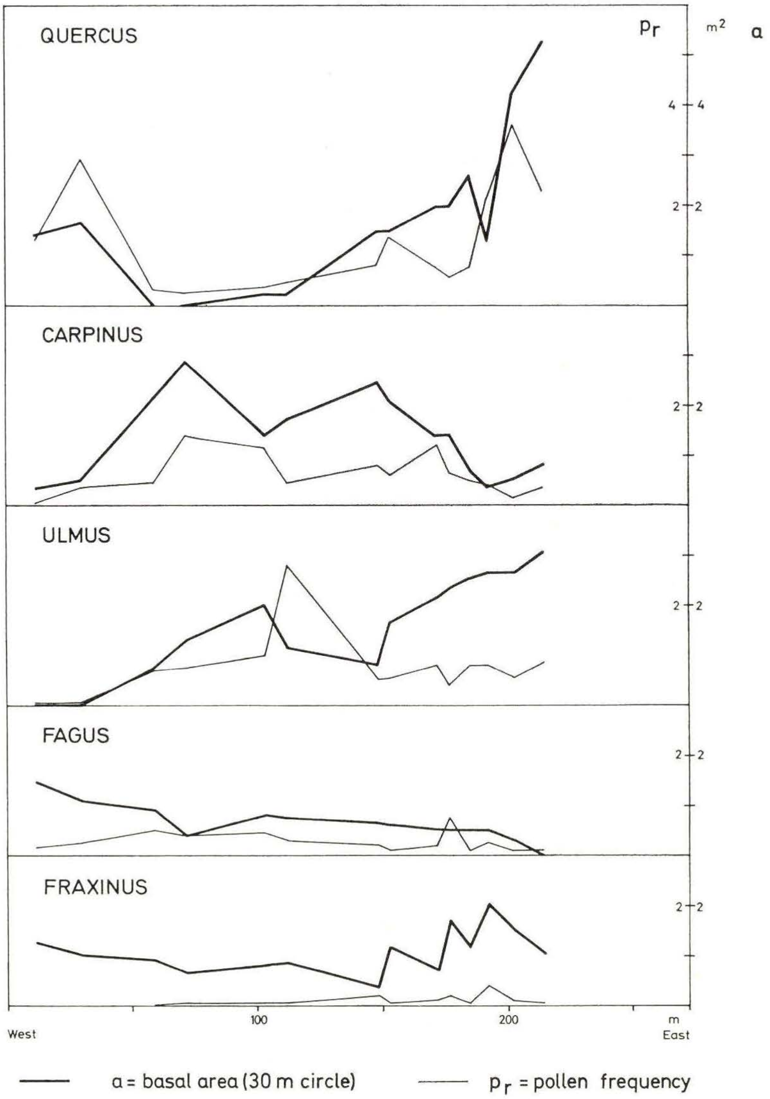

QUERCUS
pr
m²
a
4
4
2
2
CARPINUS
2
2
ULMUS
2
2
FAGUS
2
2
FRAXINUS
2
2
West
100
200
m
East
a = basal area (30 m circle)
pr = pollen frequency

PLATE VI

Longelse forest. Pollen frequencies and tree basal areas in the 30 m sample plots. Regression lines with 2 standard error limits. p_r = relative pollen deposition. N = sample number. r = correlation coefficient. + = sample with "overrepresentation". ○ = sample with more than 50% corroded grains

