Forest development, soil genesis and human activity illustrated by pollen and hypha analysis of two neighbouring podzols in Draved Forest, Denmark

BY

Bent Aaby

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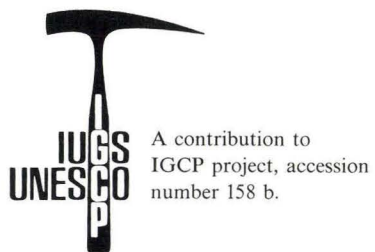
By
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Vignet: *Viscum album* pollen.
By *Ingeborg Frederiksen*

Contents

Abstract

A small investigation area, located in an old natural *Fagus-Quercus* forest, was selected for an analysis of vegetational development, soil genesis, human activity, and interaction between the processes. Podzol soils dominate the investigation area. The thickness of the humus cover varies between 5-52 cm. Two sections were excavated and material collected for pedological and microfossil analysis. Sites only 7 m apart were chosen to illustrate short-distance similarities and dissimilarities in soil development and pollen representation. Sediment accumulation curves are constructed on the basis of historical information on changes in forest composition dating back to AD 1750. Older sediments are dated from their pollen content, assuming a constant pollen influx, similar to the period AD 1750-1980. The accumulation curves reach back to the Subboreal and to the Middle Ages respectively. Relative and absolute pollen diagrams are constructed to show forest development. Concentration diagrams are calculated for the period prior to AD 1750, and an influx diagram covers the period AD 1750-1980.

A primeval *Tilia* forest dominated the area until Late Subboreal, when human interference is first detected in one of the diagrams. Leaf-hay gathering by shredding, which did not substantially change the forest composition, was practiced until late in the Middle Ages, and the mixed *Tilia* vegetation persisted until about AD 1650 when the *Tilia* trees were felled and succeeded by a *Quercus-Fagus-Betula* vegetation which has dominated the area since. Changes in the use of the forest caused the death of the *Tilia* forest. *Viscum album* was present in Draved Forest until the eradication of its host. The presence of *Viscum* in the 16th-18th centuries indicates that this species tolerates lower summer temperature than earlier supposed.

Comparison of the two percentage diagrams shows significant differences in pollen frequency, although the sites are located only 7 m apart. Similar pollen influx rates were calculated for both sites AD 1750-1980. The mean total pollen influx amounted to about 44000 pollen $cm^{-2}year^{-1}$ or 12-15000 APcorr. $cm^{-2}year^{-1}$. Distinct influx variations were recognized within smaller time units.

Two types of pollen deterioration, corrosion and thinning, were distinguished and their influence on the pollen spectra analysed. The conclusion being that the pollen spectra are only slightly influenced by pollen deterioration, and differential pollen destruction does not seem to be an important source of error in pollen analysis from the raw humus stage, the arthropod humus stage, and the lumbricid humus stage. Pollen destruction was important only in the lumbricid humus stage, and both types of pollen deterioration are involved.

Fungal hypha analysis includes total length measurements as well as the relative size distribution of hypha fragments. Litter composition strongly influences the annual growth of brown-coloured hyphae. The rate of litter decomposition is another important factor. The hypha production was slow in the lumbricid humus stage and accelerated in the arthropod- and raw humus stages. Hypha fragments in the soil show characteristic length-frequency distributions which indicate comminution by macro- and microarthropods during burial.

The investigation has demonstrated a close relationship between soil development, forest composition and human activity. Anthropogenic disturbance and a changing forest composition accelerate soil development, which is also depending on lithology and topography. The development of a podzol was completed within a period of only 300 years in one of the sections, while it took more than 2000 years to reach the same state of maturity at the other site, only 7 m away.

The investigation are in forest part 365. Old *Fagus Sylvatica-Quercus* robur vegetation.

Introduction

In recent years attention has been paid to pollen analytical studies of terrestrial soils to obtain information about successions of forest ecostystems. Andersen (1970) has shown that pollen sampled from the woodland floor originates chiefly from the surrounding 20-30 m and, because the pollen source area is very restricted, the level of spatial detail is high. In particular, small hollows with gyttja or peat deposits, and podzols with deep humus layers accumulated in the course of centuries or millennia, have furnished much knowledge about forest development on dry soil (e.g. Iversen 1964, 1969; Andersen 1973, 1978a, 1979; Dimbleby 1962; Guillet 1970; Smith and Taylor 1969; O'Sullivan 1973; Birks l982). In addition, these studies are of great importance for the interpretation of pollen diagrams from larger open sites, such as lakes and bogs, that serve as primary sites for the description of past regional vegetation. Open sites are recommended as reference sites for the IGCP project no. 158 (Berglund l979), but the large pollen-source areas associated with such sites renders a detailed reconstruction and description of the spatial vegetational pattern on the upland impossible. Pollen diagrams from open sites, representing the regional vegetation should therefore be supplemented with forest diagrams to illuminate also local plant distributions and soil conditions.

The interpretation of pollen diagrams from podzols necessitates close consideration of the processes contributing to the development of the pollen profiles, eg. mixing of pollen into the soil as a result of biological activities, downwash of pollen, (differential) deterioration and destruction of pollen. These processes have been illuminated in recent years, but relatively seldom have the profiles been located within the same pollen-source areas. It has therefore been difficult to fully establish controls for the mentioned processes. In the present study, two podzols, located only 7 m apart, have been investigated. Since soil genesis was asynchronous at the two sites, the effects of the deterioration, etc. on pollen of the same age found in different soil stages could be compared with confidence.

Dating the soil matrix in which the pollen grains are found is one of the difficult tasks to overcome in describing vegetational development from podzol pollen analysis. Sharpenseel (1971) has reviewed the problems of

instability and mobility of humus carbon in soil profiles, particularly in podzols, and questioned the validity of radiocarbon dates from such sites. Despite serious problems, humus horizons were dated in order to try to establish a time scale for vegetation history and soil development (Cruickshank and Cruickshank 1981, Hassko et al. 1969). The soil matrix in the present study is dated from historically documented vegetational changes and from its pollen content. The constant pollen influx method, previously used to date Eemian sediments (Dabrowski 1971), is based on the assumption that the amount of pollen deposited per time unit in the past was similar to that found today, and that the pollen stratigraphy was not disturbed after deposition. These demands are assumed to be also fulfilled in the present study, and the sediments belonging to the raw humus and arthropod humus stages have been dated by this method.

The present study attempts to continue the research on forest history, soil genesis and human activity in Draved Forest, that was initiated by the late Johs. Iversen and published up until 1971. Pollen analytical investigations were previously concentrated in the western part of the forest where deep humus layers are present. Hence, little was known about the eastern part. The research was originally started to improve the basis for the development of a nature conservation plan for parts of the forest.

Material and methods

Draved Forest is located in SW Jutland, 10 km N of Tønder and 20 km from the North Sea (fig. 1). The annual precipitation at the Draved meteorological station is about 830 mm (1952-1978, range of variation, 530-1240 mm) and the mean annual temperature 7.4°C, July temperature 15.4°C, and January temperature 0.3°C (Løgumkloster, 1886-1925). The forest covers about 200 ha mainly with deciduous trees. The substrate is dominated by fertile till from the Saalian or aeolian sand blown in from the surrounding outwash plains during the Weichselian.

Forest part 365 is found in the eastern part of the forest with the oldest stands in the forest, dominated by a mixed *Fagus-Quercus* vegetation (fig. 2). The small investigation area, 36x30 m is located in the center of forest part 365.
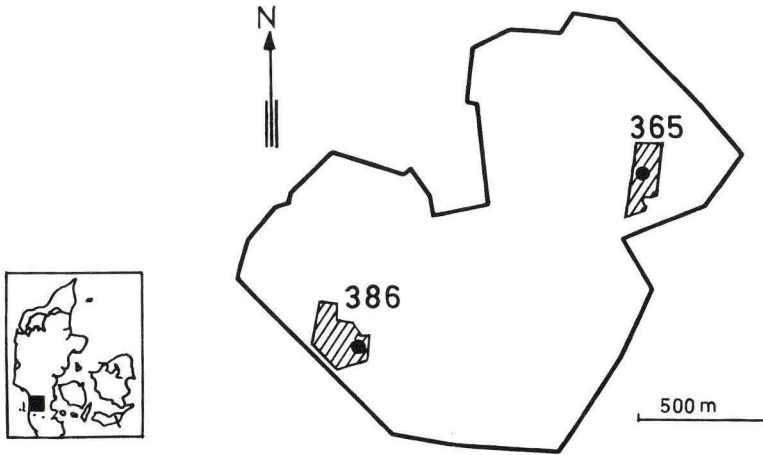
Fig. 1. Locality map showing Draved Forest in SW-Denmark, forest parts 365 and 386 and the positions of the investigated areas.

Field techniques

Present vegetation. A 2x2 m grid was established in the 36x30 m investigation area and all trees and shrubs were measured. The ground flora was analysed by noting the taxa present within a radius of 0.5 m from the 270 crosspoints in the grid.

The diameter of the trees was measured at 1.3 m above the ground. At the same level, samples for counting tree-rings were taken from three *Fagus* and three *Quercus* trees, by use of hand-operated drilling equipment. The ages of the trees were estimated by adding 10 years to the measured age. The projection of the tree crown area on the ground was measured by direct inspection in the field.

Lithology. At each of the cross-points in the grid, a boring was made with hand-operated drilling equipment to determine the composition and the stratigraphy of the uppermost soil layers. Only a few borings were more than 1 m deep.

A systematic, overall survey of the geology of Draved Forest had previously been undertaken by Sigurd Hansen, State Geologist at the Geological Survey of Denmark, making use of hand-operated drilling equipment. The depth of each boring was 1 m and the survey-grid was about 40x40m. The map showing the thickness of the aeolian sand layer (fig. 7), is based on this work.

The present humus types were mapped by Johs. Iversen, State Geologist at the Geological Survey of Denmark, and his colleagues in 1963. The vegetation and the pedology was analysed at intervals of 30-40 m. Only superficial soil samples were inspected for the purpose (fig. 6).

Sampling from sections. A 1 m deep and ca. 2.5 m long section was excavated at two sites, sections 365:1 and 365:2. Parts of the sections were selected for detailed studies of the stratigraphy and lithology. Samples for pollen analysis, measurements of physical properties, etc. were collected from vertical monoliths. The uppermost humus layer, which was coherent due to a relatively low content of inorganic matter, was cut out of the profile as an entire monolith (surface area 20x20 cm), wrapped in plastic, and frozen. Samples with a higher content of inorganic matter were collected directly form the profile as 10x10x1.5 (2.0) cm samples and stored in plastic caps for laboratory treatment.

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Laboratory techniques

Sample slicing. The upper coherent humus layer was deep frozen for 2-3 days and then sliced vertically into two subcolumns. One was stored for reference, while the other was cut horizontally into samples of 1.0 or 1.5 cm thickness by a hand-operated saw. The freezing procedure facilitates a high slicing accuracy, as the ice stabilizes the sediment, and solid tree roots and twigs are easily cut without displacing the adjacent, less stable material. Only stones cause trouble. In addition, a high degree of accuracy in volumetric measurements can be secured. Here, volumetric calculations were based on measurements from frozen material, as the volume of frozen samples does not differ significantly from that of unfrozen material in cases where, as here, the sediments are not water saturated.

Physical properties. Fresh samples were dried for 24 hours at 100°C and ignited at 550°C. The degree of humification was measured by a colorimetric determination of an alkaline extract of the sediment. The alkali absorption is proportional to the amount of humic matter dissolved and the degree of humification was calculated relative to a humic acid standard (Bahnson in Aaby and Tauber 1975). The dry density in the coherent humus was calculated from volumetric determination of the frozen sample and measurement of the weight after drying at 24 hours at 100°C. The sediment volume of the mineral soil samples was measured by filling a box with sediment and exerting an artificial compaction. The accuracy in determining the sediment volume by this procedure is supposed to be fairly good as sediment elasticity was low. The procedures for dry density, ignition residue, and degree of humification measurements are in accordance with the proposed standards for the IGCP project no. 158 (Aaby 1979).

Pollen analysis. All samples used for pollen analysis were subjected to uniform chemical treatment (Fægri and Iversen 1964). The material was mounted in silicone oil, the slides were kept unsealed, and all measurements were made shortly after preparation. About 1000 tree pollen (AP) were identified, in addition to non arboreal pollen and spores (NAP). About 5-15 *Lycopodium* tablets were added for concentration measurements, each tablet containing c. 12500 *Lycopodium clavatum* spores (Stockmarr 1971).

The pollen diagrams. The tree pollen values are calculated relative to the corrected tree pollen sum (APcorr.). The within-forest correction factors proposed by Andersen (1970, 1978a, 1980) have been adapted here for several reasons: first, these values were based on investigations made in Draved

Forest, as is the present study; second, the crown coverage in the forest areas studied by Andersen (op. cit.) was similar to that in the present investigation area; and finally, mature forest sites were studied in both cases. The Andersen (op. cit.) correction factors are:

Alnus, Betula, Corylus, Quercus and *Pinus*	x0.25
Carpinus	x0.33
Ulmus and *Picea*	x0.50
Fagus	x1.00
Tilia, Fraxinus, and *Acer*	x2.00

Hedera and *Viscum* were tentatively treated like *Tilia*. Introduction of correction factors for NAP has not been attempted, as their pollen production and dispersal can vary considerably depending on light conditions, wind velocity etc. Accordingly, the NAP is shown relative to the total number of pollen and spores(P). The tree pollen types are devided into two categories, local and exotic, depending on the species have been present within the pollen source area.

The herbaceous pollen flora is grouped into ecological categories and pollen types which may originate from other or more than one of the mentioned categories are classified as 'uncertain'. Only the most important species are mentioned in the diagrams, either as separate pollen curves or by letters in column 'DIV'. The letters refer to the species-key in the percentage diagrams, and they all represent percentage values below 0.5 % of P. Pollen types not mentioned in the diagrams are shown in appendix 1 and 2. The pollen sum of each ecological category is shown in column 'TOTAL'.

Absolute pollen values have not been corrected and they are calculated as grains g(organic matter)$^{-1}$ in the pollen concentration diagrams; and as grains cm^{-2}year^{-1} in the influx diagrams. The pollen influx diagrams cover the period since AD 1750, whereas the pollen concentration diagrams cover the period prior to that time.

The percentage pollen diagrams were divided into local forest pollen zones based on the calculated pollen values, after correction of the AP values. Section 365:1 is the type section. The zones have been applied to the influx and concentration diagrams. Too little material was available for calculating influx values at 3-4 cm in section 365:1.

Pollen deterioration. The analysis of pollen deterioration includes *Alnus, Betula, Corylus, Tilia* and *Fraxinus,* which represent types of tree pollen with a smooth or regular pollen exine. The *Fraxinus* results were later omitted due to scarce representation. The pollen grains were classified as well-preserved,

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corroded(in the sence of Cushing 1967b), corroded and thinned, or thinned (see p. 47). The pollen frequencies of the different categories were expressed relative to the total number of pollen when 10 or more grains were counted.

Brown hypha analysis. Hypha fragments were measured in samples prepared for pollen analysis, drawn on paper by means of a Leitz drawing apparatus and measured with a ruler. The class unit was 2 μm. If curved, the total length of the fragment was measured (Andersen 1979). The frequency of hyphae, relative to the pollen concentration, was calculated by using an eye-piece micrometer to determine the number of points at which the index lines touch the various constituents. Counting was done at regular intervals throughout one or two slides, which was the procedure used by Iversen (1964) on podzol samples. The calculation basis in the present paper was APcorr., whereas Iversen expressed the amount of fungal hyphae in relation to total pollen, considering the annual pollen deposition rate to be constant in time (op.cit.). Although the area around sections 365:1 and 365:2 has always been forested, the tree composition and the $AP \times APcorr^{-1}$ ratio has varied considerably in time (see plates 1 and 2). It is therefore supposed that the APcorr. value is the more stable basis for calculating the relative frequency of fungal hyphae.

The influence of pollen grain size on the result is considered insignificant because the forest in the lower part of the section was dominated by *Tilia* and, in upper part, by *Fagus* with pollen of approximately equal size.

The absolute hypha concentrations were calculated from the same slides by counting the total hypha length in an area with l00 tree pollen. The AP weight and volume values were used to calculate the hypha length in $m \times g^{-1}$ and $m \times cm^{-3}$. The sediment accumulation values were used to calculate the annual hypha production.

Terminology

Humus stages

Forest soil terminology is rather confusing, according to Kubiena (1953) and Hartmann (1965) - partly due to the ambiguous definition of the term 'humus form' which was used to denote both a single humus layer (e.g., Albert 1929), as well as the sum of all layers forming a soil profile (e.g., Kubiena 1953). This term should accordingly be avoided and, in the present paper, the terms 'brown earth', 'podzoloid', and 'podzol' are used to refer to entire soil profiles (adopted from Andersen 1979). The stages in which humus, associa-

ted with each of the soil profile types, is accumulated, are termed 'humus stages'.

The pedogenesis generally cause a succession of various soil profile types at the same place. Therefore a former stage is mostly completely obscured by the recent stage, texture, colour, degree of humification, water content, etc. Thus in palaeoecology the various soil stages cannot be defined with reference to their physical and chemical soil properties alone.

Humus formation is intimately related to the dominant soil fauna fragmenting and digesting the available organic material (Müller 1878, 1884, Andersen 1979). The definition for the humus stages as applied in this paper account for this principle as it refer to the humus produced in each of the former or recent soil stages by their soil fauna and which is not later displaced. Therefore often only a small fraction of the actual humus content characterize the layer; eg. the humus connected with a former brown earth is almost completely extinct from a present podzol soil. The pollen and the hypha fragments are the only elements remindering the former humus stage.

In accordance with Hartmann (1965), the zoogenous humus formation stages are divided into a 'lumbricid humus stage' and an 'arthropod humus stage.' A third stage with both mycogenous and zoogenous decomposition is termed 'raw humus' (Albert 1929) because the biological activity is much lower here than that found in the other stages. Each soil profile type has a specific humus formation: lumbricid humus is accumulated in brown earth, arthropod humus in podzoloid, and raw humus in podzol soils. The different layers in a soil profile are named after the stage in which the primary located humus elements are accumulated; lumbricid humus (layer), arthropod humus (layer), and raw humus (layer).

Characteristics of the humus stages

The lumbricid humus stage
Upper boundary. The transition from the lumbricid humus stage to the arthropod stage is gradual and cannot be based on a single parameter.

The pollen assemblages are differentiated at 35 cm in section 365:1(plate 1) and at 20 cm in section 365:2(plate 2), indicating decreased bioturbation. The distinct variations in the relative abundance of hypha fragment classes at similar levels is also in agreement with the assumption that the fauna composition has changed, initiating the accumulation of arthropod humus (fig. 29).
Diagnosis. The content of organic material is low and often dominated by secondary humic matter, and the degree of humification is accordingly high.

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The pollen assemblages are very similar because of intensive animal soil mixing. The pollen deterioration is generally high, and corroded and thinned grains are common. The concentration of brown-coloured hypha is low and the comminution more or less intensive, depending on the frequency of arthropods, which is possibly related to soil humidity (p. 91).

The arthropod humus stage

Upper boundary. The transition to the raw humus is drawn where the dry density and the ignition residue decrease - at 22 cm in section 365:1 and at 9 cm at 365:2. The total pollen deterioration also diminishes, indicating increasing soil acidity unfavourable for a rich arthropod fauna.

Diagnosis. The content of organic material is rather high and the degree of humification moderate to high. The content of macroscopic plant material is low. The pollen concentration is generally high and shows considerable vertical and horizontal fluctuations depending upon soil genesis and humus structure. Modification of the successive pollen assemblages is moderate to low due to the inadequate mixing capacity of the arthropods. Most pollen types are corroded or thinned, but still easily recognizable as only few pollen grains are badly damaged. The brown-coloured hypha production is distinctly higher than in the lumbricid humus stage(table 13), and the hyphae are bitten into small fragments by the rich arthropod fauna(figs. 28 and 29).

The raw humus stage
Upper boundary. Not defined.
Diagnosis. The content of macroscopic plant material is moderate to high and the degree of humification moderate to low, decreasing upward. The pollen concentration is low and the original pollen stratigraphy well preserved because of insignificant soil mixing. The pollen preservation is excellent. The brown-coloured hypha production is high and the hyphae are less comminuted than those found in the arthropod humus.

Local forest pollen zones

The concept of the term 'pollen assemblage zone' (Cushing 1967a), being a biostratigraphic unit based on pollen stratigraphy, has been widely accepted as far as regional or local pollen spectra from open areas are concerned. Pollen stratigraphy from forest soils may also be subdivided into assemblage zones, but in areas where the relative pollen productivity of the species is

known and the amount of non-arboreal pollen is low, it may be more convenient to introduce the term 'local forest pollen zone'. These pollen zones are considered to apply only to very confined areas, and are not conveyable to other parts of the same forest. The calculation basis was APcorr. for the trees and P for other taxa.

The present vegetation

Forest part 365 is dominated by an old, mixed *Fagus sylvatica-Quercus robur* vegetation. *Betula verrucosa, Frangula alnus* and *Ilex aquifolium* are fairly frequent on podzol with a deep humus cover, whereas *Sorbus aucuparia, Corylus avellana, Alnus glutinosa,* and a few *Fraxinus excelsior,* are found on brown earth in the southern part. The canopy is dense and the ground flora generally rather sparse.