PLATE VI

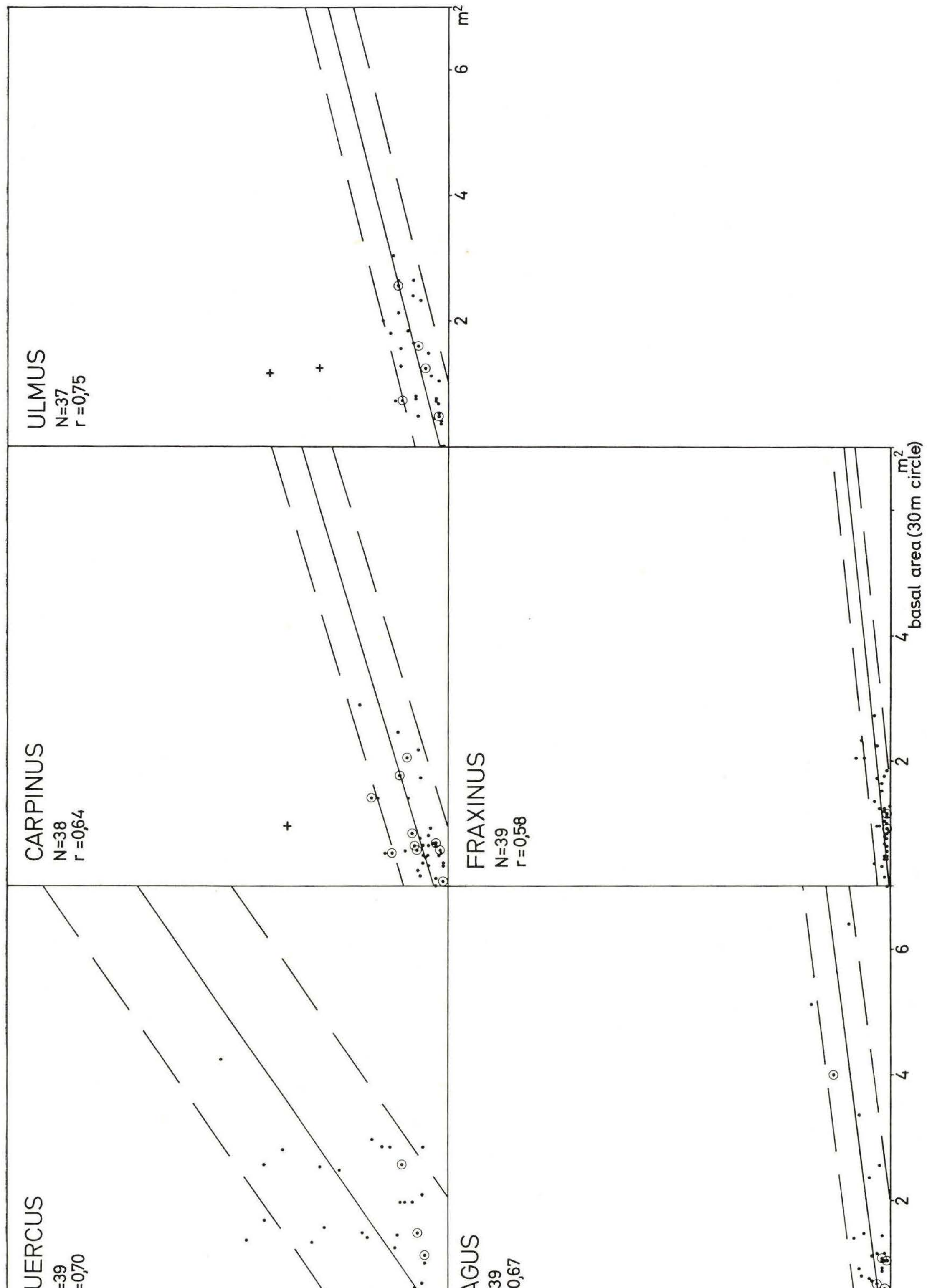
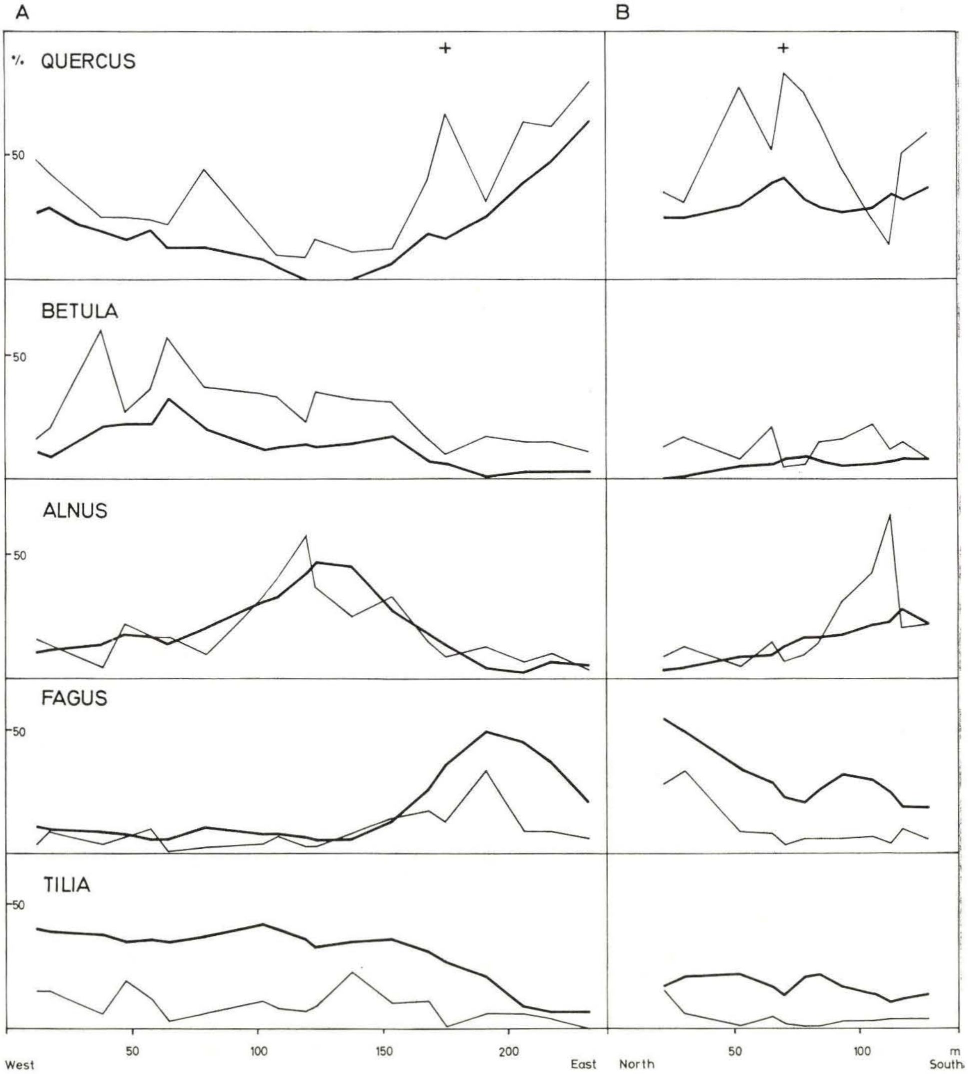

QUERCUS
N=39
r =0,70
FAGUS
N=39
r =0,67
CARPINUS
N=38
r =0,64
FRAXINUS
N=39
r =0,58
ULMUS
N=37
r =0,75
Pr
4
4
2
4
6
m²
2
4
6
m²
2
4
m²
basal area (30 m circle)

PLATE VII

Draved forest, 386. Transects A and B. Pollen frequencies as percentages of the tree pollen totals and areal frequencies as percentages of the total crown areas in the 30 m sample plots.



— crown area, % (30m circle) — pollen frequency, % of AP

PLATE VIII

Draved forest, 370. Transects A, B and C. As PLATE VII.

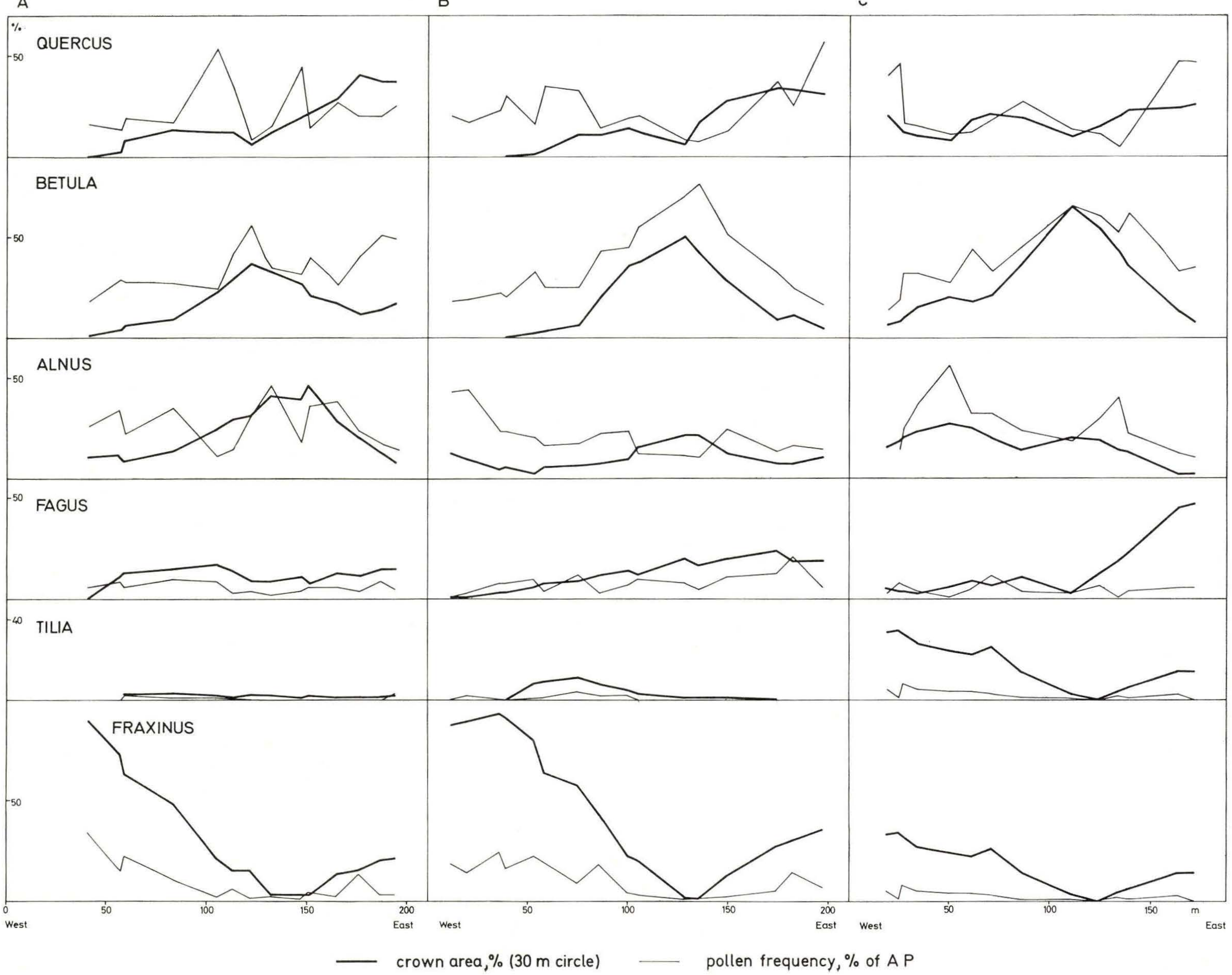

A
B
C
%
50
QUERCUS
BETULA
50
ALNUS
50
50
FAGUS
40
TILIA
FRAXINUS
50
0
50
100
150
200
West
East
West
50
100
150
200
East
West
50
100
150
m
East
crown area,% (30 m circle)
pollen frequency, % of A P

PLATE VIII

PLATE IX

Longelse forest. Transect. Areal frequencies as percentages of the total basal areas in the 30 m sample plots, otherwise as PLATE VII

PLATE IX

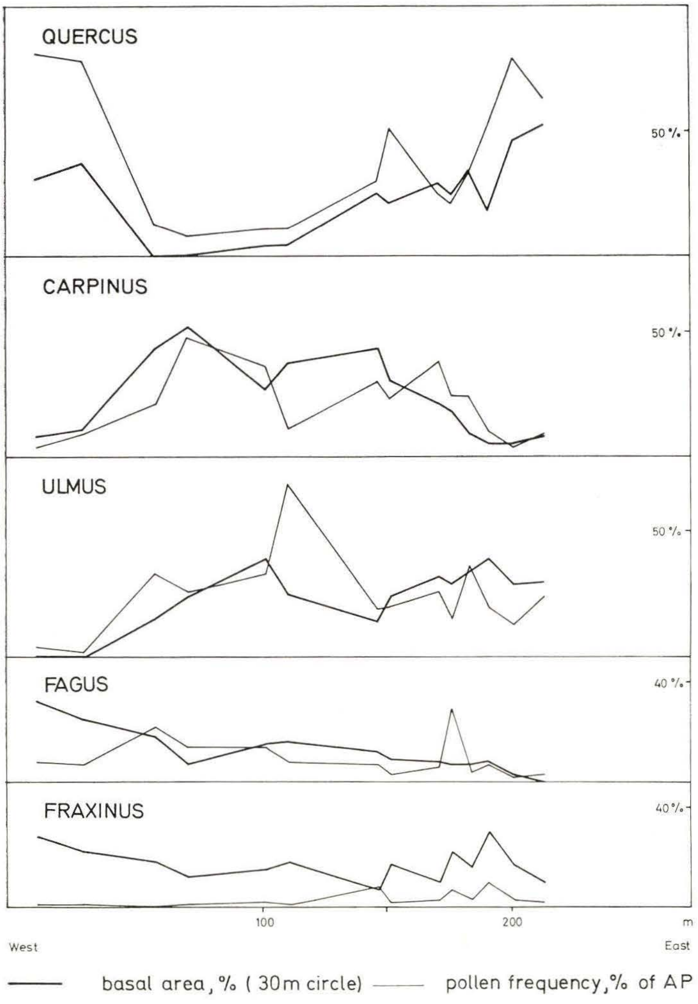
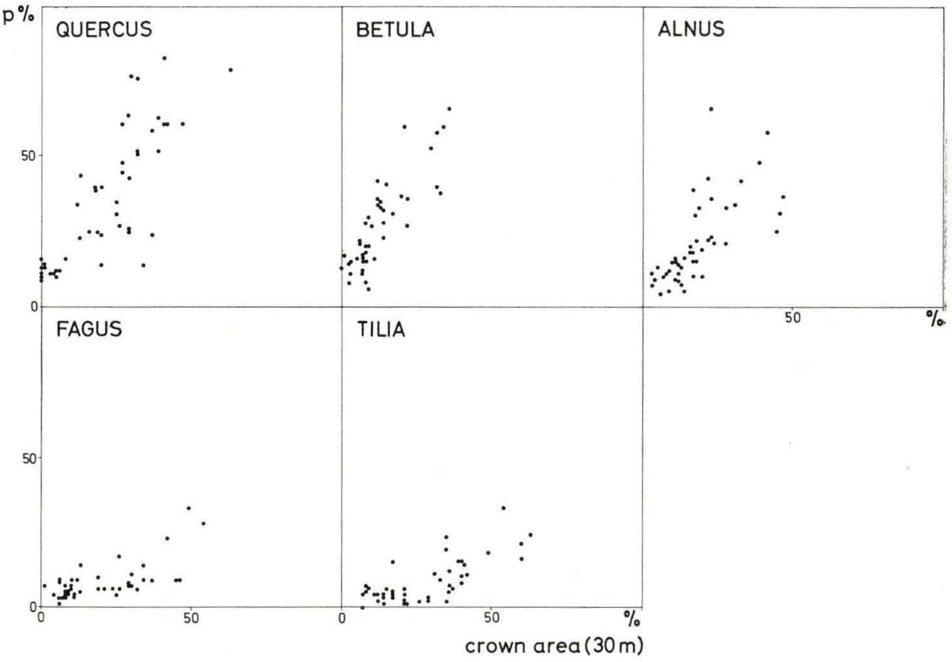

QUERCUS
50 %
CARPINUS
50 %
ULMUS
50 %
FAGUS
40 %
FRAXINUS
40 %
100
200
m
West
East
basal area, % (30m circle)
pollen frequency, % of AP

PLATE X

Draved forest, 386 (above) and 370 (below). Pollen frequencies as percentages of the tree pollen totals and areal frequencies as percentages of the total crown areas in the 30 m sample plots. p = pollen frequency