The investigation area is dominated by the same tree vegetation (figs. 2 and 3). The undergrowth is rather sparse (fig. 4), and tree reproduction, in particular, has been very low during recent years, even after a small clearance 20 years ago. This is partly due to a relatively large roe-deer

365:2   **365:1**

Fig. 2. The investigation area in Draved Forest, part 365, seen from the east and the location of sections 365:1 and 365:2.

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TREES	STEM DIAMETER	STUMPS

	Quercus	< 30 cm	·	Betula	△
	Fagus	30-64 cm	•	Quercus	▲
	Alnus	> 64 cm	●		
	Sorbus				
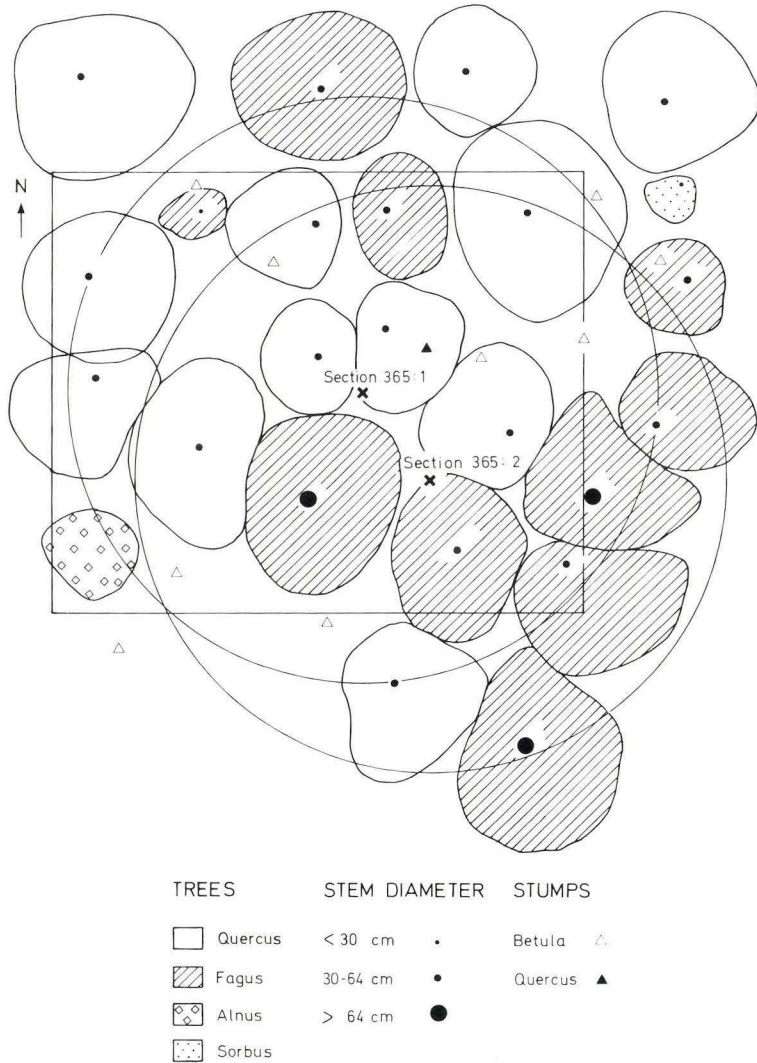
Fig. 3. The canopy vegetation near the investigation area. The investigation area and circles with a 20 m radius from the sections are shown.

population which severely impedes tree reproduction. Only *Ilex* seems to be more successful, with its reproduction by suckers which are able to persist in spite of heavy browsing. Fertile *Ilex* trees are present within the area.

The canopy is rather dense, and the projection of the crown area is about 70% of the total area. If the exposed undergrowth is included, the value

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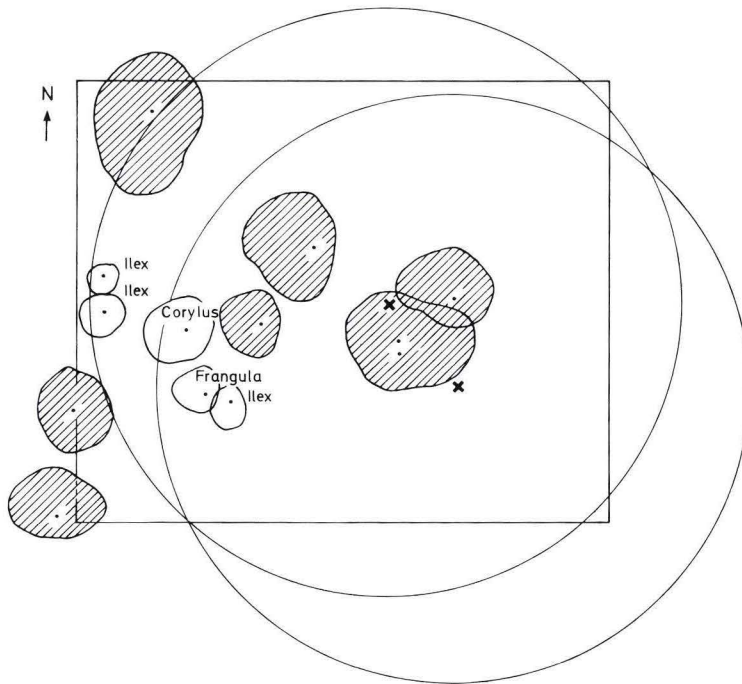
Fig. 4. The understory vegetation near the investigation area. For explanation of symbols see fig. 3.

increases to about 80% (table 1). Similar results have been obtained from other areas in Draved Forest having a mature tree vegetation (Andersen 1970).

The ground flora is rather sparse on podzols in the western and southern parts of the investigation area due to strong shading, mainly from the *Fagus* trees. *Dryopteris carthusiana, Convallaria majalis, Lonicera periclymenum, Hedera helix* and *Ilex aquifolium* are present in heavily shaded ground, whereas *Deschampsia flexuosa,* and *Trientalis europaea* dominate on less shaded ground.

The eastern and northern parts of the area are only moderately shaded as six *Betula verrucosa* trees and a single *Quercus robur* were felled here in the winter 1960-1961. (see fig. 3). The relatively dense ground flora is dominated by *Pteridium aquilinum, Deschampsia flexuosa, Vaccinium myrtillus, Stellaria holostea, Trientalis europaea, Molinia coerulea, Lonicera periclymenum,* and small *Ilex aquifolium* shrubs. Thus the vegetation is characterized by

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acidophilous species, and only a few neutro-basidophilous species such as *Alnus glutinosa, Corylus avellana* and *Deschampsia caespitosa* show that fertile till is present close to the surface in the southwestern part of the area (fig. 6).

	Section 365:1 r = 20 m % af total area	Stection 365:2 r = 20 m % af total area
Canopy		
Fagus	30.0	38.7
Quercus	38.7	30.9
Various	0.6	–
Total	69.3	69.6
Understory		
Fagus	11.0	9.1
Various	3.2	2.6
Total	14.2	11.7

	Investigation area, 30×36 m % of total area
Canopy	
Fagus	25.7
Quercus	45.6
Alnus	2.6
Total	72.9

Canopy + exposed understory 79.9% of total area.

Table 1. Relative tree crown coverage within the investigation area and around sections 365:l and 365:2.

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Historical notes on the composition of the forest AD 1100-1850

The history of Draved Forest has been studied by A. Andersen (1980 and unpublished data) and I. Brandt (unpublished data). I. Brandt has kindly given me access to information of relevance.

Draved Forest is known to have changed hands a number of times prior to AD 1173. In that year, a monastery was founded at Løgum, 4 km. north of the forest, and it is possible that the monastery acquired some areas in the forest as well. A hundred years later, in the year 1263, Duke Erik I settled a controversy between the monks and one Jacob Tuesen concerning the ownership of parts of the forest. The monks were given custody of the disputed areas and, later, acquired the entire forest, but they were often forced to assert their legal right to it because of the infringements of a neighbouring lord and other persons. By the time of the Reformation in 1536, the monastery had lost all rights to the forest, which was handed over to Duke Hans the Elder.

Written sources from the Middle Ages mainly deal with struggles over the use of the forest as a resource for wood, whereas there is little mention of the tree composition, animal browsing, or the forest management practiced during the period. The first information of the latter kind is dated to the year 1568, when it was noted that in favourable years about 2oo pigs were grazed in Draved Forest and three other woods. The mast-trees, *Fagus* and *Quercus* were common at that time. In the first general description of the forest (1607), Draved was characterized by *Betula, Alnus* and *Populus tremula;* whereas *Quercus* and *Fagus* were probably less important, as it was stated that the forest was 'without fruit'. In the year 1704, only 12-16 pigs were fed in Draved and Løgum forests and, at that time, the pigs had only been grazed in the forest twice during the previous 16 years. Accordingly the wood was of little value for feeding at that time. In contrast to the small number of pigs in the wood after AD 1600, a considerable number of horses and young cattle were grazing there. It is known that in 1704, both horses and about 100 young cattle were being kept in the forest and, in 1764, the number had risen to about 250-300 cattle.

In 1762 the wood was dominated by *Betula, Populus* and *Alnus,* but *Fagus,* mixed with some old *Quercus,* was also present. In 1785 the grazing was

brought to an end and a bank was built to protect the forest. At that time, a more rational forest management was introduced and the forest began to recover. Records show that by 1801 and 1839, the forest was dominated by younger *Betula, Alnus* and *Fagus,* the latter growing on dry soil. Some old *Quercus* and *Fagus* stands were also present.

Forest composition since 1850 in forest part 365

The historical documents regarding Draved Forest describe the wood in very general terms and only few references or events in the forest can be geographically located with confidence. Not until the first management plans were laid down by the forestry service can we find detailed information about well defined areas (forest parts). The oldest available management plan for the investigated forest part 365, dates from the year 1868; later plans are dated 1922, 1937, 1952 and 1964.

The 1868 management plan. Betula and *Alnus,* aged about 20-25 years, dominated, mixed with some 50-70 year old *Quercus.* The canopy was closed. The adjacent areas show a related tree composition. No mention of *Fagus* was made in this plan.

The 1922 management plan. Quercus, 130 and 70-100 years old, mixed with *Fagus,* 70-100 years old. In addition, *Betula, Sorbus,* and *Alnus* were present. Some *Picea abies* stands occurred, about 50 years old.

The 1937 management plan. The forest composition had not changed substantially, with the exception that some of the old *Quercus* had been felled. The canopy was closed. Nine *Tilia* trees were registered at this time, 14 m high with a mean diameter of 14 cm. From 1937 to 1952, about 20 ha. were cleared in the surrounding forest but not near the investigation area.

The 1952 management plan. 150 year old *Quercus* and ca. 100 year old *Fagus* trees dominate, mixed with 100 year old *Betula* and *Alnus. Sorbus aucuparia* was about 35 years old. The canopy was closed. During the period 1952-1964, about 80 m³ of *Betula* (50 trees), *Quercus* (14 trees) and *Fagus* were cut outside the investigation area. In the winter 1960-1961, six *Betula* and one *Quercus* were felled inside the investigation area (pers. comm. from State Forester N. L. Thomsen, 1979).

The 1964 management plan. The area was dominated by a mixed *Fagus* and *Quercus* vegetation, with some *Alnus* and *Betula* (see table 2).

The management plans show that the investigated area has not been seriously affected by forestry practices during the last century.

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Calculation of tree ages

The approximate ages of the trees are adopted from the 1964 management plan (table 2). The ages are based on tree-ring calculations done on stumps, and only the mean values are given in the plan, although a considerable variation can be expected. The ages of the individual stands are updated from the previous management plans; the ages of the oldest stands should therefore be viewed with reservation (pers. comm. from State Forester N.L. Thomsen, 1979).

Several *Fagus* and *Quercus* trees were drilled and the number of tree-rings measured, in order to verify the ages given in the management plan. The results are shown in table 2. The few ages calculated seem in general to confirm the ages given in the 1964 plan, except that the *Quercus* originates from a younger generation than indicated there. The 1922 management plan shows that at least two *Quercus* generations were present in the area, the youngest being about 140 years old today (table 2), and the old trees belong to the latter generation.

The diameters of the trees and stumps were measured (fig. 5). The stem diameters of *Quercus* are grouped, which may indicate that the *Quercus* trees originate from two different populations, one being about 105 years old, the other about 145 years old. The diameters of the *Fagus* trees show more variation. The largest trees are possibly about 135 years old, while one of the smaller trees was only about 75 years old.

The difference of 30 or 60 years between the populations may indicate forest management at constant time intervals. The 1839 management plan

	1964-plan	1868-plan	Drilling
Quercus	168	162–182	145, 145, 105
Fagus I	129	–	135, 135
Fagus II	68	–	75
Betula	129	135	–
Alnus	129	135	–

Table 2. Estimated ages of tree stands calculated from tree-ring countings and forest management plans. All values are transferred to ages in year 1980.

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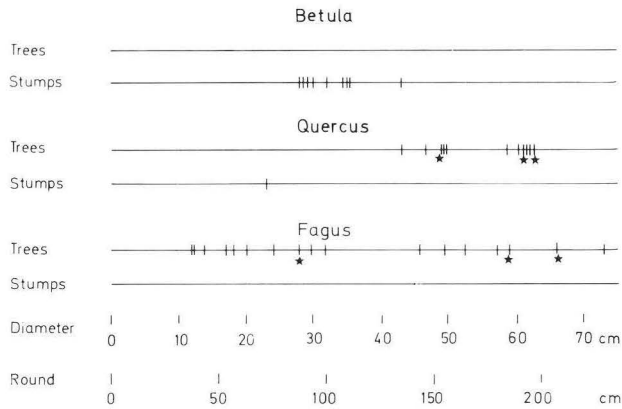
Fig. 5. Measurements of tree and stump diameters at 1.3 m and 0.2 m respectively. Trees selected for tree-ring countings are denoted by an asterisk.

indicates that the forest was managed either in 'Mittelwaldbetriebe', in which large areas were divided into rectangular areas each operated at constant intervals, or in 'Compositionsbetriebe', where no division was intended. In the latter plan, *Quercus* and *Fagus* were to be the canopy trees, the other species, mainly *Betula,* dominating the undergrowth. The rotation time was 35 years for the undergrowth and somewhat longer for the canopy trees. The effect of this management practice can still be seen in part 365.

Judging from the pollen diagrams (plates 1 and 2), *Fagus* has been frequent in the area for an extended period of time, and no clear indications of extensive *Fagus* felling are reflected in the diagrams, whereas the *Quercus* curves show distinct changes indicating tree cuttings (see p. 62).

Although the management plans do not clarify whether or not the present trees are remnants of older native populations, it is supposed that the *Fagus, Alnus* and *Betula* trees are of local provenance. The question of whether this is also true for the *Quercus* trees remains unsolved.

The geology

Forest part 365 is 2.6 ha, with the till exposed only in the central areas, the remainder being covered by aeolian sand (fig. 7). The deepest aeolian sand layers are found in the northern and southernmost areas. The general topography does not reflect the differences in the thickness of the sand layer, but shows a gradual rise from SE to NW (fig. 6).

The 36x30 m investigation area is located about 15-20 m N of the exposed Saalian till (fig. 6). The soil is identified as a podzol with a well-developed humus cover, 5-40 cm thick. A 10-30 cm aeolian sand layer is found in the NE area, but is often too thin to be traced outside this area.

The lithology of the mineral soil is rather complex. Sandy till dominates the area, but glaciofluviatile sand also appears and the sediments vary within short distances. A deep and almost impermeable iron-humus pan has developed in the till areas, whereas the pan is only weakly developed in the coarse glaciofluviatile deposits. Gley features are common below the pan - especially in the low-lying western part of the area. The general topography of forest part 365, as outlined on figs. 6 and 7, is not reflected in the investigation area, fig. 8. Here the highest elevation of the mineral soil surface is found to the NE, and the lowest to the SW. The map shows that although the isohypses run in the NW-SE direction, a distinct microtopography is present with small isolated depressions, often 20-30 cm deep. Most depressions are oblong in the N-S direction, and often sharply delimited. Small ridges are often located near the depressions on the eastern or western side. These ridges consist mainly of aeolian sand and the microtopography may have orginated in the Weichselian with the ridges being small dunes; but some of the features may be younger, formed by large trees which have been ripped up by hurricanes, exposing a hemisphaerical soil- and root cake and leaving one or two depressions and a ridge (Iversen 1969). According to Iversen (op.cit) this phenomenon is seen at several places in the forest, often in areas with a relatively high groundwater table and a thin sand layer above the till, as in the present area.
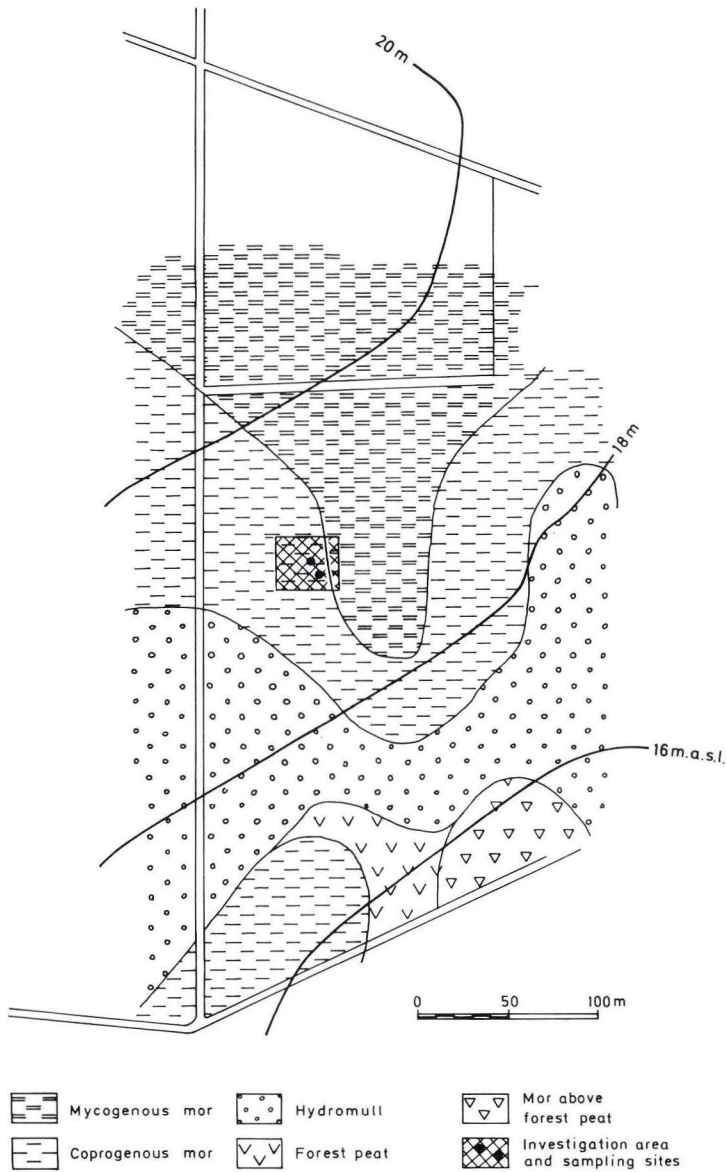
Fig. 6. Humus types in forest part 365 and surrounding areas. Terminology according to
Iversen (1964) (Geological Survey of Denmark, Inger Brandt and Johs. Iversen 1963,
unpublished).

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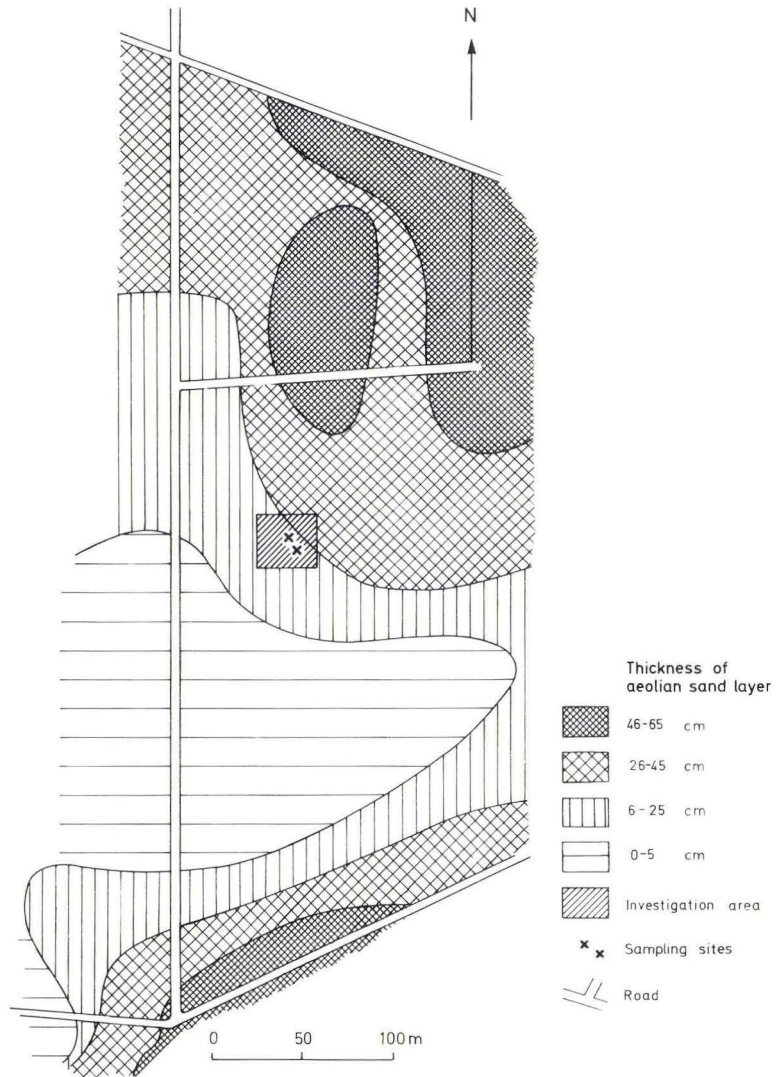
Fig. 7. Thickness of the aeolian sand in forest part 365 and surrounding areas. (D.G.U.)

Soil stratigraphy at section 365:1

(fig. 9)

Section 365:1 is a podzol on glaciofluviatile sand, located in a relatively small oblong depression, ca. 4x10 m (figs. 2 and 8). The humus cover(A_0 horizon) was about 25-40 cm or about 10-15 cm thicker than the humus layer outside
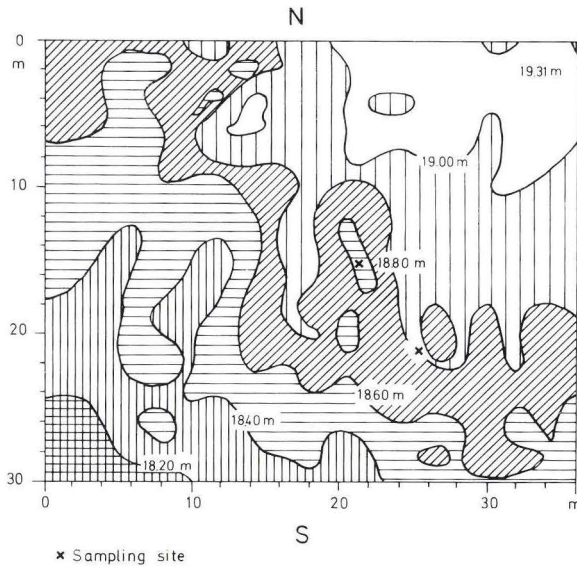
Fig. 8. Topography of the mineral soil surface, below the humus cover. Section 365:1 is located in an oblong depression and section 365:2, SE of 365:1, on higher, levelled ground. Isohypses in m a.s.l.

the depression (see fig. 12). The canopy above the section is entirely closed, and the depression does not support any ground flora. The subsoil is waterpermeable and the ground water table located at a depth of about 1 m below the surface (August 1975).

The stratigraphy at the sampling site is as follows:

A_{00}	0	cm	Litter, 18.78 m a.s.l. A ca. 2 cm layer of unconsolidated litter was collected separately and assigned a depth of 0 cm.
A_0	0-3	cm	Light brown, weakly consolidated humus. Most plant remains are easily distinguished.
A_0	3-9	cm	Reddish-brown, consolidated humus. Larger remains are distinguishable.
A_0	9-15	cm	Brown consolidated humus with only a few macroscopic remains visible.
A_0	15-20	cm	Dark brown, compressed, and homogenous humus layer. The content of inorganic matter is very low.

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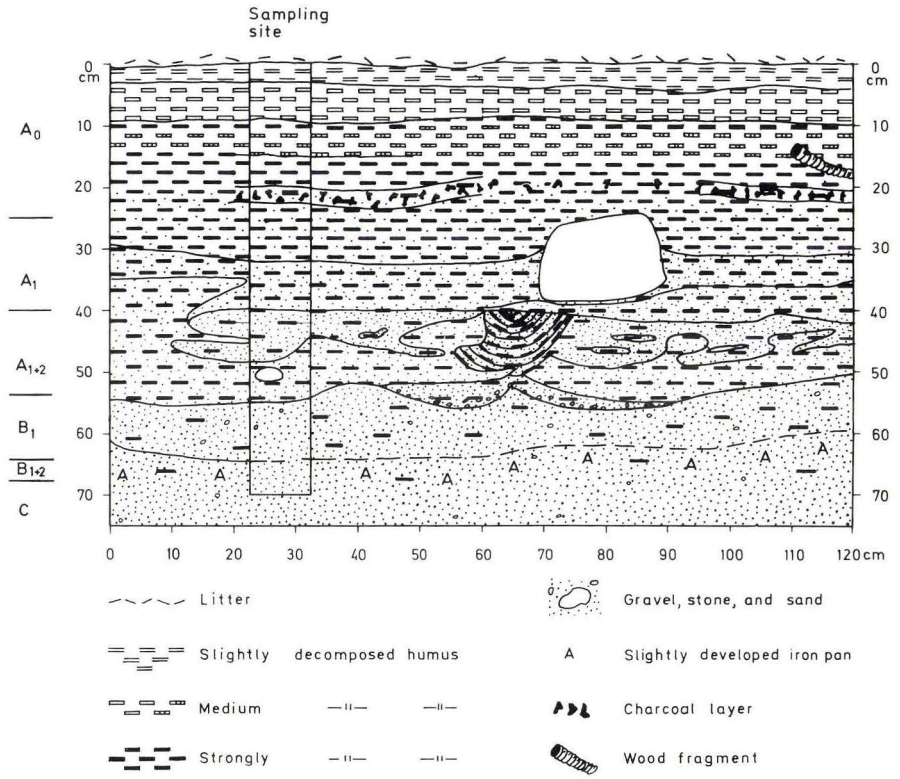
Section 365:1

Fig. 9. Soil stratigraphy at section 365:1.

A_0	20-25	cm	Blackish-brown, greasy humus, without macroscopic remains. The sand content gradually increases downward. Two charcoal layers are visible and macroscopic charcoal found.
A_1	25-35	cm	Dark brown or grey-brown humus with a relatively high sand content.
A_1	35-40	cm	Grey-brown humic sand.
A_{1+2}	40-46	cm	Grey sand with humus.
A_{1+2}	46-55	cm	Grey-brown humic sand containing some gravel and a few stones.
B_1	55-64	cm	Grey sand with humus and gravel.
B_{1+2}	64-78	cm	Rust-coloured sand with gravel.
C	68-	cm	Yellow-grey sand.

30
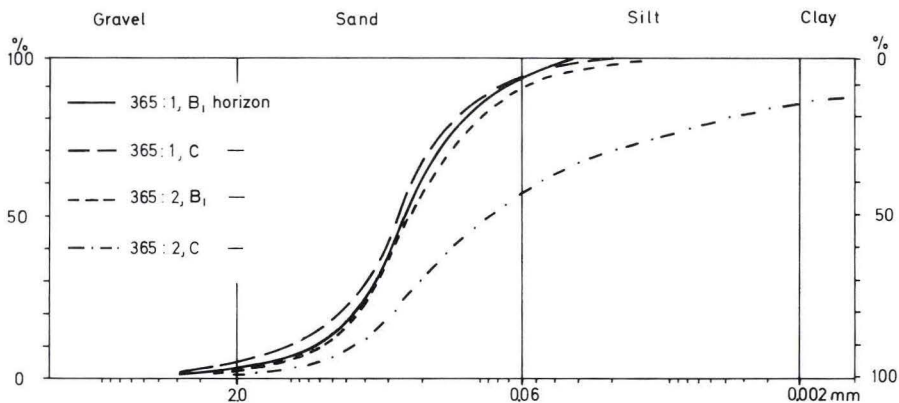
Fig. 10. Grain size distribution of glaciofluviatile sand in sections 365:1 (55-57 cm and 68-72 cm) and till in section 365:2 (30-32 cm and 100-102 cm).

The lower part of the section consists of well-sorted medium-coarse sand (fig. 10), and a boring showed that the layer could be traced to more than 2 m below surface(b.s.). Small lenses of gravel and small stones were found at 65-70 cm b.s. The lithology of the bottom sediments shows that they are of glaciofluviatile origin and the distinct double-bowed lens at 50-55 cm b.s., indicates water erosion.

The concentric and horizontal humus layers at 55-40 cm b.s. are probably formed by secondarily deposited humus, which has been washed out from organic material, inasmuch as no plant remains and only a few strongly decayed pollen grains were found in the bands. Laboratory analysis also shows that the humic matter was totally dissolved in KOH.

The inorganic fraction dereases gradually upwards from about 40 cm and, at about 20 cm, it was low. A large quartzitic sandstone with windpolish facets was found at 38-25 cm. This and other stones found in the area originate from the Saalian till and were possibly exposed in Weichselian time. It is difficult to determine whether all the mineral sediments are glaciofluviatile, or whether a thin layer of aeolian sand was deposited at the top, because the upper mineral soil layers have been bioturbated.

A charcoal layer was observed at 20-25 cm. In general, the layer was easily recognizable except to the left of the sampling site. Only small variations in stratigraphy were observed in the upper part of the humus layer which was strongly decomposed to about 15 cm, and overlain by slightly to moderately decomposed humus to about 3 cm. The uppermost humus layer was weakly consolidated and most plant remains were easily distinguishable. A 2 cm thick layer of unconsolidated litter was found at the top of the profile.

Soil stratigraphy at section 365:2

(fig. 11)

Section 365:2 is a podzol on sandy sediments overlying silty till. The formation of the upper deposit is rather uncertain, but includes possibly aeolian sand. The site is lying on almost level ground gently sloping towards the west (fig. 8). The ground flora is sparse, dominated by a few *Deschampsia flexuosa* and *Molinia coerulea* plants. An almost water-impermeable iron pan, 30-45 cm thick, is responsible for a local ground water table, which may be temporary.

The stratigraphy at the sampling site is as follows:

A_{00}	0	cm	Litter, 18.92 m a.s.l. A ca. 0.5 cm layer of litter was collected and assigned a depth value of 0 cm.
A_0	0-2	cm	Light-brown, weakly consolidated humus layer. Larger remains distinguishable.
A_0	2-9	cm	Brown consolidated humus layer with only few macroscopic remains visible.
A_0	9-14	cm	Grey-brown strongly consolidated humus with a rather low content of inorganic matter.
A_1	14-19	cm	Grey-brown humic sand. Humic lenses present.
A_2	19-24	cm	Light-grey sand with a few pebbles.
A_2	24-30	cm	White-grey sand with a few stones.
B_1	30-40	cm	Blackish-grey humic sand with a few stones. The humus content seems to be relatively high.
B_{1+2}	40-45	cm	Blackish red-brown sand with greyish lenses of sand.
B_2	45-52	cm	Blackish rust-brown, strongly congregated sand with a few stones.
B_2	52-85	cm	Reddish yellow-brown, strongly congregated sand/silt with a few stones.
B_2	85-95	cm	Less congregated yellow sand/silt with blue-grey lenses. The clay content is rather high and a few stones are present.
C	95-	cm	Yellow-grey sand/silt with a few grey or red-brown lenses. The clay content is rather high.

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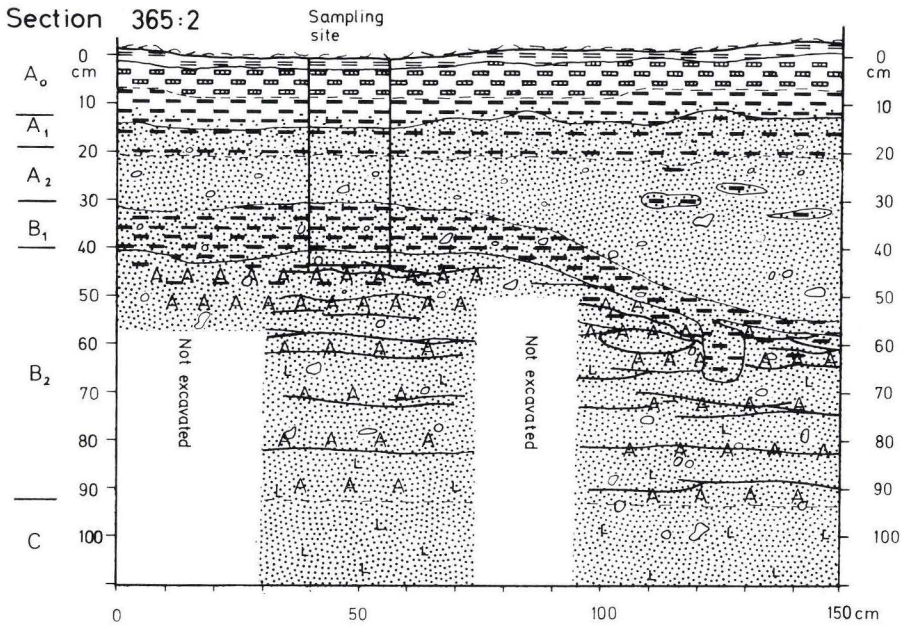
Fig. 11. Soil stratigraphy at section 365:2. The horizontal lines in the B₂ horizon indicate red-brown humic lenses. For further explanation of symbols see fig. 9.

The till in the C-horizon was investigated at the sampling site and in the eastern part of the section, and consists of silt with lenses of clayey or sandy material (fig. 10). A very strongly congregated B_2 horizon, about 30-45 cm thick, has developed. The upper surface of the B_2 layer shows distinct vertical fluctuations whereas the lower boundary seems to run smoothly. The observed variations in thickness are possibly caused by distinct heterogeneity in the initial mineral deposits which were cryoturbated during the Weichselian. The B-horizon is thickest where the A_2 horizon is rather fine-grained; it becomes thinner and is located deeper below coarse-grained deposits. The vertical extension pattern of the B_1 horizon is similar to that found for the B_2 horizon. A distinct white to light-grey bleached sand layer(A_2 horizon) with little gravel and few stones was seen at 20-35 cm in the left part of the section, and it becomes thicker to the right. Here, the colour was generally more greyish, and a few humus lenses were present. The composition of the sediments above 20 cm was rather uniform, with a 5-10 cm thick A1 horizon, overlain by 15 cm humus which was rather decomposed except at the top. The A_1 horizon, which at the sampling site belongs to the arthropod humus stage, contains no coarse mineral particles such as stones or gravel, as these have been too large for incorporation by the arthropod fauna. A few distinct cylindric humic sand layers were found in

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the rather homogenous humus layer and are supposed to represent fossil mouse holes.

It is uncertain whether the tendency to lower clay content toward the top at the sampling site is a primary feature, or the result of lessivation. The mineral particles are well rounded in the A horizon and it is therefore possible that some of the material may have an aeolian origin.

The sediments

Thickness of the humus cover

(fig. 12)

The thickness and the composition of the humus layer(A_0 horizon) was studied at 270 points regularly distributed within the investigation area. The sediment was characterized as humus when the organic content was estimated as 3/4 or more of the sediment volume.

The depth of the humus layer varied between 40cm to less than 10cm, being in general 10-30cm. A comparison of the topography of the mineral soil surface (fig. 8) and the humus isopachyt map (fig. 12) shows that the humus cover was generally deepest in the mineral soil depressions. The surface

× Sampling site
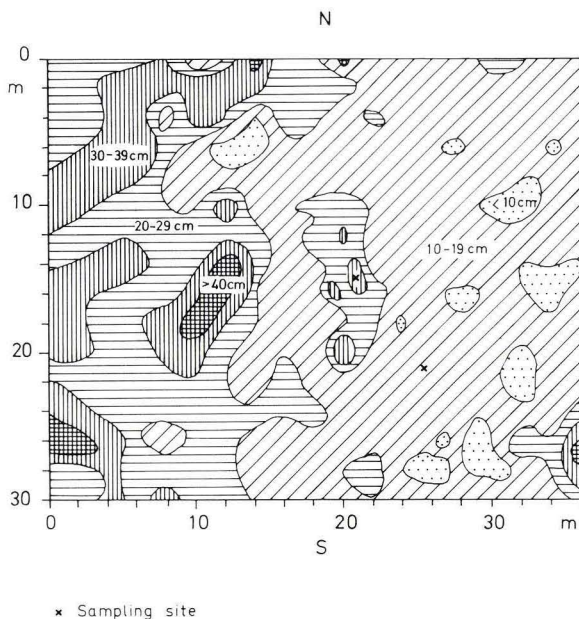
Fig. 12. Thickness of humus cover within the investigation area.

microtopography has thus been levelled by the formation of the humus cover. The comparison shows other trends when attention is directed towards the macrotopography; while the isohypses have a general NW-SE direction, the humus isopachytes run in the N-S direction, with the deepest humus cover in the western part of the area. Therefore the general trends in the thickness of the humus cover do not reflect general trends in the mineral soil topography. Also the lithology seems to have little influence on the humus thickness, as podzols with similar lithology as at section 365:2, are found in the western part of the investigation area, having a much thicker humus cover. The main difference was, that pronounced gley horizons were found in the low-lying western part with thick humus deposits, whereas such horizons were absent, or weakly developed, in the eastern area with its thin humus deposits. The hydrology of the area is therefore considered to have had an important influence on the humus formation in the area.

Initiation of humus accumulation; synchronous or asynchronous?

The question of whether the accumulation of organic matter was contemporanous in the eastern and western parts of the area was considered. During
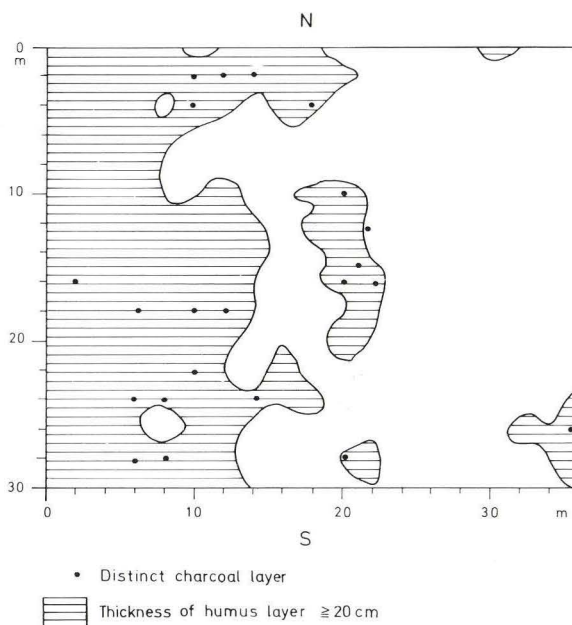
Fig. 13. Distribution of a distinct charcoal layer. The charcoal layer was only distinguished in areas with a humus cover thicker than about 20 cm.

36
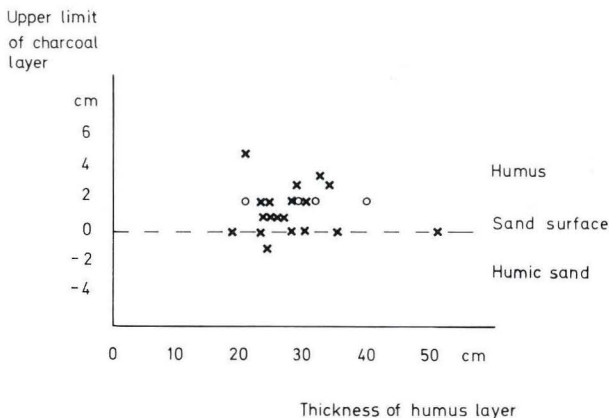
Fig. 14. Upper limit of distinct charcoal layer in relation to mineral soil surface (sand surface) and thickness of humus layer. The charcoal layer was only recorded in the borings when lying above or near the mineral soil surface, due to inadequate bioturbation at these sites at the time of burning which was dated to the Middle Ages. Brown earth was present in areas which today have a humus cover less than 20 cm thick. The upper limit of the charcoal layer was narrow (x) or diffuse (0).

the field work, a distinct horizon with charcoal dust, about 3-4 cm thick, was found in several borings (fig. 13). Sometimes the horizon could be subdivided into two separate thin layers, as at section 365:1, but when found in a boring, only a single charcoal horizon was recognized. The high content of strongly decomposed humic matter obscures the presence of charcoal, making the identification of the charcoal horizon difficult. This may explain why the charcoal horizon was recognized in only some of the borings on deep humus.

The charcoal horizon observed in the borings was supposed to originate from the same period. This statement is based on two findings; first, charcoal horizons were not found in areas with a humus cover less than 18 cm deep (fig. 14), although about 130 borings on thin humus were performed. This result is confirmed by the microscopic analysis from section 365:2, located on thin humus (see plate 2). Second, the results from section 365:1, located on deep humus, show that during the last 2000 years, macroscopic charcoal has only accumulated at a single horizon (see fig. 9 and plate 1).

The position of the upper limit of the charcoal horizon was related to the mineral soil surface and the thickness of the humus layer (fig. 14). It appeared that the charcoal layer is always found near the mineral soil surface, regardless of the humus thickness. This apparently is due to low matrix accumulation rate near the mineral soil surface.

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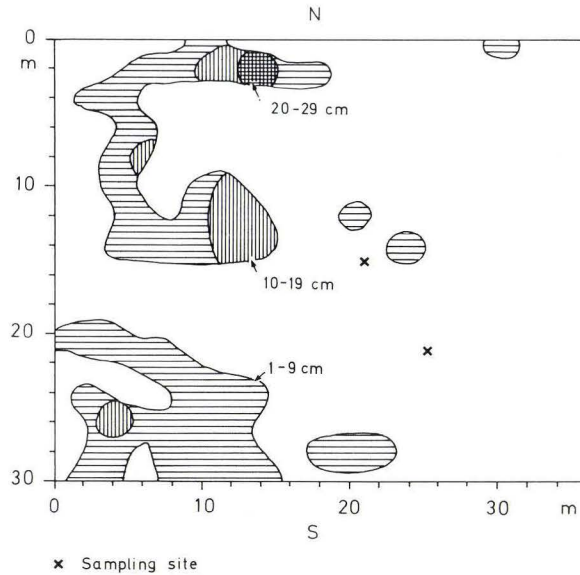
Fig. 15. Thickness and distribution of the 'pollen mor layer', a sediment with a yellow-brown or olive-brown colour originating from the colour of the pollen exines. The layer is restricted to areas with a humus cover thicker than about 20 cm, cf. fig. 13.