PLATE X


p %
QUERCUS
BETULA
ALNUS
FAGUS
TILIA
50
0
50
0
0
50
0
50
50
%
%
crown area (30 m)

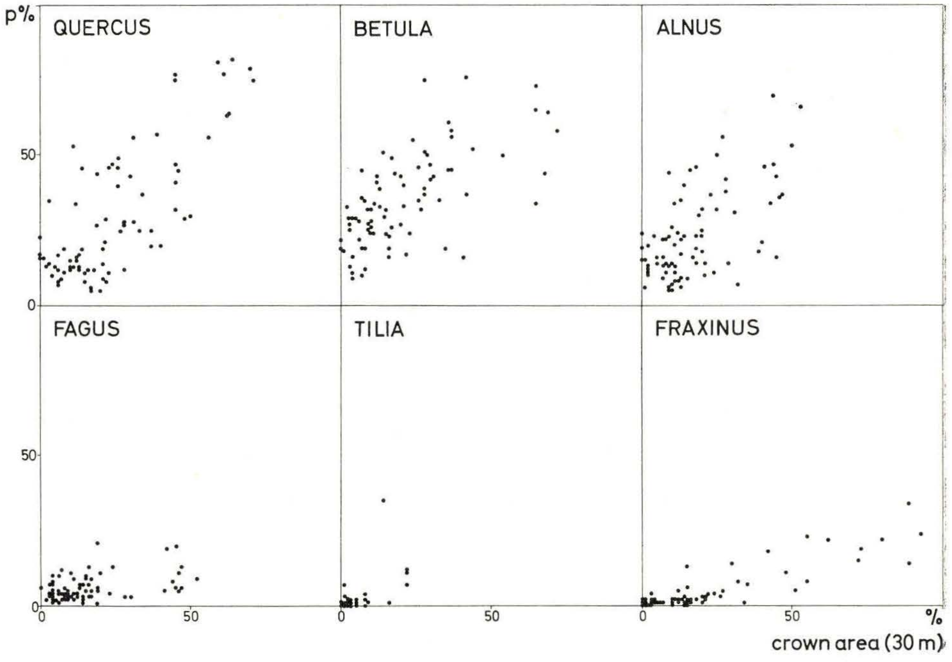

p %
QUERCUS
BETULA
ALNUS
FAGUS
TILIA
FRAXINUS
50
0
50
0
0
50
0
50
0
50
%
crown area (30 m)

PLATE XI

Longelse forest. Areal frequencies as percentages of the total basal areas in the 30 m sample plots, otherwise as PLATE X

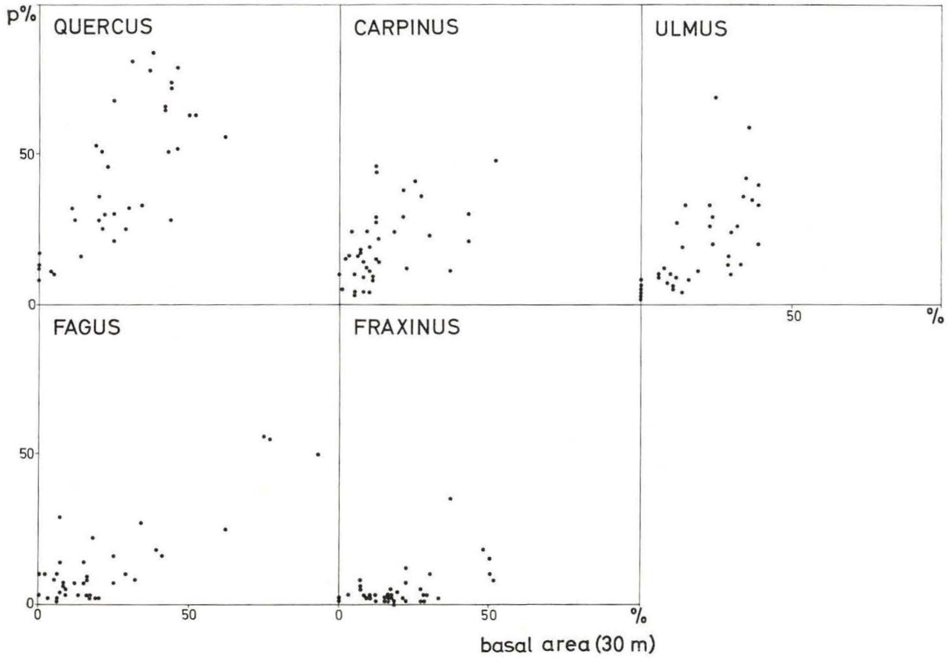

p%
QUERCUS
CARPINUS
ULMUS
FAGUS
FRAXINUS
50
0
50
0
0
50
0
50
50
%
%
basal area (30 m)

PLATE XII

Draved forest, 386. Transects A and B. Corrected pollen frequencies as percentages of the corrected tree pollen totals and areal frequencies as percentages of the total crown areas in the 30 m sample plots. + = sample with more than 50% corroded grains