Charcoal horizons were not recognized in the mineral soil, except in one boring, possibly because the fires occurred when brown earth existed in areas which today have a humus cover less than 18 cm thick. Due to intensive bioturbation in these areas, the accumulated charcoal was vertically dispersed and, therefore, not recognized during the field work. The charcoal horizon present in section 365:1 was dated to late Medieval Time, AD (1200)1300-1600 (see plate 1); thus the initiation of humus accumulation is asynchronous - being younger in the eastern part.

That humus was accumulated long before Medieval Time in the western part is emphasized by the observation of 'pollen mor' at several sites (fig. 15). 'Pollen mor' originates from an arthropod humus in which the humus has been comminuted and fungal brown hyphae are sparsely represented (Iversen 1973). Since nearly everything except pollen decomposes, a dense greasy mass is built up in the course of time. The sediment is only termed 'pollen mor' when a characteristic yellow-brown or olive-brown colour is seen. This colour is only observed when the organic fraction of the sediment consists of almost pure pollen. A high content of humic matter or charcoal dust blurs the colour of the pollen exines and, although the pollen concentration in

these sediments is just as high as in the yellow-coloured 'pollen mor', they are not classified as such.

The 'pollen mor' was only found in areas with a humus cover of at least 20 cm (fig. 13). The matrix accumulation rate is very low in 'pollen mor' and, accordingly, the initiation of humus formation is supposed to be very old, as the thickness of the 'pollen mor' layer was more than 10-20 cm at several places. ÄPollen morÄ has been found in other areas of Draved Forest, and has been dated to the Subboreal (Iversen 1969).

In section 365:1, it is calculated that the change from the lumbricid humus stage to the arthropod humus stage, initiating the humus accumulation, possibly took place in the Late Subboreal (see fig. 24). It is difficult to say whether this dating is general for the whole western investigation area, or is true only for the section site.

Physical properties

Relation between loss on ignition and dry density

Comparisons of different soil-element frequencies are generally best made on a volume basis. This is particularly true where soil bulk density may vary considerably, as in podzol profiles. The bleached sand often has a dry density ten times that of unconsolidated humus. A relationship between dry density and loss on ignition has been found by Gorham (1953) in his work on forest humus and brown earth, and by Jeffrey (1970) on a wide range of uncultivated soils. These investigations concern top samples which are presumed to be unconsolidated.

The present study deals with the mentioned relationship in two sections, in which all samples except the uppermost represent consolidated sediments. At both sites, a continuous series of samples has been measured. From section 365:1 51 samples, and from section 365:2 32 samples were analysed(fig. 16).

The regression, calculated according to Jeffrey (op. cit.), for section 365:1 was:

$$Y = 1.6451 - 0.3027 \ln X; (r = 0.9733, t = 29.6819, P < 0.001), A + B \text{ horizons}$$

and for section 365:2 was:

$$Y = 1.4980 - 0.2836 \ln X; (r = 0.9703, t = 13.8947, P < 0.001), A \text{ horizons}$$

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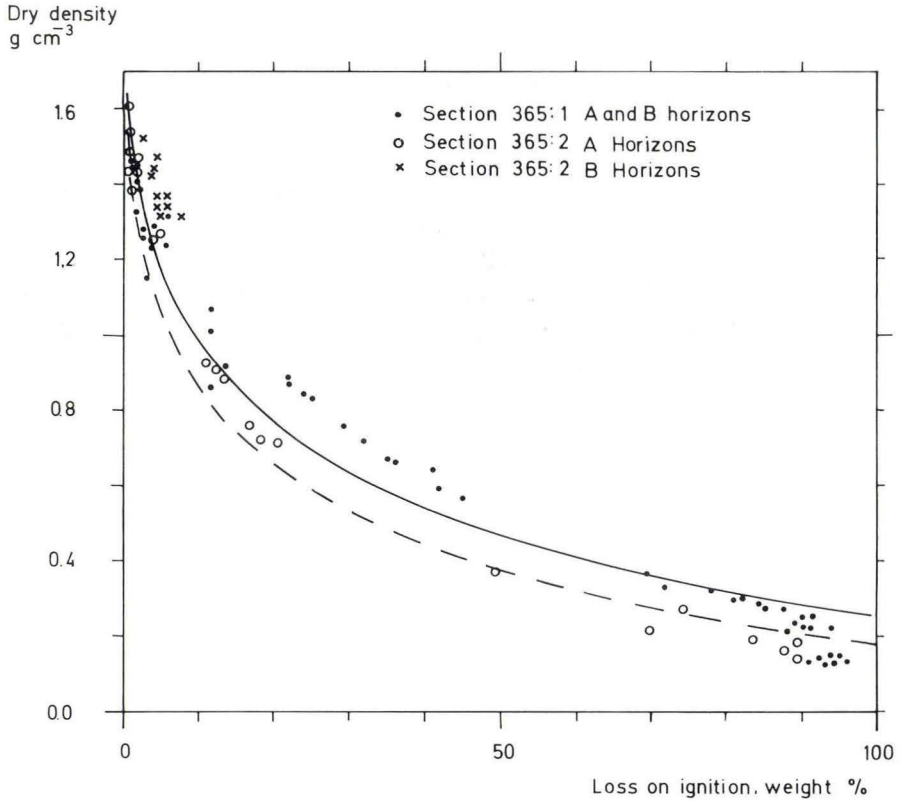
Fig. 16. Relation between loss on ignition and dry density at sections 365:1 and 365:2. Logaritmic curves for section 365:1 A + B horizons (full line) and section 365:2, A-horizons (dashed line) are shown.

$Y = 1.6825–0.3247 \ln X; (r = 0.9624, t = 14.6080, P < 0.001), A+B$ hor.

$(Y =$ dry density, $X =$ loss on ignition).

Jeffrey's conclusion (op. cit.) yielded the equation:

$Y = 1.482–0.6786 \ln X; (r = -18.7311, t = -0.9045, P < 0.001)$

The variations in the relationships obtained by Jeffrey and those found in the present investigation are supposed to be due mainly to variations in sediment autocompaction.

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Relation between ignition residue weight and volume percentages

The calculation of element volumes is often time consuming and requires a number of laboratory procedures. It may, therefore, be appropriate to estimate volume values from weight values which are produced by much simpler laboratory techniques.

In terms of ignition residue, the investigated soil profiles may be regarded as a two-component system, comprising a non-ignitable mineral material, and an ignitable largely organic component. The content of clay and silt was low at all levels in section 365:1 and in the A horizon and the upper part of the B_1 horizon in section 365:2 (fig. 10). The weight of the ignition residue was, therefore, considered to equal the inorganic fraction weight in section 365:1, and the A and B_1 horizons in section 365:2. This was proved from samples in the C horizon in section 365:1, where the ignition residue dry weight values deviate only slightly ($<0.05\%$) from the sediment dry weight.

The dry density of the ignition residue has been measured at three different levels above the B_2 horizon in each of the sections, at 42, 36, and 26 cm in section 365:1 and at 28, 22, and 18 cm in section 365:2. The dry density was 1.58 in section 365:1 and 1.63 in section 365:2. The value 1.60 was taken as general for the two sections.

The volume of the ignition residue at different levels was calculated relative to one cm³ of material with a 1.60 density (see figs. 18 and 19). The regression between ignition residue weight % and volume % has been calculated, and was for section 365:1:

$$Y = 1.1093e^{0.0455X}; (r = 0.9737, t = 23.0147, P <0.001), A+B \text{ horizons}$$

and for section 365:2:

$$Y = 0.8816e^{0.0466X}; (r = 0.9946, t = 23.5274, P <0.001), A \text{ horizons}$$

$$Y = 0.8637e^{0.0472X}; (r = 0.9951, t = 26.7851, P <0.001), A+B1 \text{ horizons}$$

(X = ign. res. weight %; Y = ign. res. volume %)

The relation between ignition residue weight % and volume % shows that half the volume is inorganic matter when the weight % is about 85-90% (fig. 17). The calculations were based on the assumption that the lithology of the mineral fraction was constant throughout the sections. The calculation neglects the intergranular space which contains organic matter, water, air,

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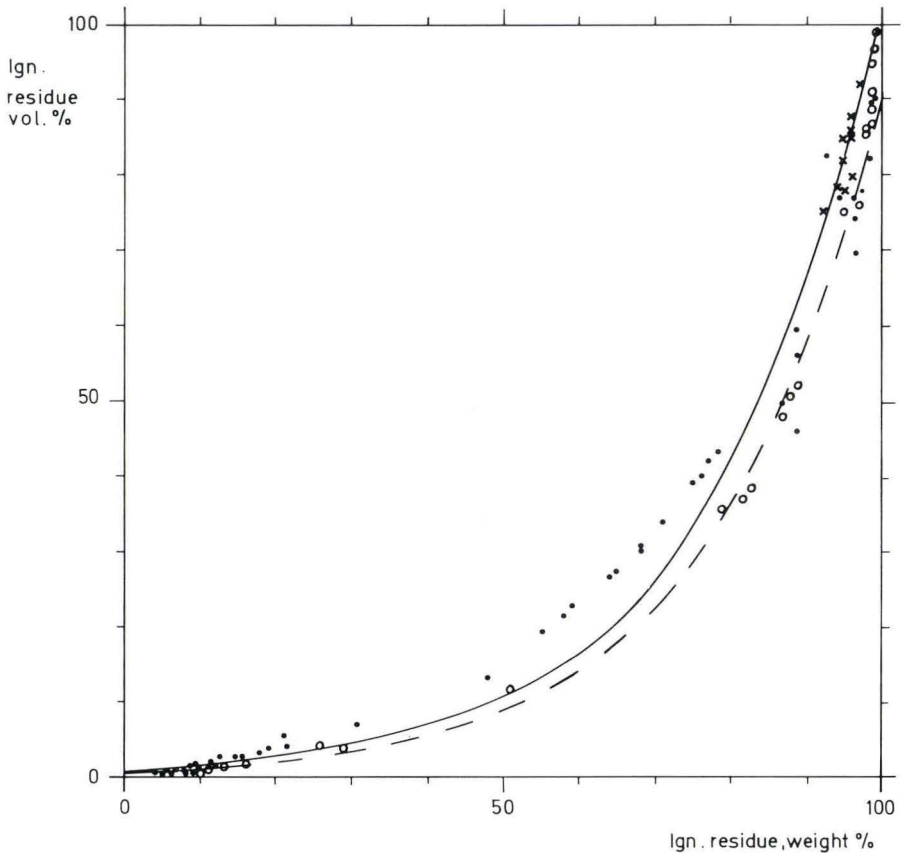
Fig. 17. Relation between ignition residue weight and volume percentages. Exponential curves for sections 365:1 and 365:2 are shown. Explanation of symbols and curves, see fig. 16.

etc. Accordingly, the results cannot be used to calculate the volumetric relations between the inorganic and organic fractions.

Slightly different relations were calculated for the two sections because of variations in sediment structure. In section 365:1, the samples with weight % between 15 and 85, have higher volume % than that measured in section 365:2, which indicates that the ignition residue has a lower density in section 365:1.

Content of KOH-soluble humic matter

The amount of humic matter dissolved in an alkaline extract has been measured in samples from the two sections and expressed as degree of humification. The degree of humification is shown as measured values and as

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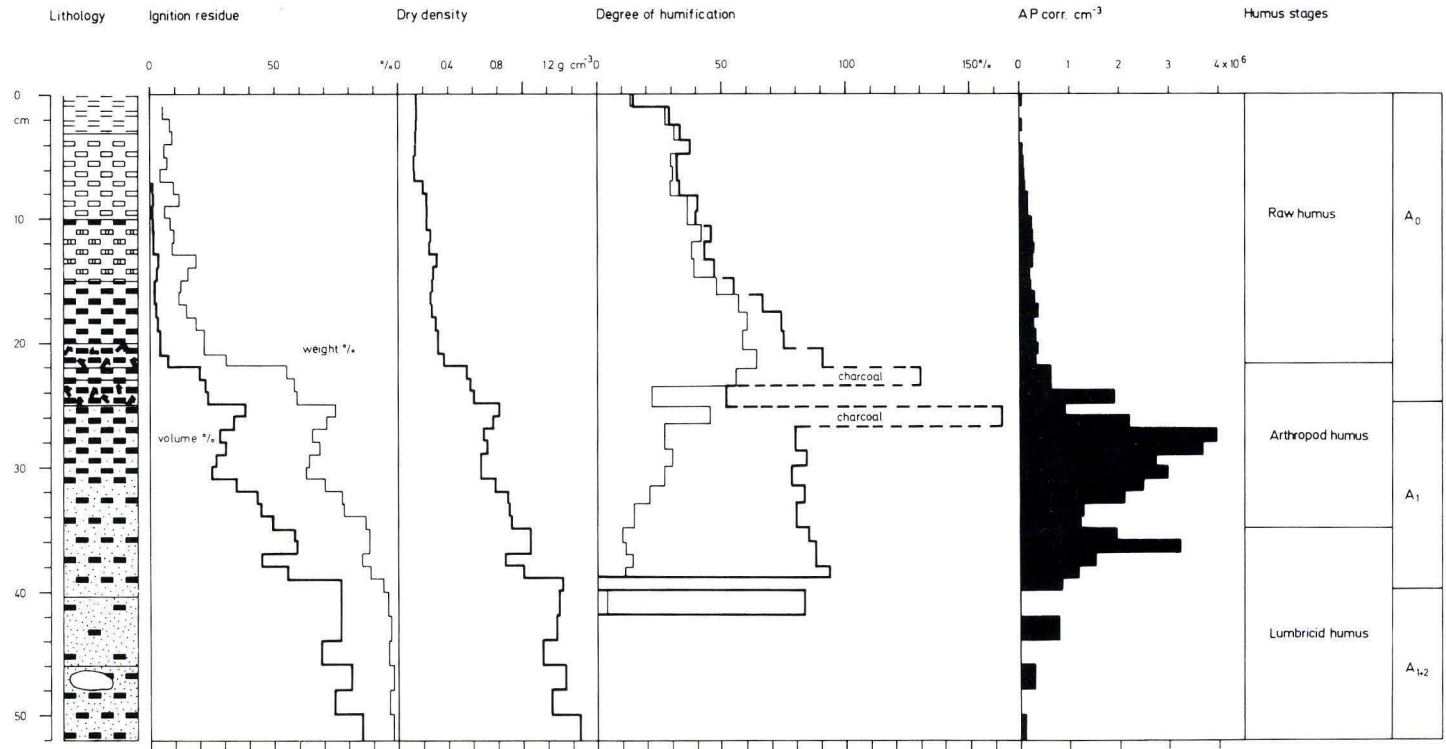
Fig. 18. Measurements of physical properties, degree of humification, and AP-corr.cm(matrix)$^{-3}$ at section 365:l. The degrees of humification are shown as measured values based on the sediment weight (thin line) and after correction for inorganic matter content (heavy line). For explanation of symbols see fig. 9.

values based on the organic matter weight after correction for inorganic matter content (see figs. 18 and 19). Only the corrected values are discussed.

Section 365:1. The degree of humification was very low in the litter layer (ca. 15%). In the moderately consolidated raw humus at 1-8cm, the values were relatively low and constant. The humification increases very little down to 15 cm, then increases gradually from that level, reaching about 80-90% at about 22 cm, and this humification level was general for the deeper part of the section. Thus, a high content of soluble humic matter, relative to the total amount of organic matter, was found in the lower part of the raw humus and below.

At two levels, 23 cm and 26 cm, in the upper part of the arthropod humus, charcoal dust was found in very great quantities. Therefore, the humification values exceed those of the standard, and satisfactory results cannot be obtained at these levels.

Section 365:2. The measured humification values differ somewhat from the values in section 365:1. In the raw humus, the degree of humification was constantly low, about 30-40%, and the humification values increase slightly to about 50% in the upper part of the arthropod humus. At 16-18cm, the values show a distinct increase, to about 80-90%. Similar values are found in the lumbricid humus, at 30-45cm, in a layer rich in organic matter.

The analyses show that the content of KOH soluble humic matter was not related to humus stages, as high humification values were measured in the lower part of the raw humus in section 365:1, whereas the same values were first found in the lower part of the arthropod humus in the other section. Similarly, no relation to soil genesis was found when soluble humic matter was expressed in terms of the volumetric content of the mineral matter.

It may be questioned whether the KOH-soluble humic matter was produced by decomposition processes at the level on which it was found (primary location), or whether it originated from younger strata and has been washed down (secondary location).

The relation between the degree of humification and the number of pollen grains present in the sediment is an argument for the presence of displaced humic matter. Bioturbation is insignificant in the raw humus, where the precipitated amount of pollen is embedded in the litter layer, and no later secondary displacement occurred (Andersen 1979). Decomposition of organic components increase pollen concentration, and humification values should, accordingly, be correlated to pollen concentration - if the soluble humic matter is primarily located. The pollen concentration has been expressed as APcorr. to compensate for variations in tree pollen producti-

Section 365:2
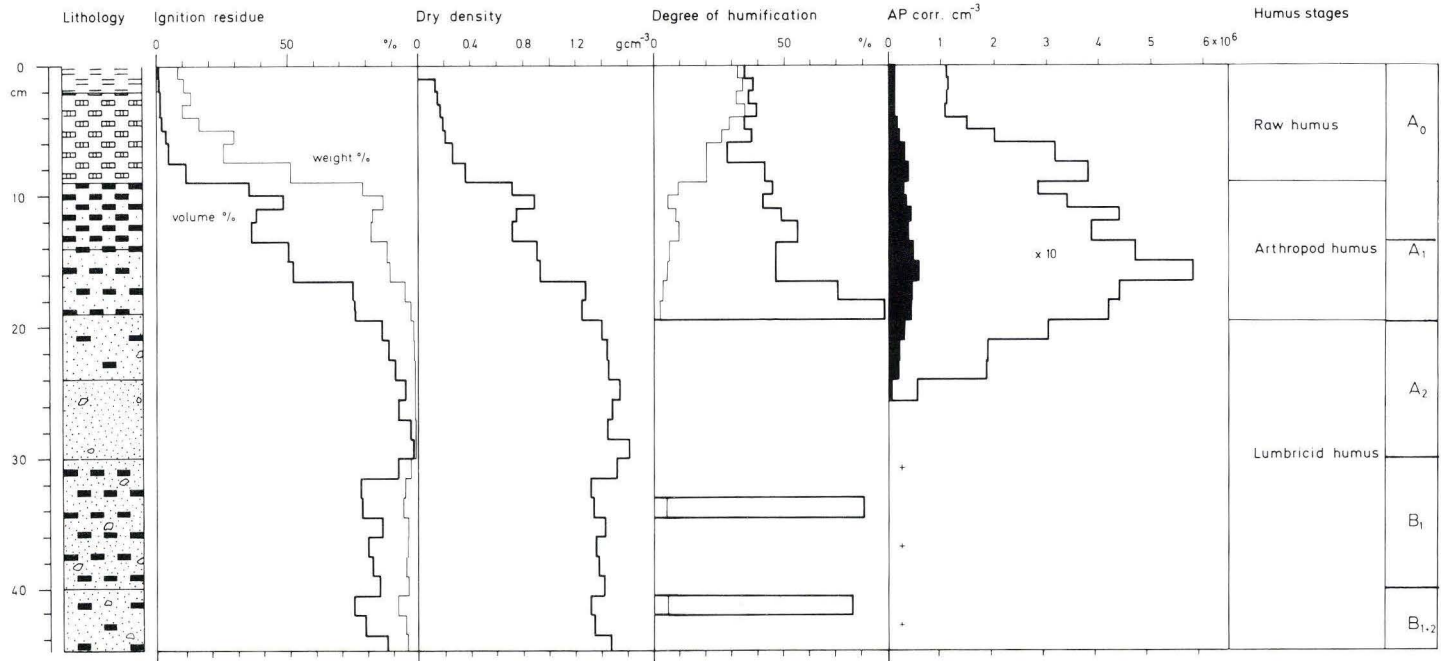
Fig. 19. Measurements of physical properties, degree of humification, and APcorr.cm(matrix)$^{-3}$
at section 365:2. For explanation see fig. 18.

vity. In section 365:1 (fig. 18), the general increase in humifiction values, from about 40% at 11cm to about 80-90% at 20-22cm, is not accompanied by the same increase in pollen concentration values. In section 365:2 (fig. 19), the degree of humification was constant in the raw humus despite increasing pollen concentration values to below.

The pollen concentration values found in the arthropod humus stage also vary independently of the humification values. Bioturbation had more influenced the lower part of the arthropod humus, but possibly not to the extent as to seriously disturb the pollen stratigraphy. The destruction of pollen grains was insignificant both in the raw humus and the arthropod humus.

Because the humification curves are related neither to the pollen concentration nor to humus stages, it is assumed that the displacement of soluble humic matter has been considerable and that the content of secondarily deposited humus was therefore high in the lower part of the sections, especially in the B_1 horizon.

Pollen preservation

Pollen deterioration

To derive the maximum benefit from the data obtained by pollen analysis, it is necessary to determine the effect of pollen deterioration and destruction on the pollen assemblages. Particularly with regard to mineral soils, it has been argued that the pollen composition can easily be changed by selective deterioration (Cushing 1967b, Godwin 1956, Havinga 1974). Fægri and Iversen(1964) also advise against palynological investigations of sediments containing pollen in a state of poor preservation, recommending discard, if more than 50% of the pollen grains of deciduous trees show traces of deterioration.

Physical, chemical and biological processes affect pollen grains from the moment they are liberated from the anthers and, depending upon environmental conditions, the intensity and type of deterioration may vary (Havinga 1971l). Cushing (1967 b) recognized 5 classes of deterioration: 1)corrosion, 2)degradation, 3) crumbled and exine thinned, 4)crumbled but exine normal, and 5) broken. A modified classification was used by Delcourt and Delcourt (1980) based on the primary processes responsible for pollen deterioration. They also distinguished 5 classes: 1)corrosion and 2)degradation, in which the pollen exine was biochemically or chemically deteriorated; and physical types of deterioration including: 3)mechanical damage, 4)concealment by authigenic minerals, and 5)concealment by detritus.

Similar definitions for corrosion were adopted by the mentioned authors; ie., distinctive etching or pitting of the pollen exine (perforation corrosion, Havinga 1971). Biochemical oxidation, related to localized fungal and bacterial activity, was supposed to be responsible for the primary etching process(es) (Goldstein 1960). Pitting - the simple circular to slightly irregular perforations about 0.25-2.0 μm in diameter found, for example, in *Polypodium* spores (see fig. 21). - is possibly caused by chemical oxidation (Brooks and Elsik 1974).

Degradation, according to Delcourt and Delcourt (op. cit.), includes thinning of the exine, fusion of sculptural features, or fusion of structural elements which form the wall layers. This type of deterioration is mainly

A

B

C

D

E
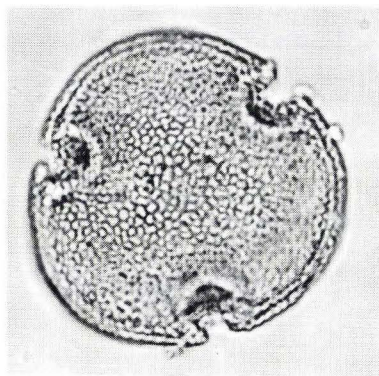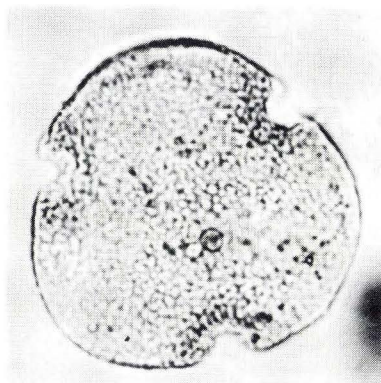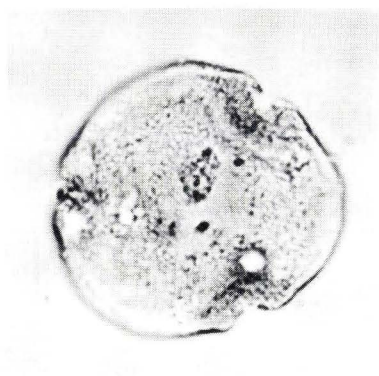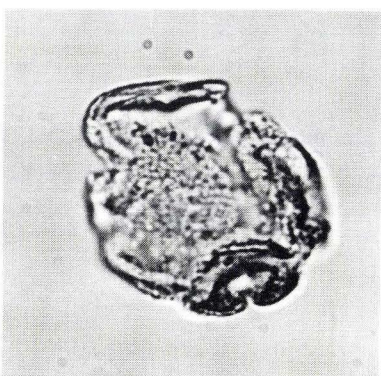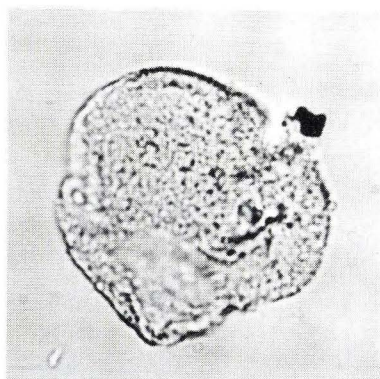
0   20   40 μm

caused by chemical oxidation in aerial or subaerial environments (Havinga 1964). Cushing (1967b) uses the same term in a stricter sense for an exine which has undergone structural changes, so that sculptural and structural details are resolved only with difficulty. The process affects the entire exine which become opaque and has been described as resembling a 'warmed-up wax ball' (Birks and Birks 1980).

In podzols, thinning is a very important type of deterioration (cf. Havinga 1971), whereas degraded grains - sensu Cushing (1967b) - are of little or no importance. Thus, in order to simplify matters, a distinction has been made between two main types of degradation - i.e., fusion and thinning. The first type being identical to Cushing's degradation class, whereas the latter is distinguished by an exine which is noticably thinner than that of normal grains. Structural elements seem to be unaffected, and the loss of material is possibly confined mainly to the endexine (see also Cushing 1967b). The thinning process may affect the entire exine area but it often has a differential appearance, as shown on fig. 21, D and H.

The other classes of deterioration mentioned by Cushing, and by Delcourt and Delcourt are mainly caused by abiotic conditions and considered to be of minor importance here in illuminating soil development, biological activity and pollen representation in podzols.

In the present study, the corrosion and thinning categories have been measured for *Alnus, Betula, Corylus* and *Tilia* (figs. 20-23). Corrosion, thinning and total deterioration (including both categories) are treated separately in tables 3, 4, and 5.

Fig. 20. Pollen deterioration.
A. *Tilia* cf. *cordata.* Section 365:2, 19.5-21.0 cm. Well-preserved pollen grain. The fossulate sculpture is distinct and the endexine and ektexine can be separated. Costae pori are clearly seen.
B. *Tilia* cf. *cordata.* Section 365:2, 19.5-21.0 cm. Thinned and corroded pollen grain. The fossulate sculpture is present and only slightly affected by corrosion, but the exine cannot be separated into two layers. The endexine and the costae pori are more or less obscure. Exine corroded over less than 50% of the pollen surface area.
C. *Tilia* cf. *cordata.* Section 365:2, 19.5-1.0 cm. Thinned and corroded pollen grain. Exine perforated over less than 50% of the pollen surface area. The fossulate sculpture has been damaged in several areas.
D. *Tilia* cf. *cordata.* Section 365:2, 19.5-21.0 cm. Thinned and corroded pollen grain. Differential thinning and corrosion appear. Two pores are strongly deteriorated whereas the third pore is well preserved. Exine corroded over less than 50% of the pollen surface area.
E. *Tilia* cf. *cordata.* Section 365:2, 19.5-21.0 cm. Thinned and corroded pollen grain. Exine corroded over more than 50% of the pollen surface. Costae pori indistinct or totally dissolved.

A

B

C

D

E

F

G

H

I
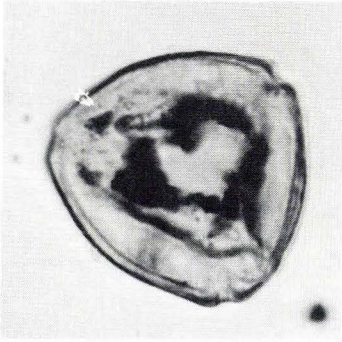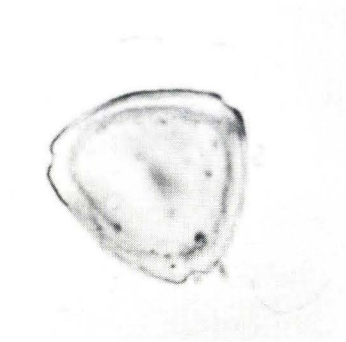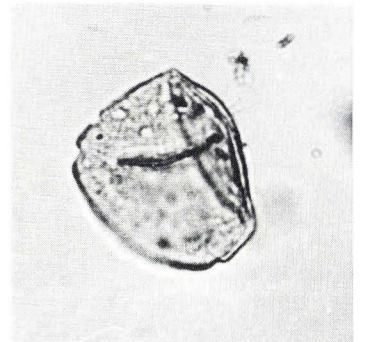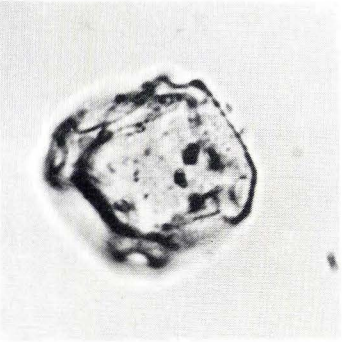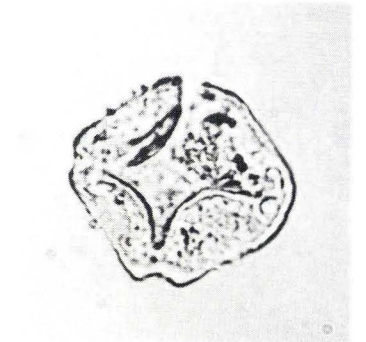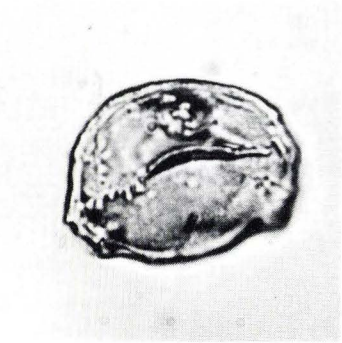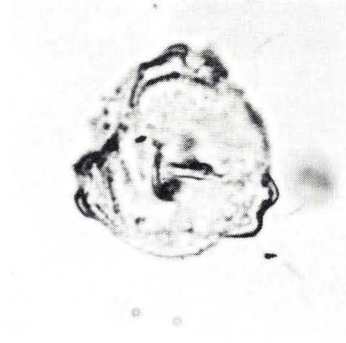
0   20   40 μm

Corroded pollen. Only few grains of *Alnus, Betula,* and *Corylus* were corroded in the raw humus (about 6-8%, table 3), whereas *Tilia* showed distinctly higher values (about 30%). The low number of *Tilia* pollen counted (56 grains) may influence the result, which seems to indicate that *Tilia* is more sensitive to corrosion than types having an almost smooth pollen surface. Corrosion was more intensive in the arthropod humus in both sections (about 25-35%), and *Tilia* shows the highest values in this stage as well. The number of *Tilia* pollen examined was sufficiently high to conclude that *Tilia* has a higher corrosion factor in arthropod humus than other pollen types. Most of the pollen grains in the lumbricid humus (about 50-80%) were corroded in both sections and here the *Tilia* values did not vary from the other species.

Thinned pollen. Thinned pollen grains are frequent in the raw humus in both sections (about 25%, table 3) and, although *Tilia* again shows the highest value, it does not deviate significantly from those of the other species. About half the pollen grains were thinned in the arthropod humus in both sections. The frequency of thinned grains increases with depth and, in the lumbricid humus, about 60-80% of the grains were affected. The thinning percentages

Fig. 21. Pollen deterioration.
A. *Corylus avellana.* Section 365:2, 19.5-21.0 cm. Well-preserved pollen grain. The exine is thick and the endexine is sharply delimited.
B. *Corylus avellana.* Section 365:2, 19.5-21.0 cm. Thinned pollen grain. The pollen surface is smooth and distinct whereas most of the endexine has disappeared.
C. *Corylus avellana.* Section 365:2, 15.0-16.5 cm. Corroded and thinned pollen grain. Exine etched over less than 50% of the pollen surface area.
D. *Alnus glutinosa.* Section 365:2, 15.0-16.5 cm. Thinned pollen grain. The interpore area is especially affected, whereas most of pores and arci are well-preserved.
E. *Alnus glutinosa.* Section 365:2, 19.5-21.0 cm. Thinned pollen grain. The exine is strongly deteriorated. Pores and arci are difficult to observe. Although the exine is very thin, no perforations are observed. Two inclusions of immersion oil are seen.
F. *Alnus glutinosa.* Section 365:2, 19.5-21.0 cm. Corroded and thinned pollen grain. More than 50% of the pollen surface area is corroded.
G. *Betula* sp. Section 365:2, 19.5-21.0 cm. Corroded pollen grain. Ektexine etched over less than 50% of the pollen surface area. Endexine well-preserved.
H. *Betula* sp. Setion 365:2, 19.5-21.0 cm. Corroded and thinned pollen grain. The grain is differentially deteriorated. The pores are well-preserved, whereas the interpore area has been attacked. The exine is corroded over more than 50% of the pollen surface area.
I. *Polypodium vulgare.* Section 365:2, 19.5-21.0 cm. Corroded grain (pitted). Concentric perforations are seen in the spore wall, caused by chemical oxidation (cf. Brooks and Elsik 1974). Magnification x2.

Table 3. Mean pollen corrosion, thinning and total deterioration percentages of *Tilia* (T), *Alnus* (A), *Corylus* (C), *Betula* (B) and x̄(T+A+C+B) calculated for each of the humus stages in sections 365:l and 365:2. The number of samples is shown in brackets.

Corrosion*

Section 365:1	*Tilia* x̄	n	*Alnus* x̄	n	*Corylus* x̄	n	*Betula* x̄	n	T+A+C+B/4 x̄	n
Raw humus	33.30	(1)	6.83	(3)	8.93	(3)	7.27	(4)	9.45	(3)
Arthropod humus	28.81	(6)	22.62	(6)	18.97	(6)	20.47	(6)	22.72	(6)
Lumbricid humus	43.30	(4)	48.97	(4)	47.35	(4)	–	–	46.04	(4)
Section 365:2										
Raw humus	–	–	7.10	(3)	5.30	(1)	4.67	(3)	5.72	(3)
Arthropod humus	46.30	(4)	31.70	(4)	36.25	(4)	32.25	(4)	35.95	(4)
Lumbricid humus	72.30	(2)	73.20	(2)	70.90	(2)	74.60	(2)	72.75	(2)

Thinning*

Section 365:1	x̄	n	x̄	n	x̄	n	x̄	n	x̄	n
Raw humus	34.40	(1)	28.06	(3)	19.30	(2)	24.36	(3)	24.52	(3)
Arthropod humus	53.31	(6)	62.06	(6)	43.30	(6)	62.10	(6)	55.19	(6)
Lumbricid humus	54.92	(4)	70.90	(4)	58.02	(4)	–	–	61.20	(4)
Section 365:2										
Raw humus	–	–	37.53	(3)	35.80	(1)	12.03	(3)	24.46	(3)
Arthropod humus	57.55	(4)	65.55	(4)	55.52	(4)	53.35	(4)	58.03	(4)
Lumbricid humus	74.35	(2)	76.95	(2)	74.80	(2)	81.55	(2)	77.91	(2)

Total Deterioration **

Section 365:1	x̄	n	x̄	n	x̄	n	x̄	n	x̄	n
Raw humus	64.88	(5)	39.23	(22)	27.78	(26)	25.83	(22)	31.54	(22)
Arthropod humus	64.97	(13)	68.49	(13)	46.62	(13)	70.64	(11)	62.24	(13)
Lumbricid humus	67.15	(8)	85.05	(8)	68.50	(8)	–	–	73.65	(8)
Section 365:2										
Raw humus	–	–	33.18	(8)	22.75	(4)	13.10	(8)	21.81	(8)
Arthropod humus	73.96	(7)	75.38	(8)	70.56	(8)	62.67	(8)	70.25	(8)
Lumbricid humus	87.83	(4)	97.48	(4)	91.13	(4)	97.08	(4)	93.28	(4)

*Selected levels   ** All levels

of *Tilia* greatly resemble those of other species at both high and low mean values. The observed relation between thinned *Alnus* and *Tilia* pollen agrees with the results of Havinga (1963), who showed that *Alnus* was most readily affected by oxidation, especially in an alkaline medium.

Total deterioration. The total chemical and biochemical pollen deterioration, defined as the proportion of pollen with corrosion and/or thinning marks, has been calculated for the four species in the two setions. About 20-30% of the grains in the raw humus were deteriorated, and thinning was about 2-3 times as frequent as corrosion (table 3). Pollen deterioration reached about 60-70% in the arthropod humus and, particularly in the lumbricid humus, the grains were badly affected with both thinning and corrosion common. *Tilia* showed greater total deterioration at low mean values than did the other species, whereas the opposite was found at high mean values. *Alnus* was generally further deteriorated than *Corylus* and *Betula,* independent of mean values.

The deterioration measurements show that more pollen grains were affected by thinning than corrosion at all levels in the podzols. This relation was most distinct in the raw humus and in the upper part of the arthropod humus. Corrosion was important mainly in the lumbricid humus and the lower part of the arthropod humus.

Chemical oxidation is supposed to be the primary process responsible for pollen exine thinning. The fact that the thinning percentages show no tendency toward smaller values in the youngest deposits in the raw humus may indicate that the oxidation takes place prior to or contemporaneous with the embedding of the pollen into the sediment, when they are exposed to aerial or subaerial environments (see figs. 22 and 23). This is in agreement with Zetsche and Kalin (1931), who showed that sporopollenin prepared from *Picea* and *Pinus* was subject to oxidation when exposed to the air for long periods, and they concluded that sporopollenin may also be oxidized under natural conditions. Further, the experiments of Havinga (1967, 1971) show that the thinning process is active in podzols in the A_1 horizon at 5 cm with, after only six months, about 1/3 of the embedded grains showing signs of deterioration, mainly thinning. Pollen analytical investigations from natural podzols in the Netherlands have almost invariably shown that the main process during the often severe deterioration of the pollen exine is thinning (Havinga 1971).
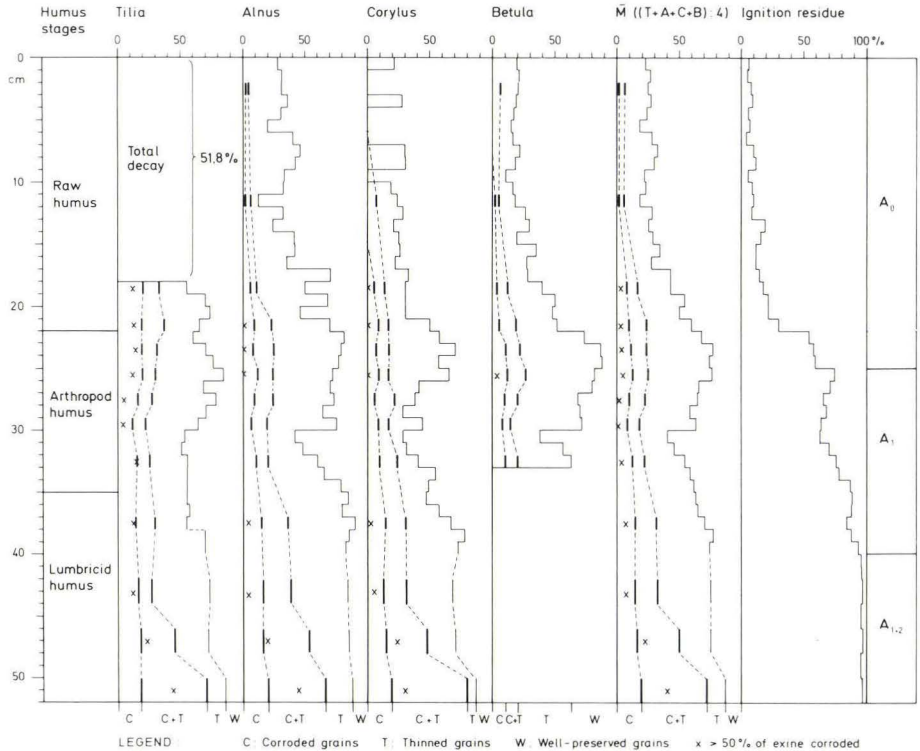
Fig. 22. Section 365:1. Pollen deterioration diagram for *Tilia* (T), *Alnus* (A), *Corylus* (C), *Betula* (B), and the mean deterioration for the four species. The following deterioration categories are measured: corroded (C) and thinned (T), in addition to well-preserved (W) pollen. X indicates the frequency of pollen with 50% or more of the pollen surface area corroded. The total deterioration was measured at all levels, whereas the corrosion and thinning frequency was analysed at selected levels. The diagram shows that thinning is generally more frequent than corrosion, and strongly corroded grains are of importance only in the lowermost samples.

The dependence of pollen deterioration upon soil stages and litter composition

A correlation of the species mean pollen deterioration shows that the raw humus values are significantly different from the arthropod humus values, which differ in turn from the lumbricid humus values (table 4). The results were valid for all categories of pollen deterioration in both sections. The significance test of probability is positive only when the standard deviations

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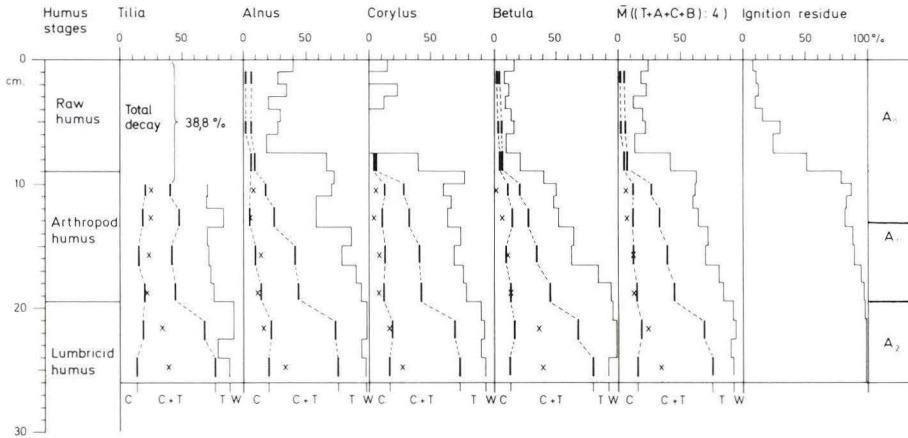
Section 365:2

Fig. 23. Pollen deterioration diagram from section 365:2. For explanation of symbols see fig. 22.