PLATE XII

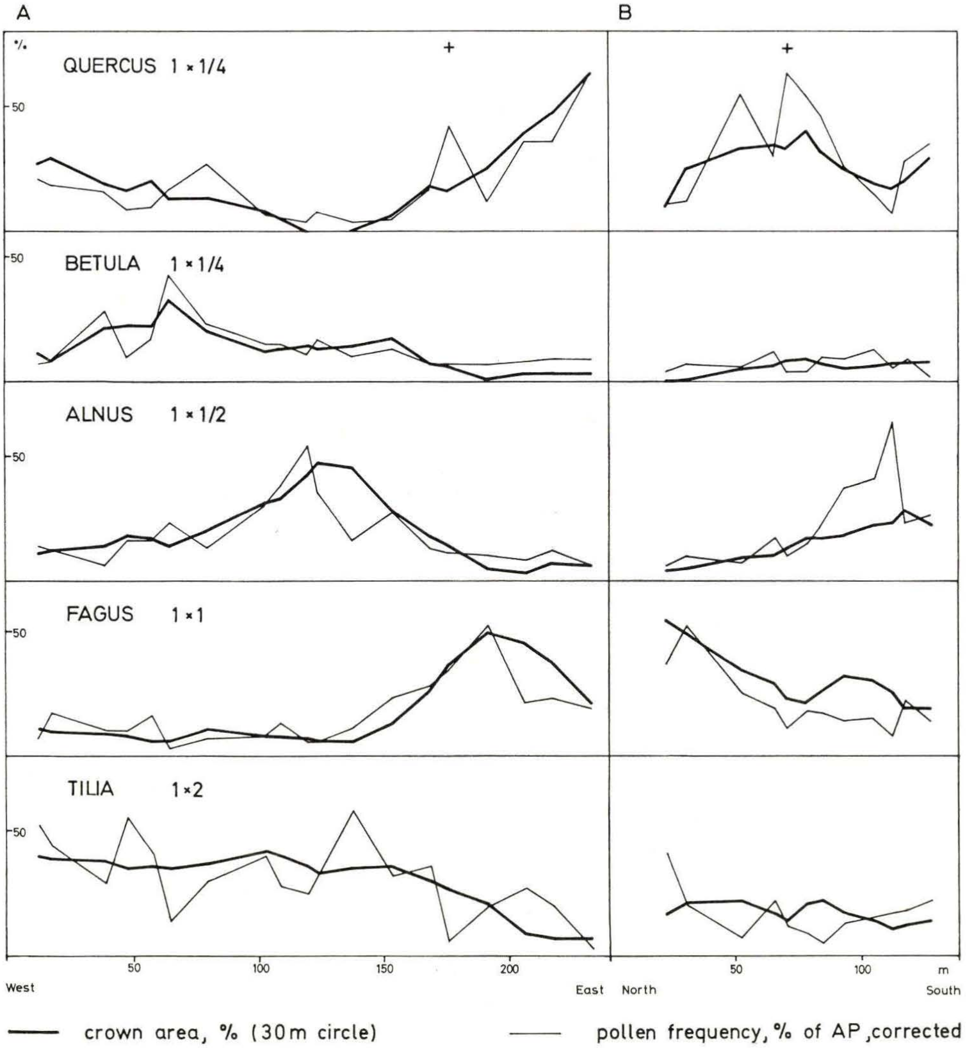

A
B
%
QUERCUS 1 × 1/4
BETULA 1 × 1/4
ALNUS 1 × 1/2
FAGUS 1 × 1
TILIA 1 × 2
50
+
+
50
100
150
200
West
East
North
50
100
m
South
crown area, % (30m circle)
pollen frequency, % of AP, corrected

Plate XIII
Draved forest, 370. Transects A, B and C. As Plate XII

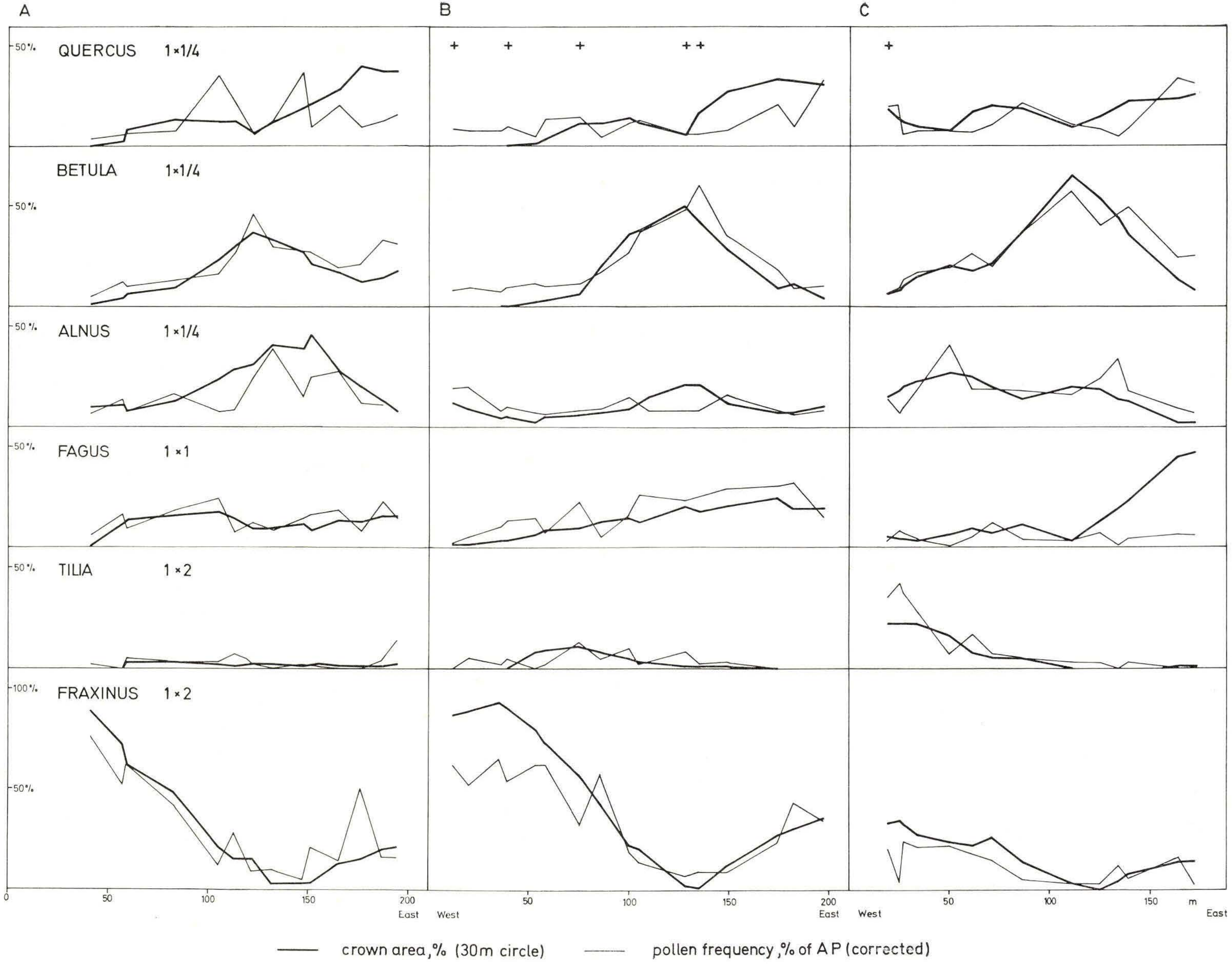

A
B
C
QUERCUS 1×1/4
BETULA 1×1/4
ALNUS 1×1/4
FAGUS 1×1
TILIA 1×2
FRAXINUS 1×2
50 %
100 %
+ + + + +
+
0
50
100
150
200
East
West
m
crown area, % (30m circle)
pollen frequency, % of AP (corrected)

PLATE XIII

PLATE XIV

Longelse forest. Transect. Areal frequencies as percentages of the total basal areas in the 30 m sample plots, otherwise as PLATE XII