Table 4. Comparison of mean pollen corrosion, thinning and total deterioration percentages for differing soil stages in sections 365:l and 365:2. Uncertain values are shown in brackets. A variance ratio test and a t-test have been used.

	365:1			365:2		
	s diff.		$\bar{x}$ diff.	s diff.		$\bar{x}$ diff.
CORROSION*	P	DF	P	P	DF	P
Raw h. – Arthropod h.	0.11	7	0.006^{xx}	0.001^{xxx}	5	(0.002^{xx})
Arthropod h. – Lumbricid h.	0.001^{xxx}	8	(0.01^{x})	0.32	4	0.003^{xx}
THINNING*						
Raw h. – Arthropod h.	0.30	7	0.002^{xx}	0.29	5	0.003^{xx}
Arthropod h. – Lumbricid h.	0.17	8	0.24	0.05	4	0.04^{x}
TOTAL DETERIORATION**						
Raw h. – Arthropod h.	0.40	33	$<0.0001^{xxx}$	0.33	14	0.0001^{xxx}
Arthropod h. – Lumbricid h.	0.16	19	0.02^{x}	0.004^{xx}	10	(0.001^{xxx})

* Selected levels ^{x} P$<$0.05
** All levels ^{xx} P$<$0.01
                     ^{xxx} P$<$0.001

of the means are similar; therefore, the results are shown in brackets when the probability of standard-deviation similarity is less than 0.05. The calculations show that thinning and corrosion do vary dependent on stage conditions, indicating that different chemical and biochemical environments prevailed during the various stages of soil genesis.

The two investigated podzols developed similarly but the humus stages were asynchronous, and forest composition at the two sites differed in the same humus stages. For example, the arthropod humus in section 365:1 was

55

Table 5. Comparison of mean pollen corrosion, thinning and total deterioration percentages for similar stages in sections 365:1 and 365:2. Uncertain values are shown in brackets. A variance ratio test and a t-test have been used.

	s diff.	365:1		365:2			x̄ diff.
	P	x̄	s	x̄	s	DF	P
CORROSION*							
Raw humus	0.01^{xx}	9.45	± 6.84	5.72	± 0.75	4	(0.40)
Arthropod humus	0.07	22.72	± 3.84	35.94	± 7.53	8	0.007^{xx}
Lumbricid humus	0.06	46.23	±17.62	72.75	± 4.90	4	0.01^{x}
THINNING*							
Raw humus	0.42	24.52	±10.59	24.46	±11.63	4	0.99
Arthropod humus	0.45	55.19	± 8.48	58.03	± 8.75	8	0.62
Lumbricid humus	0.14	61.20	± 5.11	77.91	± 2.04	4	0.011^{x}
TOTAL DETERIORATION**							
Raw humus	0.45	31.54	±11.76	21.81	±11.84	28	0.06
Arthropod humus	0.42	62.24	±10.95	70.25	±10.07	19	0.10
Lumbricid humus	0.05	73.65	± 7.65	93.28	± 3.08	10	0.0006^{xxx}

* Selected levels ^{x} $P < 0.05$
** All levels ^{xx} $P < 0.01$
           ^{xxx} $P < 0.001$

formed prior to about AD 1650 in a *Tilia*-dominant forest, whereas the same type of humus formation took place about AD 1600-1850 in section 365:2, when *Fagus* dominated the forest vegetation. A correlation of pollen assemblages from similar stages in the two sections may therefore illuminate whether the pollen deterioration was related to stages, litter composition or other factors.

The statistical test shows that the amount of corroded pollen was the same at both sites in the lumbricid humus - and possibly in the raw humus as well - whereas in the arthropod humus stage, more pollen were corroded at section 365:2 than at section 365:1 (table 5).

The probability of similar degrees of thinning decreases from raw humus and arthropod humus to lumbricid humus, where pollen from section 365:2 were distinctly more thinned than those from section 365:1.

The total deterioration was the same in the raw humus and the arthropod humus stages at the two sampling sites, although the significance levels were rather low. The total deterioration was significantly lower in the lumbricid humus at section 365:1 than at section 365:2 which was located on levelled and well-aerated ground with a relatively rich subsoil, in contrast to section 365:1 which was found in a small depression on poor glaciofluciatile sand. Thus local hydrological- and lithological conditions contribute to the observed variations in pollen deterioration from the lumbricid humus.

The litter composition is possibly of only minor importance in determining the rate of pollen deterioration, as a *Tilia*-dominated forest prevailed during

Table 6.. Comparisons of the mean pollen percentages of *Alnus, Betula, Corylus,* and *Tilia* in raw humus from section 365:1, and arthropod humus from section 365:2 to test the probability of no difference between contemporary pollen spectra, due to differential pollen destruction. A variance ratio test and a t-test have been used. Uncertain values are shown in brackets.

	s diff.	Pollen % (AP corr.), zones E–F					x̄ diff.
		365:1		365:2			
	P	x̄	s	x̄	s	DF	P
Alnus	0.33	3.80	± 1.66	5.87	± 1.89	17	0.31
Betula	0.13	29.96	±18.00	19.52	±12.04	17	0.17
Corylus	0.002[xx]	3.64	± 1.11	5.40	± 2.93	17	(0.08)
Tilia	0.17	6.97	± 4.05	11.82	± 5.49	17	0.05

the formation of the lumbricid humus at both sections, but resulted in different total deterioration values. The litter composition varied at the formation of the arthropod humus (*Tilia* forest and *Fagus-Quercus* forest) and, here, similar total pollen deterioration values were obtained from the two sections(table 5).

It is concluded that the chemical and biochemical environment on the soil surface and in the bioturbated zone strongly influences the susceptibility of pollen to deterioration, as the experiments of Havinga (1971) have also shown.

Pollen destruction

Differential pollen deterioration and destruction may influence pollen assemblages (Hall 1981; Havinga 1971, 1974; Cushing 1967b). To illuminate the extent to which the pollen assemblages may have changed due to differential destruction, the corroded pollen have been divided into two categories: those with more than 50% of the pollen surface area affected, and those with less. This method of analysis was originally used by S.Th. Andersen, Geol. Surv. Denm. Due to difficulties in precisely delimiting areas of thinned exine, deterioration by thinning was excluded from the examination.

All pollen grains which are undergoing destruction due to corrosion will sooner or later, by definition, be included in the first - 'more than 50%' - category, and the size of this category gives a clear impression of the degree of destruction in the various humus stages. Seriously corroded grains were rare in the raw humus at both sections (figs.22 and 23). The destruction of pollen due to corrosion was, therefore, considered insignificant at this stage. Similarly, the arthropod humus from section 365:1 contains only few seriously corroded pollen and, in section 365:2, only about 5-10% of the *Alnus,*

Table 7. Comparison of the mean pollen percentages of *Alnus, Betula, Corylus* and *Tilia*, in arthropod humus from section 365:1, and in lumbricid humus from section 365:2, to test the probability of no difference between contemporary pollen spectra due to differential pollen destruction. A variance ratio test and a t-test have been used. Only the *Tilia* values varied, whereas all the other dominant tree species show similar percentages. This was also valid for *Quercus* ($\bar{x}$ diff., P = 0.98). The mean pollen deterioration percentages from the same species in the same zone have also been compared to test the possibly of no difference. A variance ratio test and a t-test were used. Uncertain values are shown in brackets.

| | s diff. | Pollen % (AP corr.), zone D | | | | | $\bar{x}$ diff. |
| | | 365:1 | | 365:2 | | | |
	P	$\bar{x}$	s	$\bar{x}$	s	DF	P
Alnus	0.48	9.40	± 1.82	8.70	±1.82	5	0.63
Betula	0.05	3.22	± 1.18	2.90	±0.41	5	0.64
Corylus	0.01[x]	13.77	± 3.72	12.03	±0.90	5	(0.40)
Tilia	0.47	53.80	± 2.95	60.88	±2.91	5	0.025[x]

| | s diff. | Pollen deterioration (T+A+C+B/4) | | | | | $\bar{x}$ diff. |
| | | 365:1 | | 365:2 | | | |
	P	$\bar{x}$	s	$\bar{x}$	s	DF	P
Corrosion	0.003[xx]	23.93	± 0.28	72.75	±4.91	2	(0.005[xx])
Thinning	0.07	56.81	±10.82	79.92	±2.95	2	0.10
Total deterioration	0.08	68.18	± 8.40	93.17	±3.35	4	0.007[xx]

[x] $P < 0.05$
[xx] $P < 0.01$
[xxx] $P < 0.001$

Betula and *Corylus* pollen are seriously corroded, with a higher frequency (25%) for *Tilia*. Although differential pollen destruction cannot be excluded, it has no serious influence on the pollen spectra in the arthropod humus stage, as indicated by a comparison of the *Alnus, Betula, Corylus* and *Tilia* spectra from local forest pollen zones E and F at the two sites. The zones are found in raw humus in section 365:1, with insignificant pollen destruction and in arthropod humus in section 365:2, (table 6).

The frequency of seriously corroded pollen increases in the lumbricid humus, especially in the lower spectra. pollen destruction is considered to be restricted mainly to this stage and comparisons of contemporary pollen assemblages found in arthropod humus at section 365:1 and in lumbricid humus at the other site, may indicate whether differential pollen destruction was of importance in the lumbricid humus, as claimed by, e.g. Havinga (1971,1974), Godwin (1956), and Hall (1981). Table 7 shows that dispite significant variations in pollen corrosion and total pollen deterioration, the pollen assemblages were similar, except for *Tilia,* which has about 6% higher

Table 8. Comparisons of the APcorr. percentage pollen spectra and the percentage pollen spectra of ecological groups in the lumbricid humus from each of the sections 365:1 and 365:2 to test the probability of no difference between pollen spectra due to changes in pollen concentration. A paired observation t-test has been used. The total pollen concentration g(organic matter)$^{-1}$ is also shown.

	Levels		$\bar{x}$ diff.	Total pollen x 10^3
	cm	DF	P	g (organic matter)$^{-1}$
Section 365:1	35–36/50–52	10	0.82	18.8/3.7
	42–44/50–52	10	0.12	18.0/3.7
Section 365:2	19.5–21/24–25.5	10	0.40	24.6/9.0
	21–22.5/24–25.5	10	0.46	19.1/9.0

in the lumbricid humus. Spatial variation in pollen deposition may account for this difference in *Tilia* pollen representation, as it is of the same order as registered i contemporary pollen spectra in raw humus and arthropod humus, with insignificant pollen destruction (table 9). Thus it is concluded, that differential pollen destruction by corrosion and thinning, was not an important source of error in the palynology of the two podzols investigated. Similar results were obtained from analyses of pollen corrosion in subrecent moss-humus samples (Andersen 1970) and gyttja and soil samples (Andersen 1978a). Also the finding that the pollen spectra remain almost stable dispite a very distinct decrease in pollen concentration (table 8), support the result of insignificante differential pollen destruction. The conclusion is based on the assumption that the forest composition has remained stable when acidotrophic brown earth was present. This happened in pollen zone A at section 365:1 and in pollen zone D at section 365:2. The pollen assemblages in forest pollen zone A, at section 365:1 do not show any sign of human influence and a stable *Tilia*-community is supposed to have dominated. Similarly, the forest composition was rather stable in zone D, according to the percentage diagram from section 365:1(plate 1). This zone is found in arthropod humus which has not been bioturbated.

This result contradicts the hypothesis of many authors (eg. Godwin 1956) presuming that *Tilia* pollen is so highly recognizable that it can be recorded even in a very damaged or fragmentary state, and that the relative abundance of *Tilia* pollen in mineral soils is often a result of this recognition factor, coupled with a remarkable resistance to deterioration and selective preservation. The present investigation does not bear out this assumption, and the very high *Tilia*-pollen values often reported (Hyde 1936, Heim 1966, Guillet 1970) are possibly due to a local source.

It is difficult to calculate the relation between pollen destruction by thinning and corrosion. In section 365:1 the fraction of seriously corroded

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pollen increases about 10%, from 46-48 cm to 50-52 cm (fig. 22), whereas the pollen concentration diminishes about 75% (see plate 4 and fig. 18).

It is possible that the higher degree of corrosion is not solely responsible for the observed drastic fall in pollen concentration, and that destruction by thinning is also an important factor (Havinga 1971). It is therefore valuable to know the state of pollen deterioration, including both corrosion and thinning classes, when evaluating pollen analytical data from mineral soils.

Calculation
of sediment accumulation curves

Three levels in the humus layer have been dated by correlating distinct changes in the pollen stratigraphy with historically dated changes in the forest composition. This dating procedure is possible only because bioturbation and vertical mixing of the precipitated pollen was sufficiently low to allow for reliable information on past changes in vegetation.

The most recent change in forest composition can be dated to the winter 1960/61 when *Betula* trees were felled in forest part 365.
Within the investigation area, 9 trees were felled, mainly in the northern part (the position of the stumps is shown in fig. 3). In addition, one *Fagus* and one *Quercus* stump were present in the area, and they are supposed to be of the same age as the *Betula* stumps. The two stumps originate from young sterile trees, whereas the *Betula* trees were about 100 years old. The time of felling was kindly provided by State Forester N.L. Thomsen (pers. comm., 1979) and documented by air photos of the area in early spring 1961. This clearence is the most recent intervention in the area.

The next change in forest vegetation which can be dated is the flowering of *Picea*. The forest management plan from 1922 states that there were some *Picea* stands near the investigation area. They were about 50 years old at that time, and no older stands were present. *Picea abies* generally begins to produce pollen when 20-30 years old, and *Picea* pollen was accordingly supposed to be dispersed into the investigation area about AD 1890-1900.

The oldest change in forest composition which can be inferred from historical information was the felling of *Quercus* trees about AD 1790-1800. The 1868 forest management plan indicates that the *Quercus* trees in the area were about 50-70 years old and this population succeeded an older *Quercus* population which, according to the pollen diagrams, was felled about AD 1790-1800.

The following events are recognized in the pollen diagrams:

Section 365:1. The percentage pollen diagram (plate 1) shows rather constant *Betula* values, about 25-30% at 10-5 cm. A distinct decrease is observed at 5 cm and, above that level, the values are consistently 10-15%. The distinct change in the *Betula* representation at 5 cm is supposed to reflect the felling in the winter 1960/61.

The oldest layer containing *Picea* pollen is at 9-10 cm. This level was dated to AD 1890-1900 and is characterized by a distinct decrease in *Betula* and increasing *Quercus* and *Fagus* values.

A distinct decrease in the *Quercus* curve is seen at 16 cm, and the *Betula* values increase above the same level. These changes cannot be explained by any natural forest development; only by the felling of *Quercus* trees. The clearance is also reflected by increasing values for the open ground herbs. The 16 cm level is considered to date about AD 1790-1800.

Section 365:2. No distinct change in the *Betula* curve is observed which can be referred to the 1960/61 *Betula* clearence. A decrease in the *Betula*
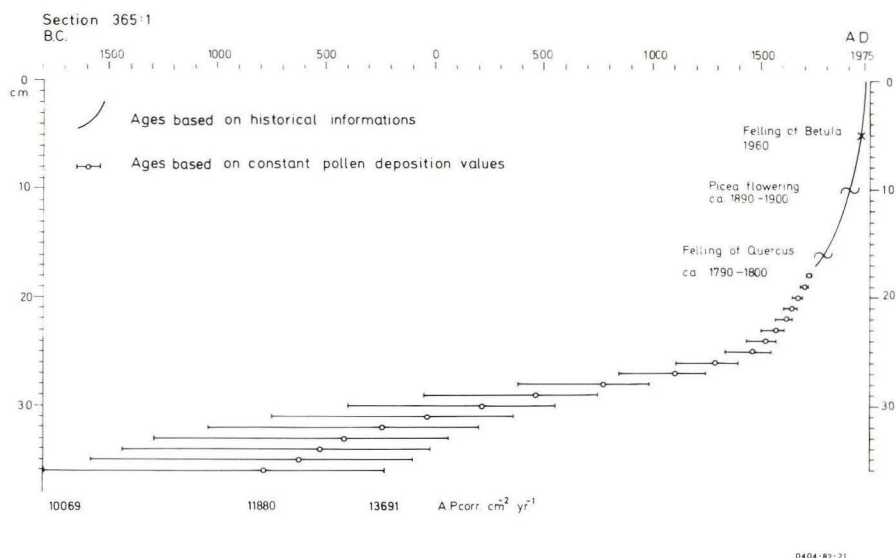
Fig. 24. Relation between sediment age and depth at section 365:1, calculated from historically documented changes in pollen composition in the period AD 1750-1975. Prior to AD 1750 the sediment age was based on a constant pollen deposition rate, equal to the mean value calculated for the period AD 1750-1975. Mean and 95% confidence interval are indicated, cf. fig. 26.

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percentage was seen at 2 cm, but this change was not considered to be synchronous with the 5 cm level in section 365:1 because, there, *Quercus* increases at the same level at which *Betula* decreases. In section 365:2, *Quercus* increases at 4 cm. Therefore the 1960 level is tentatively positioned at 3 cm.

Picea appears at 7.5 cm. The trends in the pollen diagram at that level can be correlated with the 10 cm level in section 365:1 where *Fagus* and *Quercus* increase and *Betula* decreases. The 7.5 cm level is dated to AD 1890-1900.

The forest clearance about AD 1800 is also reflected in the pollen diagram from section 365:2 at 12 cm. Here the *Quercus* values decrease, and those for the open ground herbs expand, but the changes are not as obvious as in section 365:1.

Age-depth curves based on the three dated levels and the year of excavation have been constructed (figs. 24 and 25).

Older sediments cannot be dated from historical sources due to a lack of accurate evidence of vegetational changes. Instead, they were dated by a constant pollen-influx dating method (Dabrowski 1971).

A constant pollen-influx dating method can only be applied to sediments in which the following criteria can be assumed to be fulfilled:
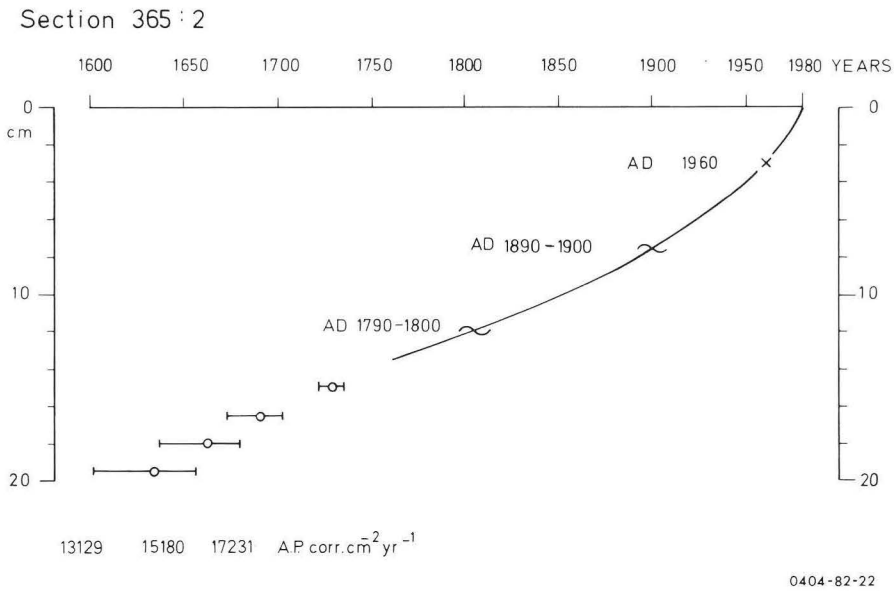
Section 365 : 2

Fig. 25. Relation between sediment age and depth at section 365:2, calculated from historically documented changes in pollen composition in the period AD 1760-1980. Prior to AD 1760, the sediment age was based on a constant pollen deposition rate, equal to the mean value for the period AD 1760-1980. Mean and 95% cinfidence interval are indicated.

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1) the influx values are almost constant in time,
2) the vertical mixing of pollen is insignificant,
3) the destruction, disintegration, or inwash of pollen is insignificant,
4) no sedimentary hiatus is present.

1) The investigation area has never been treeless or seriously cleared, according to the fairly low frequency of open ground herbs in both sections. Because the ratio AP x APcorr.$^{-1}$ shows distinct variations in the arthropod and raw humus stages (see plates 1 and 2), the annual precipitation of APcorr. is considered to be preferable to P or AP values for dating forest humus layers.

The correction factors are calculated from investigations in forest part 370 and 386 in Draved Forest (Andersen 1970). Here the tree crown coverage was calculated to be about 67% of the ground area. Similar values were obtained for the present area (table 1). The correction factors are thus supposed to be valid for part 365. The mean pollen influx values were calculated from periods in which the canopy has been closed - according to the forest management plans since 1868 - and the forest canopy has always been dominated by mature trees. Accordingly the pollen influx is supposed to have been almost constant.

2) In the lumbricid humus stage, the vertical mixing is important. Humus is transported down by burrowing animals, mainly *Lumbricus* species. Pollen spectra from this soil stage cannot be dated.

In the arthropod humus stage, soil disturbance has diminished. Large earthworms have disappeared, and the fauna is dominated by a rich arthropod fauna (Bornebusch 1930). Pollen spectra from arthropod humus show a small-to-moderate modification, as the pollen curves are stretched out because of bioturbation, compared to spectra from deep humus layers in which the mixing is insignificant (Andersen 1979).

In the raw humus stage, bioturbation is insignificant and is dominated by a sparce arthropod fauna - mainly Diplopoda, Isopoda, and Diptera, etc. (Wallwork, 1970) - which are too weakly represented to incorporate the litter into the soil (Andersen op. cit.).

In section 365:1 an insignificant mixing of the pollen assemblages was assumed above 36 cm, and in section 365:2 above 19.5 cm, the supposed transition from the lumbricid humus stage to the arthropod humus stage.

3) The different categories of pollen deterioration have been compared with the humus stages, and neither the pollen deterioration nor the destruction of pollen grains was considered to be important in the raw humus or arthropod

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humus stages (ps. 56 and 58). Secondary inwash of pollen is of no importance in terrestrial forest soils, as seen from the low pollen content in the B_1 horizon at section 365:2 (plate 4).

4) Neither the measured stratigraphy nor the pollen assemblages show any sign of a hiatus.

There thus appears to be a satisfactory basis for using the constant pollen influx dating method in sediments accumulated in the arthropod and raw humus stages at the two sites. Here, all the mentioned criteria are assumed to be fulfilled.

The deposition time for each 1 cm layer from 17 cm to 36 cm in section 365:1 and from 13.5 cm to 19.5 cm in section 365:2 has been calculated based on the APcorr. concentration values and on the assumption that the influx has been constant in time and equal to the mean influx AD 1750/60-1975/80. Both the mean and the 95% confidence interval were used in the construction of the sediment accumulation curves (fig. 24). Using the influx values, the 36 cm level in section 365:1 was dated to about 800 B.C. (1800 B.C. or 200 B.C.). In section 365:2 the level 19.5 cm was dated to about AD 1630 (AD 1600 or AD 1650) (fig. 25).

The pollen diagrams

The percentage diagrams

(plates 1 and 2)

Local forest pollen zone A. (Represented only in section 365:1)
The upper zone boundary has been fixed at the beginning of a gradual decline in the *Tilia* curve.
Description: All pollen spectra in the zone are alike, with high *Tilia* values (about 80%) and an even representation of *Alnus, Corylus,* and *Quercus* (about 5-7%). NAP values are low; only *Dryopteris* and *Polypodium vulgare* are rather frequent.

Local forest pollen zone B. (Represented only in section 365:1)
The upper zone boundary was drawn where the *Quercus* values decrease and the NAP curve rises.
Description: In the lower part of the zone, the *Tilia* curve gradually decreases whereas that of *Quercus* rises. *Betula* is represented by a few pollen grains. *Alnus* and *Corylus* increase slightly. The NAP values remain low although they are higher than in zone A.

Local forest pollen zone C. (Represented only in section 365:1)
The upper zone boundary is marked by a distinct depression of the *Quercus* curve and a contemporary rise in the open ground herbs.
Description: *Quercus* is less frequent in this zone than below, and *Fagus* is continuously represented at about 1%. *Sorbus* and *Salix* are distinctly higher than in the previous zones. NAP increases and *Melampyrum* and *Pteridium* are represented by about 1%, and a few grains of *Trifolium repens* are found.

Local forest pollen zone D
The drastic rise in the *Fagus* curve is used as the upper zone boundary.
Description: The tree pollen curves are rather constant and do not deviate considerably from the frequencies in the previous zone, except that *Fagus* has become more common. The zone is characterized by high values of Poaceae and *Melampyrum. Secale* and *Hordeum*-type pollen were found. The distinct

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maxima in the Poaceae and *Melampyrum* curves in section 365:1 were not clearly reflected in section 365:2, due to bioturbation at this site (Andersen 1979).

Local forest pollen zone E

A distinct fall in the *Quercus* curve at section 365:1 was used as the upper zone boundary. This change is more obscure in the section 365:2 diagram. Description: The *Tilia, Alnus,* and *Corylus* values are relatively low, whereas *Quercus* and *Fagus* are well represented. A *Betula* maximum appears in the lowermost part of the zone and *Viscum* is not found in this zone. The NAP values are fairly high. *Fagopyrum, Secale,* and *Trifolium repens* are present. *Dryopteris* and *Melampyrum* are rather frequent in the section 365:2 diagram.

Local forest zone F

The empirical limit of *Picea* is used as the upper zone boundary. Description: The *Alnus* and *Corylus* curves decrease. The frequency of *Quercus* is relatively low. A distinct *Tilia* maximum is reflected in the lower part of the zone at both sites. *Betula* is frequent and reaches its highest values in the upper part of the zone. The *Fagus* curve shows a minimum in the middle of the zone in both diagrams. A considerable quantity of open ground herbs are represented; *Calluna,* Poaceae and *Melampyrum* are of particular importance.

Local forest pollen zone G

The decline in the *Betula* curve, which is clearly seen in the section 365:1 diagram, is used as the upper zone boundary. For the reasons mentioned on p. 63, the zone boundary was fixed at 3 cm in the section 365:2 diagram. Description: *Quercus, Betula,* and *Fagus* dominate the pollen spectra. *Fagus* is rather constant, whereas *Quercus* reaches its highest values in the upper part of the zone. The *Betula* curve is rather constant in the section 365:1 diagram but decreases upward in the diagram from the 365:2 site. A *Tilia* maximum is found in the lower part of the zone in both diagrams. The NAP curve is constantly represented at frequencies resembling present-day values and only Poaceae pollen grains are frequent.

Local forest pollen zone H

The upper zone boundary is undefined. Description: *Fagus* and *Quercus* are constantly represented in the diagrams at high values, whereas *Betula* is much less important than below. *Picea* reaches about 2-3% in this zone. The NAP pollen spectra resemble those in Zone G.

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Table 9. Comparisons of the APcorr. pollen percentage spectra and the pollen percentage spectra of ecological groups in sections 365:1 and 365:2, to test the probability of no difference due to spatial variation in pollen deposition. A variance ratio test and a t-test have been used and only contemporary spectra from insignificantly bioturbated soils, with no differential pollen destruction, were compared.

	Pollen % (AP corr., P), zones E–H						
	365:1		365:2		s diff.		x̄ diff.
	x̄	s	x̄	s	P	DF	P
Alnus	3.49	± 1.42	4.33	± 2.10	0.05	32	0.21
Betula	25.16	+14.92	18.14	+10.36	0.21	32	0.14
Corylus	2.53	± 1.61	3.55	± 3.12	0.004[xx]	32	(0.22)
Quercus	33.99	+10.28	23.32	± 6.43	0.18	32	0.002[xx]
Tilia	3.76	± 3.60	11.71	± 9.20	0.0001[xxx]	29	(0.009)[xx]
Fagus	28.40	± 7.16	40.67	± 9.08	0.16	32	0.0001[xxx]
SHRUBS	1.07	± 0.55	1.31	± 0.62	0.31	32	0.25
HERBS, field & pasture	2.62	± 0.83	2.21	± 0.54	0.05	32	0.15
HERBS, open ground	8.95	± 5.27	11.85	± 4.90	0.50	32	0.12
HERBS, shaded ground	0.83	± 0.76	0.41	± 0.46	0.06	32	0.14
HERBS, uncertain	1.59	± 1.79	1.67	± 1.25	0.09	32	0.88

[x] $P < 0.05$
[xx] $P < 0.01$
[xxx] $P < 0.001$

The surface pollen spectrum from a moss polster on a *Quercus* stump 3 m NE of section 365:1 has a pollen composition similar to the spectra in zone H at section 365:1 (plate 1).

Comparison of the pollen percentage diagrams

Selected pollen spectra from the two neighbouring sites have been compared in order to analyse similarities and dissimilarities. Only pollen spectra from the arthropod and raw humus stages are analysed, as they represent stages in which little or insignificant bioturbation has taken place. A comparison is only possible for local forest pollen zones E,F,G, and H - as soil genesis has been asynchronous at the two sites. The pollen spectra of the individual taxa or ecological groups have not been analysed separately for each of the zones, due to the low number of observations in each zone. Therefore, only the test including the pollen zones E-H is shown (table 9).

In zones E-H, the *Alnus, Betula,* and *Corylus* pollen values are similar for the two sections, whereas *Quercus* is more frequent in section 365:1, and *Fagus* and *Tilia* more frequent in section 365:2. A similar difference between *Fagus* and *Quercus* pollen percentages was also reflected in the modern pollen spectra. The pollen spectrum from the litter layer, 0-1 cm, at section 365:1, and the spectrum from the moss polster near this section, show

distinctly higher *Quercus* values than were found in the litter layer, 0-1 cm, at section 365:2. Measurements of the crown area show that *Quercus* today occupies a larger proportion of the total crown area than *Fagus* at section 365:1, and vice versa at section 365:2 (table 1 and fig. 3). Thus, the distribution of the present tree vegetation is reflected in the surface pollen spectra, and this relation can be traced about 300 years back in time. Differences up until 10% in tree pollen representation may therefore be obtained from neighbouring sites and the differences are sertainly not caused by variations in pollen preservation.

In zones E-H the curves for shrubs and the different herb categories are similar in the two diagrams.

The influx diagrams

Comparison of pollen influx rates

The pollen influx was calculated from measurements of pollen concentration and sediment accumulation rates. The calculations include the period AD 1750-1975 at section 365:1 and AD 1760-1980 at section 365:2.

At section 365:1 the mean total pollen influx was 41456 grains $cm^{-2}year^{-1}$ since AD 1750, whereas the value was a little higher at section 365:2, 45969 grains $cm^{-2}year^{-1}$. Considering the APcorr. values, about 11880 grains $cm^{-2}year^{-1}$ were accumulated at section 365:1 and a little more at section 365:2 (table 10). Andersen (1974) calculated pollen influx in the same forest from pollen traps and moss polsters. The pollen precipitation varied from about 3000 (*Fraxinus*) to 30000-40000 (*Quercus, Betula, Alnus*) pollen grains

Table 10. Yearly pollen influx mean, coefficient of variance (C%), and 95% confidence intervals (c.i.) calculated for each of local forest pollen zones F, G, and H since 1750 (1760) at sections 365:1 and 365:2.

		P $cm^{-2}year^{-1}$			APcorr. $cm^{-2}year^{-1}$		
Section 365:1	n	$\bar{x}$	C, %	95% c.i.	$\bar{x}$	C, %	95% c.i.
Zone H	4	41030	34.17	18720–63340	13205	34.00	6060–20350
G	5	34259	27.14	22715–45803	11134	15.87	8939–13329
F	6	49230	30.14	33408–65052	12305	32.10	8093–16517
AD 1750–1975	16	41456	32.59	34257–48655	11880	28.61	10069–13691
Section 365:2							
Zone H	3	46551	27.36	14908–78194	17068	27.73	5310–28826
G	4	35752	11.77	29056–42448	12817	11.11	10552–15082
F	4	53938	17.99	38496–59380	16055	17.91	11478–20632
AD 1760–1980	12	45969	24.41	38752–53186	15180	21.01	13129–17231

Table 11. Comparison of yearly pollen influx means at sections 365:1 and 365:2 for each of the local forest pollen zones F, G, and H. A variance ratio test and a t-test have been used. C= coefficient of variance.

Σ P cm^{-2} year^{-1}

Zone in section 365:1 and 365:2	C, diff. P	DF	$\bar{x}$, diff. P
H	0.46	5	0.62
G	0.07	7	0.61
F	0.22	8	0.70
AD 1750–1975/AD 1760–1980	0.26	26	0.82

Σ APcorr. cm^{-2} year^{-1}

Zone in section 365:1 and 365:2			
H	0.44	5	0.84
G	0.35	7	0.92
F	0.28	8	0.93
AD 1750–1975/AD 1760–1980	0.42	26	0.99

cm^{-2} year^{-1}. The value for *Fagus* was about 10000 grains cm^{-2}year^{-1} in the traps, and a little less in the polsters, and this result agrees fairly well with the APcorr. influx values found in the present study.

The pollen influx at the two sites has been compared to test the probability of a similar pollen precipitation at the two sites (table 11). Including the entire period AD 1750-1980, both the total pollen influx and the APcorr. influx have been similar for the last 230 years. A comparison of the total pollen influx at the two sites for each of the local forest pollen zones within that period also showed a close agreement between the sites(table 11).

Analysis of the total pollen influx curves within the pollen zones shows interesting variations. While the mean pollen influx in pollen zone F as a whole, was about the same at both sites(tables 10 and 11), much lower influx values were registered in the lower part of this zone in section 365:1 - in contrast to the high values found in section 365:2(fig. 26, plate 3). This difference is explained by felling of *Quercus* about AD 1800 near site 365:1. The percentage pollen curves also show that the effect of felling on the 365:1 site was much greater than on the second site (plates 1 and 2). The trends in the total pollen influx curves are similar in Zone G, whereas differences are obvious in Zone H, as the superficial samples include only a few years' pollen influx and are thus influenced by considerable annual variations in pollen productivity (Andersen 1974).

Working separately for each section, the total P and APcorr. influx values were also analysed to test whether the amount of pollen precipitated was

Section 365:1

AP corr. cm^{-2} yr^{-1} Tree pollen frequency   Local forest pollen zone

0404-82-23
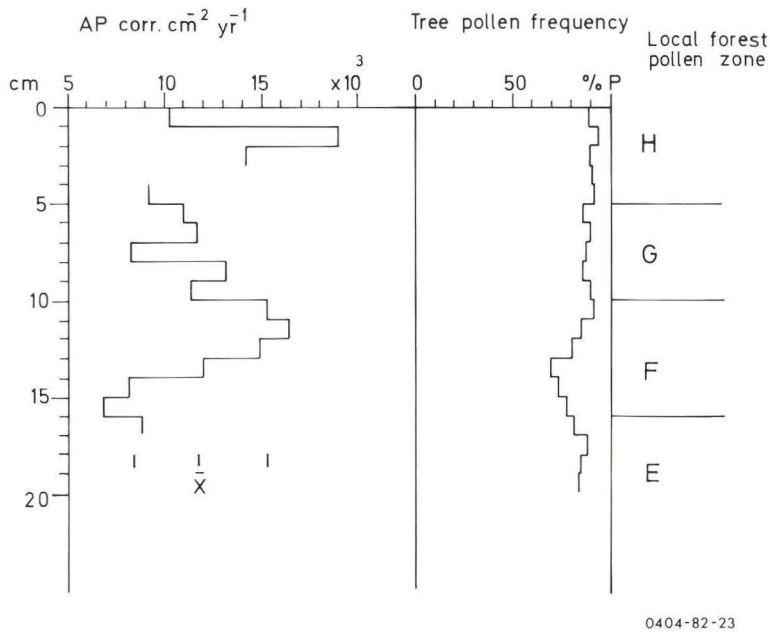
Fig. 26. Yearly corrected pollen deposition at sections 365:1 and 365:2. Mean and the 95% confidence interval calculated for the period AD 1750/60-1975/80 are indicated, cf. table 10.

Table 12. Comparison of yearly pollen influx means in local forest pollen zones G-F,H-F, and H-G from sections 365:1 and 365:2. Uncertain values are shown in brackets. A variance ratio test and a t-test have been used. Uncertain values are shown in brackets. C= coefficient of variance.

Σ P cm^{-2} year^{-1}		C, diff.		$\bar{x}$, diff.
Section 365:1	Zones	P	DF	P
	H–G	0.20	7	0.41
	H–F	0.48	8	0.41
	G–F	0.16	9	0.08
Section 365:2	H–G	0.03[x]	5	(0.17)
	H–F	0.30	5	0.42
	G–F	0.31	6	0.01[x]
Σ AP corr. cm^{-2}year^{-1}				
Section 365:1	H–G	0.03[x]	7	(0.38)
	H–F	0.37	8	0.75
	G–F	0.05	9	0.55
Section 365:2	H–G	0.02[x]	5	(0.15)
	H–F	0.18	5	0.74
	G–F	0.10	6	0.09

[x]$P < 0.05$

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constant in time (table 12; see also fig. 26). In general, the comparisons showed that this was true. The difference between some of the zones cannot be tested because the variance was too great.

Although the statistical tests indicate a constant pollen influx when comparing larger true units, such as pollen zones or the entire period AD 1750-1980, it is obvious that the pollen influx shows considerable variations when using a smaller true-scale; here, differences of factor 2 are registered - eg., in section 365:1, in pollen zone F. These short-term changes may be caused by variations in pollen productivity per crown-area unit, or variations in the total pollen producing area.

The diagrams (plate 3)

The influx diagrams are considered valuable for reconstruction of the past vegetation, as both the short-term pollen production and the sediment accumulation rates vary. If they had been almost constant, the percentage data would convey just as much information as do the influx data. The diagrams are based on calculated influx values without correction for differential pollen productivity.

Local forest pollen zone F, AD 1790/1800-1900
The mean influx of pollen was about 50 000 grains (P) $cm^{-2}year^{-1}$, with relatively large variations. In section 365:1 the smallest values were found in the lower part of the zone, possibly because the clearance about AD 1800 took place near this site and the new generation of trees had not all matured. In the diagram from section 365:1, an increased *Betula* pollen influx was registered even in the lowermost spectrum, as the 1 cm thick layer represents about 25 years and *Betula* became fertile after 10-15 years. *Quercus* mature after 40-50 years, so the young trees will have produced pollen about AD 1840-1850, and a rise of the *Quercus* pollen curve is indeed seen in the middle of the zone. At 14 cm, the influx of *Betula* pollen shows another rise, followed by high values of most NAP species, with the *Calluna* maximum especially pronounced. These changes were the result of a felling around AD 1840 (see p. 23 and table 2).

In section 365:2 the felling of *Quercus* around AD 1800 has not influenced the pollen influx seriously, whereas the clearance about 40 years later was obvious and the felling possibly included some *Alnus, Tilia,* and *Fagus* trees.

Local forest pollen zone G, AD 1900-1960

The total pollen influx was rather constant, about 35000 grains $cm^{-2}year^{-1}$, with the highest values in the lower part of the zone. About AD 1900 *Betula* trees were felled at an age of about 100 years.

This vegetational change was clearly reflected in the influx values (fig. 26, plate 3). Contrary to previous clearances, open ground areas were possibly small and the canopy quickly recovered.

The *Quercus* trees originating from the AD 1800 clearance, and some *Betula* trees, were cut in the period 1922-1937 according to the forest management plans. This felling is registered at both sections. Although influx changes are seen at 8 cm in the *Quercus* and *Betula* pollen curves from section 365:1 (plate 3), it was assumed that the clearance should be more clearly reflected in section 365:1 as 130 years earlier. Today the present *Quercus* trees are about 140 and 100 years old (see table 2) and the younger generation produced pollen from about AD 1930. Hence the decrease of *Quercus* influx due to felling of the old trees may have been counteracted by increased pollen influx from the younger *Quercus* generation at the same time.

Local forest pollen zone H, AD 1960-present

The total pollen influx values are a little higher than found in the previous zone. The felling of *Betula* trees in 1960/61 was reflected in the section 365:1 diagram, but not in that from 365:2. Only old trees were cut, leaving small glades which soon closed.

Conclusion. The calculations indicate that pollen influx is fairly constant, and the spatial variation low within the same forest community, when larger time units are considered. On the contrary distinct influx variations are found when using a smaller true-scale, which shows that the pollen source area is very small (cf. Andersen 1970). The pollen influx rates are accordingly very sensitive to local vegetational changes, which are often more clearly shown from influx diagrams than from percentage diagrams, cf. the felling of Quercus in the management period 1922-37(plates 1 and 3).

The influx diagrams show that open ground with good light conditions appeared after the felling about AD 1800 and AD 1840, succeeded by a vigorous regrowth of *Betula,* shrubs and herbaceous plants; whereas the following fellings included only smaller areas with little effect on the ground flora. The diagrams stress the importance of including the time of tree maturity when interpreting the composition of vegetation from pollen spectra which include only a few years pollen influx, as also pointed out by Andersen (1979).

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The concentration diagrams

Prior to AD 1750, sediment matrix accumulation rates cannot be calculated independently of the pollen influx, and therefore only concentration diagrams are constructed for the older layers.

Pollen concentration calculations are highly influenced by the structure and texture of the matrix. Therefore, concentration diagrams are most frequently calculated from aquatic sediments with only small changes in matrix composition. In terrestrial soils, and especially in podzols, the matrix shows considerable vertical variations and only few concentration diagrams have been elaborated (Dimbleby 1965).

Because of the matrix complexity, two concentration diagrams were constructed with differing calculation bases to minimize false information. Only the organic matter concentration diagram ($P \times g^{-1}$) is published, and the pollen diagrams are discussed for each of the humus stages as the pollen concentration is related mainly to them.

The matrix concentration diagram ($P \times cm^{-3}$). (not published)
The concentration values are mainly determined by the content of inorganic matter, structure (density), and the type of organic matter. Secondary humic matter has a distinct effect on the values in the lumbricid humus, especially in the B horizon in section 365:2, where primary humus was of little importance. The pollen concentration varies considerably within the profile and in the same humus stages at the two sites.

In section 365:1, the smallest concentration (0.1×10^6 grains x cm^{-3}) was found at 50-52cm. The concentration reached 2.5×10^6 grains x cm^{-3} at the transition from the lumbricid humus to the arthropod humus stage. The highest pollen concentration was found in the arthropod humus at 29-27cm (9×10^6 grains x cm^{-3}). The pollen concentration was low at the transition to the raw humus stage (1.5×10^6 grains x cm^{-3}).

At section 365:2, much lower values were observed in the lumbricid and the arthropod humus; eg., the maximum value in the arthropod humus reached only 2.5×10^6 grains x cm^{-3}.

Although the individual curves for species - or groups of species - vary, they all show the same trend in concentration values. The matrix concentration diagram was, therefore, supposed to be too unreliable for analysing vegetational trends and is not included here.