PLATE XIV

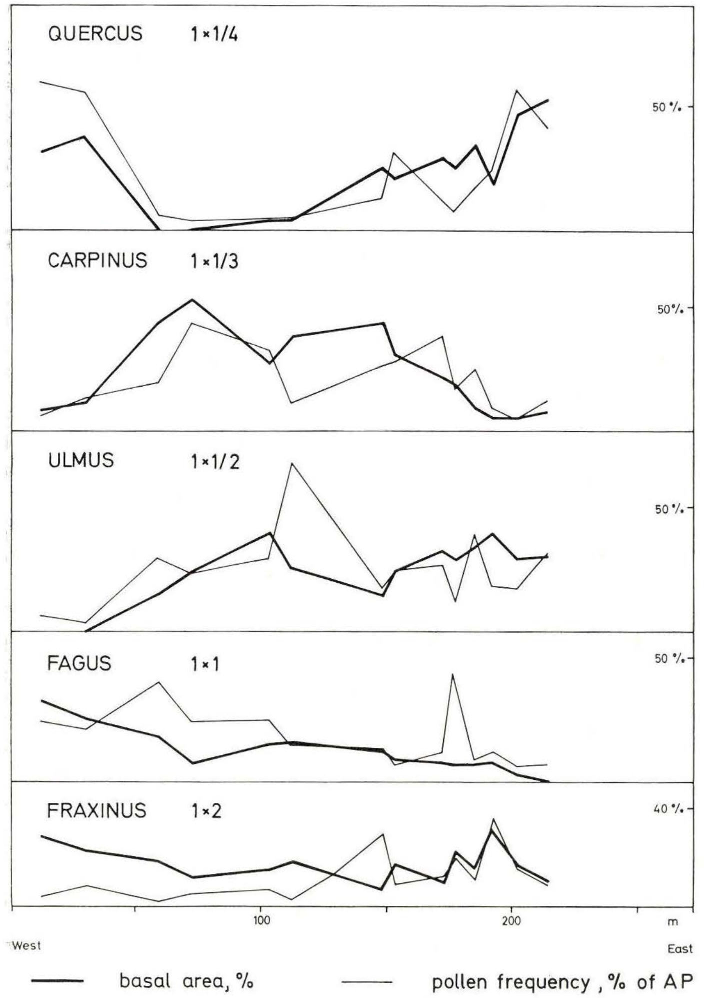
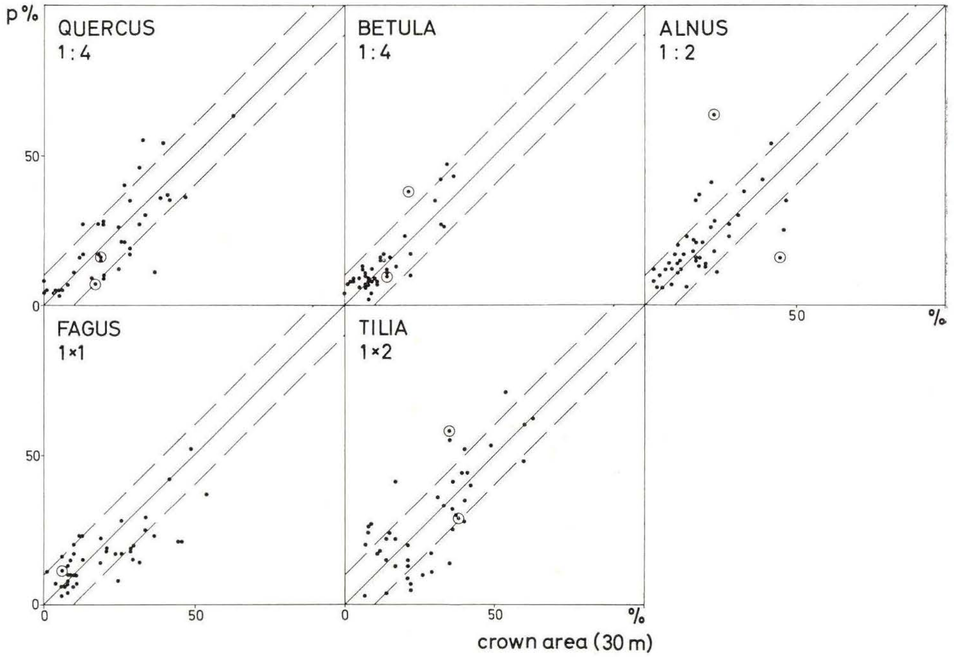

QUERCUS 1×1/4
50 %
CARPINUS 1×1/3
50 %
ULMUS 1×1/2
50 %
FAGUS 1×1
50 %
FRAXINUS 1×2
40 %
100
200
m
West
East
basal area, %
pollen frequency, % of AP

PLATE XV

Draved forest, 386 (above) and 370 (below). Corrected pollen frequencies as percentages of the corrected tree pollen totals and areal frequencies as percentages of the total crown areas in the 30 m sample plots. The straight lines indicate equal pollen and areal frequencies with ± 10% confidence intervals. p = pollen frequency. ⊙ = sample with "overrepresentation"

PLATE XV


p%
QUERCUS
1:4
BETULA
1:4
ALNUS
1:2
FAGUS
1×1
TILIA
1×2
50
0
0
50
0
50
50
%
crown area (30 m)

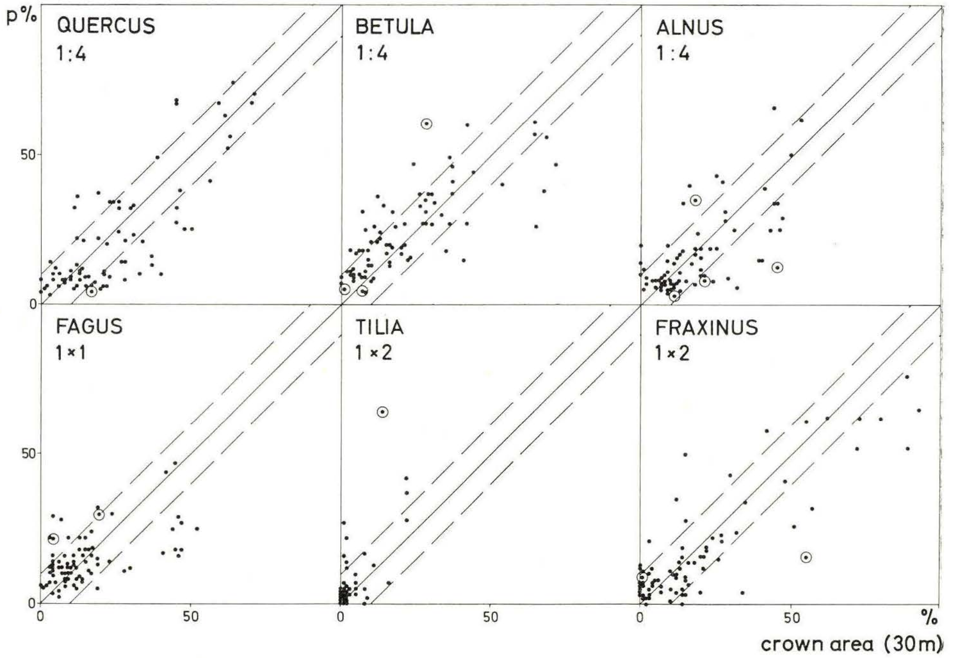
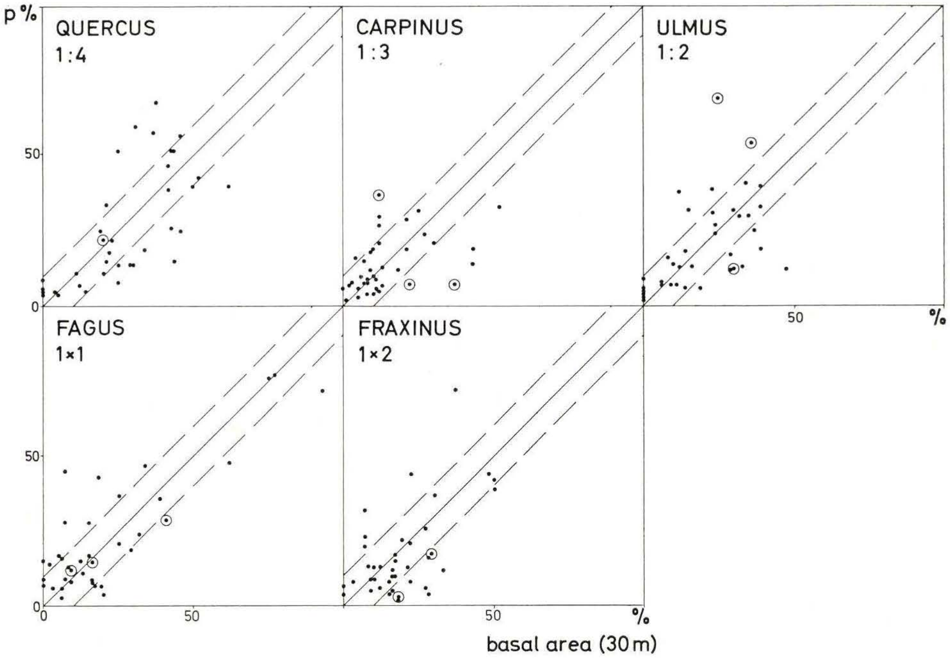

p%
QUERCUS
1:4
BETULA
1:4
ALNUS
1:4
FAGUS
1×1
TILIA
1×2
FRAXINUS
1×2
50
0
0
50
0
50
0
50
%
crown area (30m)

PLATE XVI

Longelse forest. Areal frequencies as percentages of the total basal areas in the 30 m sample plots, otherwise as PLATE XV

Draved forest, 370. *Corylus* in the transects A, B and C. Crown cover as percentages of the areas of 10 m sample plots and pollen frequencies as percentages of the corrected tree pollen total. + = sample with more than 50 % corroded pollen grains. One sample in transect B (at 36 m) with a very high pollen frequency (96 %) presumably due to "overrepresentation" was omitted


p %
QUERCUS
1:4
CARPINUS
1:3
ULMUS
1:2
FAGUS
1×1
FRAXINUS
1×2
50
0
50
%
0
50
50
%
basal area (30 m)

2

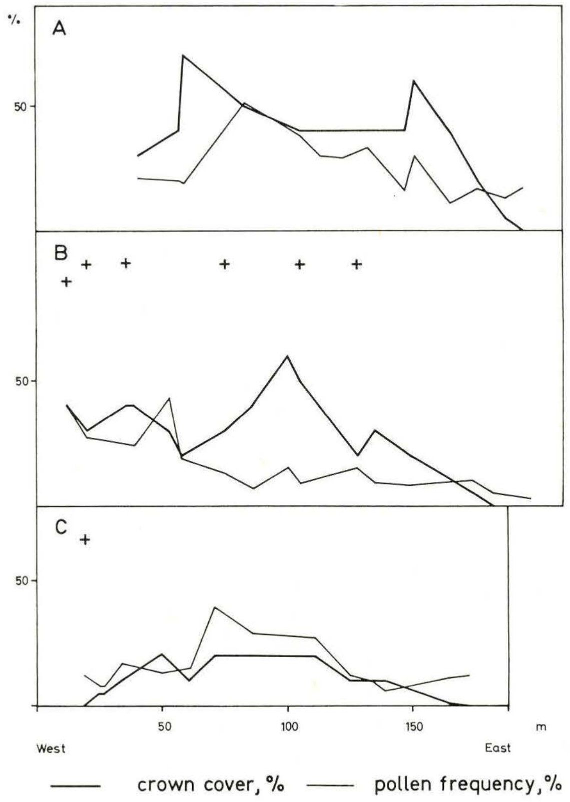

%
A
50
B
50
C
50
50
100
150
m
West
East
crown cover, %
pollen frequency,%

PLATE XVII

Draved forest, 386. Transects A and B. Herbaceous forest plants. White columns: Coverage percentages. Black columns: Pollen frequencies as percentages of the corrected tree pollen totals. + = presence of the species

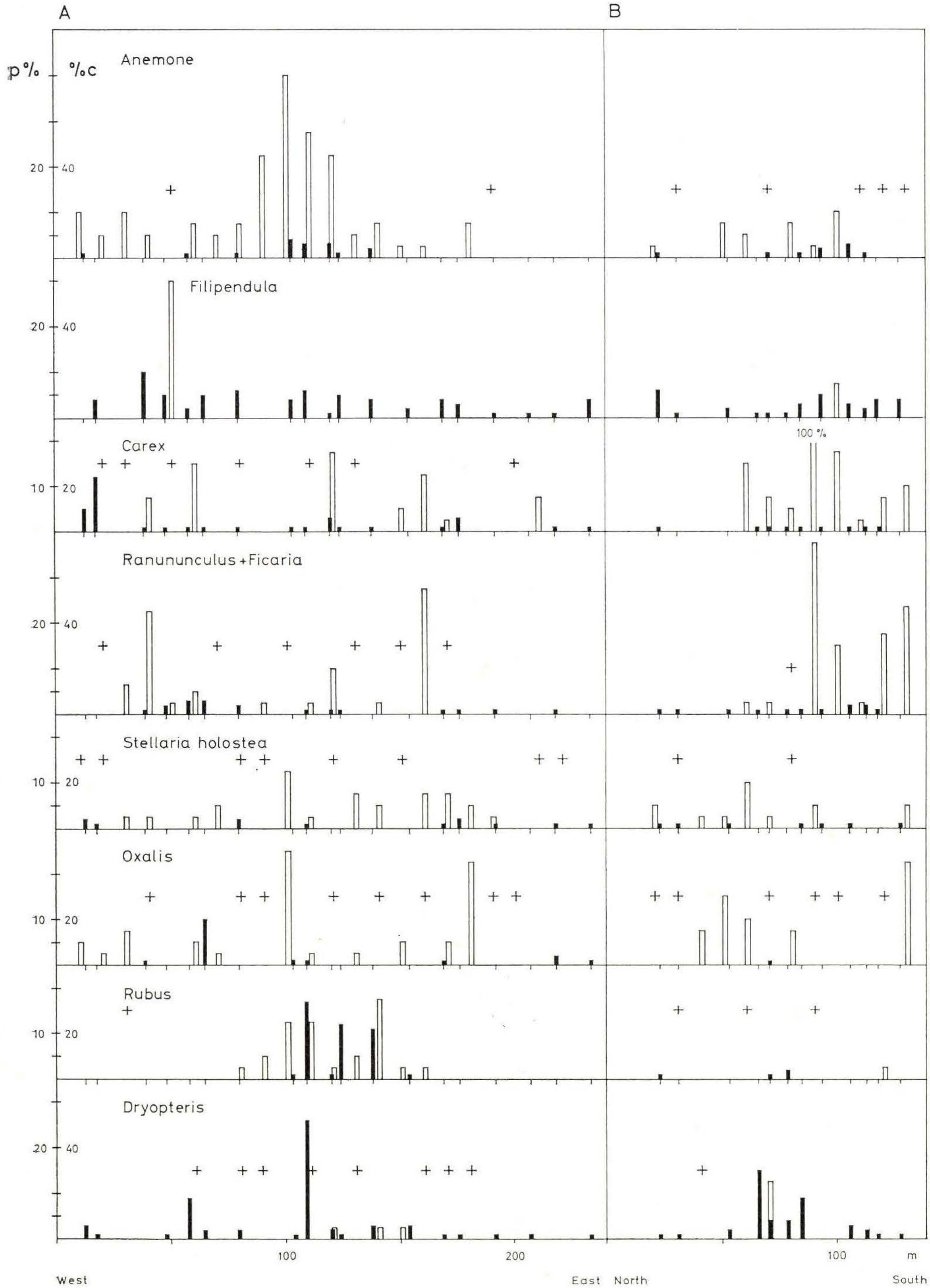
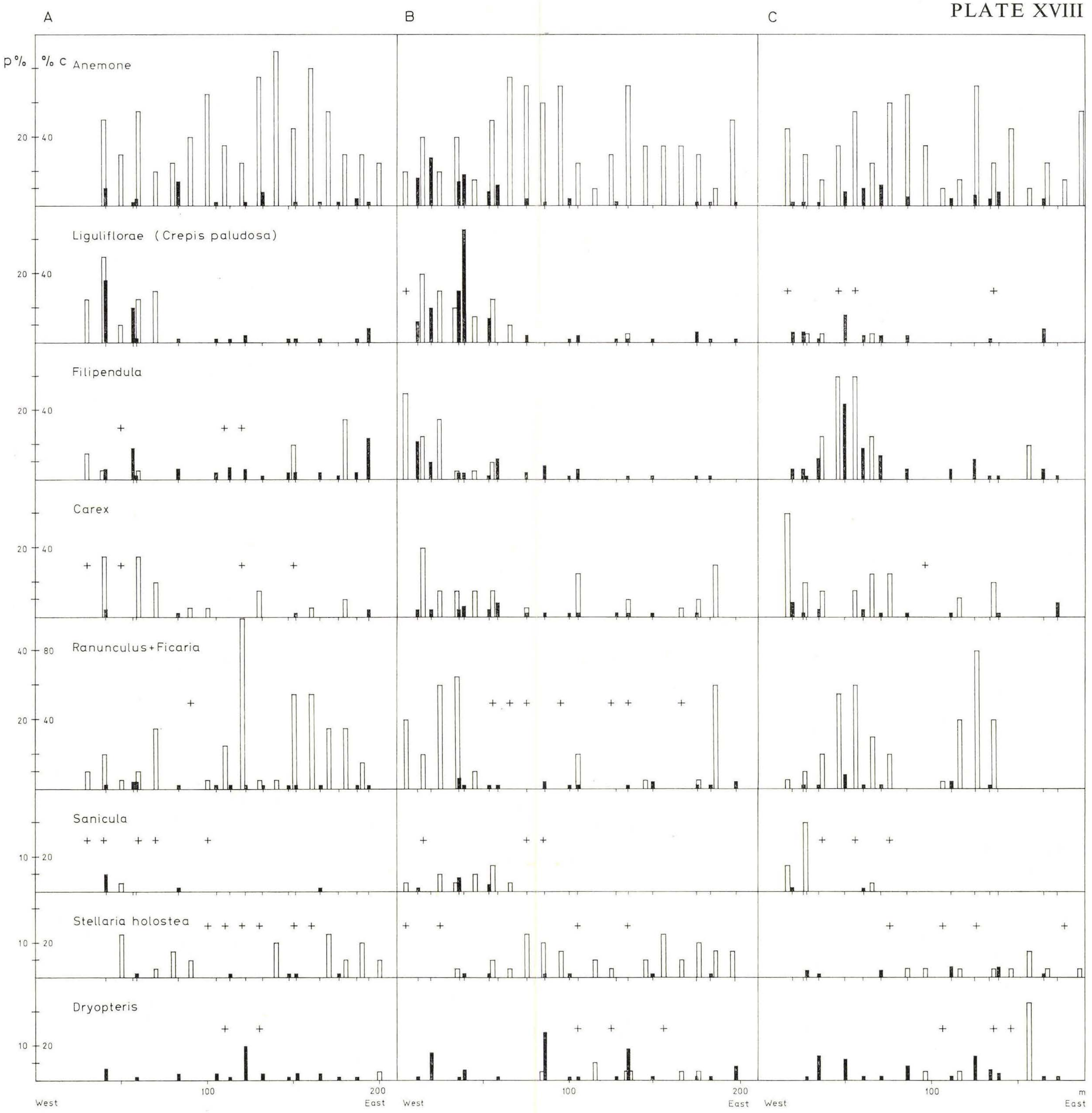

A
B
p%
%c
Anemone
20
40
Filipendula
20
40
Carex
10
20
100 %
Ranununculus + Ficaria
20
40
Stellaria holostea
10
20
Oxalis
10
20
Rubus
10
20
Dryopteris
20
40
100
200
100
m
West
East
North
South

PLATE XVIII
Draved forest, 370. Transects A, B and C. As PLATE XVII

PLATE XVIII


A
B
C
p %
% c
Anemone
20
40
Liguliflorae (Crepis paludosa)
Filipendula
Carex
Ranunculus+Ficaria
40
80
Sanicula
10
Stellaria holostea
Dryopteris
100
200
m
West
East