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The organic matter concentration diagram (P x g^{-1}). Plate 4

The concentration of tree pollen is given as AP and APcorr. values per g organic matter, and only the APcorr. values will be discussed.

Lumbricid humus stage. In section 365:1, relatively small total pollen concentration values were calculated for the lowermost level, 52-50 cm, whereas the concentration was about 7 times higher at 48-46 cm. This drastic change was supposed partly to be caused by higher content of secondary humus at the lowermost level. The decay and destruction of pollen grains may also influence the trend (see p xx). The total APcorr. concentration values were relatively constant from 48 cm and upwards except for the minimum at 40-37 cm. The *Tilia* curve shows the most pronounced minimum, which is also reflected in the other pollen curves except for that of *Quercus.* This variation in pollen curves is not reflected in the percentage diagram (plate 1). The minimum is therefore considered to originate from changes in the matrix, either its composition, origin, or accumulation rate. The pollen deterioration curves (fig. 22) show no variations at that level, but the humification curve reaches a maximum at 40-37 cm (fig. 18). It is therefore assumed that the content of secondary humic matter was higher at that level and thus may have caused the observed changes in concentration values.

In section 365:2 the pollen concentration was very low in the B_1 horizon, at 40-35 cm. The pollen concentration was about 800 times higher at 23-24 cm. and rather constant above that level.

All the pollen grains at the two levels in the B_1 horizon were strongly deteriorated and it was difficult to determine if they were secondarily deposited, or whether they originated in the brown earth.

The pollen concentration in the upper part of the lumbricid humus was about 12-15x10^6 grains g^{-1}, and similar values were found in section 365:1, dispite a metachronous formation of perhaps 2500 years.

The arthropod humus stage. At 35-29 cm in section 365:l, the total APcorr. concentration values are lower than in the upper part of the lumbricid humus. This minimum does not resemble the minimum at 40-37 cm because the different tree pollen curves and the curves for the herbaceous pollen vary independently. Accordingly the onset of the upper minimum was also clearly reflected in the percentage diagram at 35 cm (plate 1). *Alnus, Corylus,* and *Tilia* show a minimum just above 35 cm, whereas the *Quercus* and *Betula* values are similar to those in the upper part of the lumbricid humus. Only the

NAP curve shows increasing values. Above 32 cm, the concentration values for *Alnus, Corylus* and *Quercus* exceed those in the lumbricid humus, whereas *Tilia* was still represented by low concentration values. The highest values for *Alnus* appear at 32-30 cm, whereas the maxima for *Corylus* and *Quercus* were found at 29-27 cm after the termination of the *Tilia* minimum. The NAP curve and the 'open ground herbs' curve reach high values at 31-28 cm.

The minimum at 35-29 cm for the APcorr. curve and most of tree pollen curves may theoretically be caused by:
1) increased sediment accumulation rates
2) a higher content of secondary humic matter
3) increased pollen destruction
4) decreased pollen influx

1 and 2) These possibilities presuppose a general change in the organic matter and should not therefore, influence the percentage calculations. The percentage diagram from section 365:1 does show distinct changes in the pollen curves above 35 cm, and general variations in the composition of the organic matter cannot be responsible for the observed minima. In addition, the degree of humification was constant at 35-29 cm (fig. 18).

3) Theoretically, pollen decay and destruction may cause changes in both the concentration and the percentage diagrams. However, neither the pollen decay curves nor the 50% corrosion curve for the individual species (fig. 22) show variations at that level which could account for the observed concentration variations.

4) A lowering of the pollen influx is a possible explanation for the minimum. Both the concentration diagram and the percentage diagram indicate better light conditions on the ground because the 'open ground herbs' curves increases at 35 cm. The Poaceae curve shows a small maximum at 35-33 cm and *Betula* is, for the first time, sparsely represented. The decreasing influx values were possibly caused by Man's activity in the forest.

In the upper part of the arthropod humus, above 27 cm, the concentration values decrease for all the tree species. The same change was not reflected in the percentage diagram. The general trend in the concentration curves is possibly influenced by changes in organic matter composition, and perhaps reinforced by human interference.

In section 365:2 the concentration values in the lowermost part of the arthropod humus resemble those of the lumbricid humus but decrease from 18 cm, parallel with changes in humification values (fig. 19). The concentra-

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tion values in the upper part of the arthropod humus are approximately the same as found in section 365:1, 3×10^6 grains g^{-1}.

Raw humus stage. No serious change was observed at the transition from the arthropod humus to the raw humus in section 365:1, and the values in the lower part of the raw humus are rather constant. The organic matter is therefore supposed to be of relatively stable texture at that level.

Conclusion. A comparison of the concentration diagrams from sections 365:1 and 365:2 shows that the total APcorr. values are very much the same within the same stage; $12\text{-}15 \times 10^6$ grains g^{-1} in the upper part of the lumbricid humus and the lower part of the athropod humus, and about 3×10^6 grains g^{-1} in the upper part of the arthropod humus. The content of secondary humic matter has a serious influence on the pollen concentration values in the lumbricid humus stage in both profiles.

While concentration diagrams based on matrix calculations seem to be of minor importance for the understanding of vegetational development, the organic matter concentration diagrams contribute important information and are considered to be an valuable supplement to the percentage diagrams.

Forest development

The vegetational development during the past 3-4000 years within the investigation area is based on information derived from the percentage (%), organic matter concentration, and influx diagrams at sections 365:1 and 365:2.

Local forest pollen zone A, Subboreal Time

The %-spectra show that an almost pure *Tilia* vegetation dominated the area. *Alnus, Corylus* and *Quercus* were equally represented and are supposed to have been more frequently represented in the area than they are today. *Viscum* and *Hedera* were flowering in the canopy layer. Shrubs and most herbs were uncommon due to unfavourable light conditions, and only shade-tolerant species such as *Polypodium vulgare* and *Dryopteris* were relatively frequent. Lamiaceae, cf. *Ajuga repens,* indicate moist soil conditions around 365:1 - which are also inferred from the sediment structures (p. 31).

Pollen of *Sorbus aucuparia, Salix, Anemone,* Lamiaceae cf. *Ajuga repens,* and *Dryopteris,* indicating neutral-acidotrophic soil conditions, are found together with acidotrophic species as *Frangula alnus.* Thus, arthropod humus or raw humus was accumulated in the area, which was possibly dominated by neutral-acidotrophic lumbricid humus, according to the investigations of initiation of humus accumulation in the area (p. 38). Vertical mixing of the soil precludes a detailed study of the vegetational development during the period. It may yet be concluded that the pollen spectra reflect a primeval forest, natural for the area and growing on neutral-acidotrophic brown earth in an undisturbed state.

Local forest pollen zone B. Late Subboreal Time-Medieval Time (about AD 1300)

The %-pollen spectra gradually change in the lower part of the zone. A detailed analysis of the changes in the pollen concentration values at the same level (p. 76) has shown that they presumably originate from reduced tree pollen influx values, mainly *Tilia* pollen,caused by Man's interference in

the area. The small but distinct maximum for Poaceae, and the presence of *Melampyrum* and *Pteridium* suggest a slight clearing of the area. If larger areas were felled, the resulting improvement in light conditions would certainly be reflected by much more distinct rises in the 'open ground herbs' pollen curve, and/or in the presence of a *Betula* maximum such as that seen after the extensive felling of *Tilia* at 21 cm, and *Quercus* at 16 cm in section 365:1 (plate 1).

Thus, the peasants did not fell the trees, but exploited the primeval forest directly. Most likely, the reduced tree pollen influx was caused either by standard pollarding, cutting all the branches and twigs, or by shredding, a variant of pollarding in which the side branches are cut off, leaving a tuft at the top to feed the tree (see fig. 27). The concentration diagram (plate 4) cannot solve which of the harvest methods that was used. The pollen diagram (plate 1), shows that *Viscum* was present also after the human interfearence. *Viscum* is confined mainly to the small branches and twigs in the canopy and would accordingly not persist if standard pollarding was practiced, and it would possibly not manage to re-establish itself on the pollarded trees, as they were often lopped, and *Viscum* needs at least six years to mature (pers. comm. S. Ødum 1983). In the early Middle Ages the rotation time was about 6-15 years (Rackham 1980), and it is assumed that the intervals were perhaps shorter before that time. Therefore, it is assumed that the trees were shredded for leaf-hay gathering.

According to Rackham (1980), shredding is often mentioned in documents up to about AD 1600 in England, and is still practiced in parts of France and Germany, but has long been extinct in Northern Europe. Shredding is still widely practiced in Kashmir (Heybroek 1963). Therefore it is considered likely that shredding is an old tradition commonly practised in Medieval and prehistoric times in Denmark.

Trees are not seriously damaged by shredding and can be lopped over a long period. But while shredding does not inhibit all flowering, the practice does reduce the extent of the pollen producing area. This type of woodsmanship appears to have been practiced over a long period of time (1500-2000 years), and the investigation area must have been part of a larger forest area managed in this manner.

Tilia and *Corylus* in particular show low concentration values at 35-29 cm (plate 4), and they are more valuable fodder plants than *Alnus* and *Quercus*. These trends are quite different from those in the percentage diagram (plate 1) where only the *Tilia* curve decreases, whereas *Quercus* increases and the other tree species remain almost stable. The concentration diagram indicate that first of all, the *Tilia* trees, and also *Corylus, Alnus,* and perhaps *Quercus,* were lopped and the products used as leaf-fodder. Historical documents

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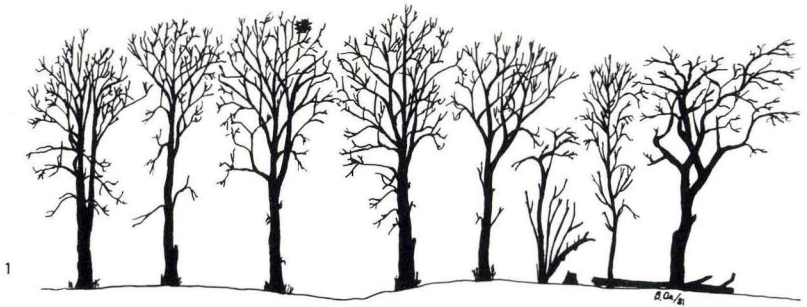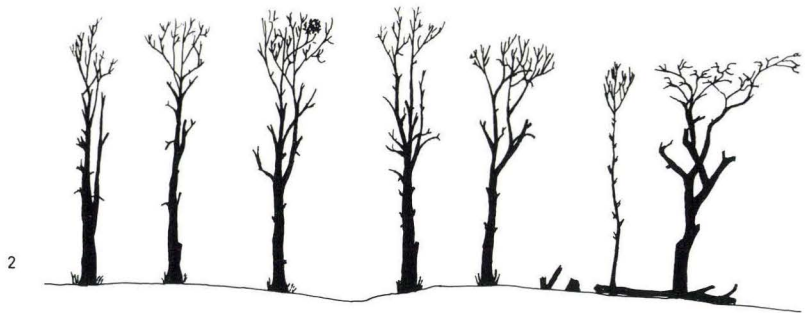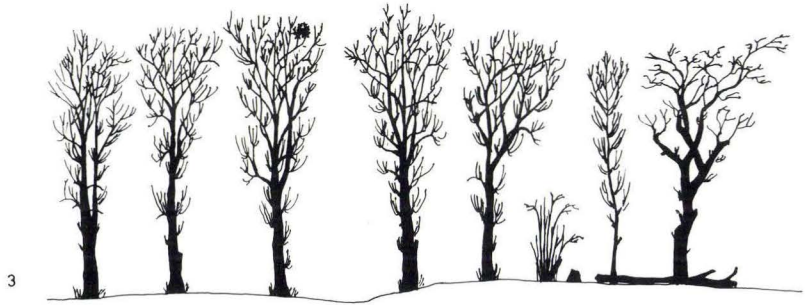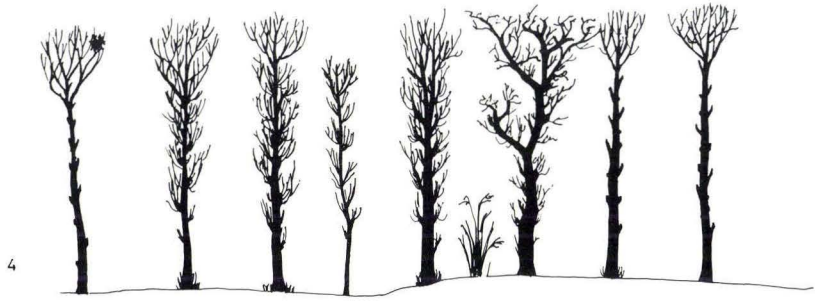
confirm that almost every tree species could be used - even *Alnus* (Rackham 1980).

The primeval forest and the first stages after the introduction of forest shredding are illustrated in fig. 27.

The *Tilia* minimum terminates at 29 cm, and a maximum in pollen concentration is seen for most trees at 29-27 cm (plate 4). The concentration values of total APcorr. at that level resemble the values at 37-35 cm and 48-42 cm, prior to the discussed human interference reflected at 35-29 cm. The frequencies of *Quercus* and *Corylus* in particular show higher values than previously, whereas *Tilia* shows the opposite trend. The shrubs and herbaceous plants are also more frequent at 29-27 cm than below 35 cm.

The *Tilia* maximum was also reflected in the %-diagram at 29-27 cm and the mentioned relations in concentration-values were also valid for the %-values, although less distinct. The observed variations at 29-27 cm in concentration- and %-pollen values were possibly caused by reduced human activity in the area, as the pollen values tend to resemble those in local forest pollen zone A. Neither the humification, dry density, ignition residue, nor pollen deterioration curves show any significant change at 29-27 cm - so the higher concentration values are therefore considered to indicate a higher deposition of tree pollen in this period.

Soil leaching became more pronounced during this zone and arthropod humus developed at site 365:1, whereas the formation of lumbricid humus continued in large areas, including site 365:2.

Because the dating method used here is based on the assumption of constant pollen influx, it is difficult to date this zone since it is supposed that the pollen influx was reduced because of shredding. It may therefore be more reasonable to use a smaller influx value for zone B than the mean value for AD 1750-1975; if, the lower value for the 95% confidence interval (10069 grains(APcorr.)$cm^{-2}year^{-1}$) is introduced, this forest stage can be estimated to have lasted for about 2700 years, including most of the Bronze Age and the Iron Age until Medieval Time. The *Tilia* maximum at 29-27 cm, possibly reflecting a reduced human interference, would therefore date to after the Roman Iron Age.

Fig. 27. Illustrations of forest architecture before and after the introduction of shredding management. 1: Primeval *Tilia* forest with *Corylus* and *Quercus. Viscum* is present in the canopy (local forest pollen zone A). 2: The same trees after being shredded. The pollen producing area has been reduced (local forest pollen zone A/B). 3: The same trees a few years later. The canopy has recovered and is relatively dense, preventing a vigerous flowering of the ground flora. 4: Several tree-generations later. The forest vegetation has not changed and the canopy continues to be relatively dense (local forest pollen zone B). (Tree architecture adopted from Rackham 1976: 21.)

Local forest pollen zone C, Medieval Time (about AD 1300-1400/1500)

The forest composition was similar to that in the preceding period except that *Quercus* was less frequent. The sudden decrease in *Quercus* %- and concentration-values at the transition from zone B to C possibly indicates felling. A distinct *Hedera* maximum appears and for the first time shrubs were able to flower luxuriantly. The light-demanding herbs, especially Poaceae, only show insignificant changes. Thus, the canopy was more open, allowing the shrubs to flower, but the light conditions remained unfavourable for the ground flora. The recorded increase in the 'open ground herbs' pollen curve may have been caused by increased long-distance transport, which may explain the increased *Fagus* percentages as well.

The forest may have been managed as in the previous periods, with *Tilia* particularly being shredded. The fact that *Betula* does not show any response to the increasing light despite adequate soil conditions, while the response of *Sorbus* and *Hedera* is clear, seems to indicate an intensive nursery of the area. *Betula* does not produce valuable leaf-hay and was accordingly expunged.

Local forest pollen zone D, about AD 1400/1500-1650

An open *Tilia* forest mixed with a few *Alnus, Corylus* and *Quercus,* dominated the forest vegetation. *Fagus* remained absent from the investigation area, as evidenced from the low percentage values.

Because of favourable light conditions, the ground flora became more luxuriant; Poaceae and *Melampyrum* were common. The shrub flora was dominated by *Sorbus, Salix* and *Frangula.*

The finds of *Trifolium repens* and *Ranunculus* pollen may indicate the presence of browsing animals (Iversen 1964,1969), but the few finds might as well be interpreted as long-distance transport, since the same pollen types are found in the modern pollen rain inside the forest (Andersen 1970). In terms of human activity, the changes in the %-and concentration diagrams are rather uncertain. The main difference between the %-values in zones C and D is the higher 'open ground herbs' pollen values in the latter zone. The high *Melampyrum* values especially, but also the distinct Poaceae maximum, indicate favourable light conditions at the section 365:1 site. The frequent occurrence of *Melampyrum* is often found after a fire (Rackham 1980, Inger Brandt, unpublished data). That burning in fact occurred at the time is indicated by the high concentration of charcoal dust in the sediment at that level (plate 1). Written sources show that the forest was also used for grazing, which was possibly less intensive than in the following period. Fire may have favoured the growth of a vigorous ground flora which is attractive to live

stock. The investigation area may therefore have served as a source for leaf-hay gathering and animal browsing.

Local forest pollen zone E, about AD 1650-1800

A drastic change in forest composition appeared in the middle of the 1600's when most of the *Tilia* trees disappeared. The sharp decline of *Tilia* %-values in section 365:1 possibly indicates that the stands were felled. Due to soil bioturbation, the *Tilia* %-values show a less distinct change in section 365:2. For the first time *Betula* was able to flower, and it reaches a maximum shortly after the clearance (plate 1). *Quercus* and *Fagus* now became the dominant tree species. *Tilia* had hosted *Viscum album* and, after its felling, mistletoe became extinct in the area. The NAP %-values were generally lower compared to the previous period. This may be caused by a decreased influx of NAP pollen in zone E, but it may as well be a function of the calculation bases. The NAP %-values are calculated from the total number of pollen counted, and this value has increased as the low pollen producer, *Tilia,* were replaced by high pollen producers, such as *Betula* and *Quercus,* at the transition from zone D to E. The ratio APxAPcorr.$^{-1}$ clearly shows this change (plate 1). The most conclusive interpretation of the NAP values is drawn from the concentration-diagram (plate 4). Only the matrix parameters in section 365:1 (see fig. 18) were relatively stable above 21 cm, and the NAP concentration curve shows decreasing values above this level (plate 4), while the total APcorr. curve remains stable. Thus, the NAP-pollen productivity was hampered, probably by grazing animals (Andersen 1979). It is known from historical records that the forest was intensively grazed by cattle and horses at that time (p. 21).

The drastic change in forest composition accelerated soil genesis. Raw humus accumulated at section 365:1 whereas oligotrophic lumbricid humus was replaced by arthropod humus at many sites, including section 365:2 (fig. 32).

The change in vegetation at the beginning of zone E possibly reflects the introduction of a new management method. The former practice of using the area mainly for collecting leaf-hay fodder was replaced by direct foraging by animals. The *Tilia* trees, not being valuable for that purpose, were accordingly felled - whereas the mast trees, *Fagus* and *Quercus,* were highly valued. A more extensive use of the forest is indicated by the high frequency of *Betula* in the area although this tree would be of little value to the foraging animals.

Local forest pollen zone F, about AD 1800-1900

Around AD 1790-1800, *Quercus* was felled in the area. The trees were possibly more than 150 years old, as no cutting of mature *Quercus* trees took place in the previous zone according to the %-diagrams. *Betula* quickly coloniced the cleared area. In the middle of the zone, the *Betula* %-values show another rise which was associated with a maximum of NAP pollen, and Poaceae and *Calluna,* in particular, became frequent. These variations indicate a new clearance probably dated to about AD 1840 (see p. 23). Thus, in the later part of the zone, two generations of *Betula* were present in the area. In addition to *Betula, Quercus* and *Fagus* occupied the cleared area, and some of the present day trees originate from that time, about AD 1840 (table 2).

The forest was fenced in the year 1785 to protect the wood from grazing cattle and horses. The ground flora which appeared after the clearances in AD 1790-1800 and around 1845 was therefore not hampered by grazing, and a relatively high NAP pollen influx was recorded. At the end of the zone the herbs and shrubs again produced less pollen, possibly because of shading. Soil leaching proceeded and raw humus now prevails in the area (fig. 32).

Local forest pollen zone G, around AD 1900-1960

The vegetation was dominated by *Quercus, Fagus* and *Betula.* At the beginning of the zone old *Betula* trees, originating after the clearance AD 1790-1800, were felled. *Quercus* shows a minimum in the %- and influx diagrams in the middle of the zone. From the forest management plans it is known that these trees were felled in the period AD 1922-1937 at an age of about 130 years. The fellings are also reflected in the NAP values, but the increase of herbaceous pollen is much smaller than found after felling of trees in previous periods. This was probably due to the extraction of single trees which increased the light on the ground only in a very restricted area, while the clearances in earlier times affected larger areas.

Local forest pollen zone H, AD 1960- present

In the winter 1960/61 a number of scattered *Betula* trees were felled. Their positions, shown by the stumps which are still found in the area (fig. 3), indicate that larger openings in the canopy did not appear after the fellings. Forestry has not been practiced in the area for the last 20 years and, today, a mixed *Fagus-Quercus* vegetation dominates with a few *Alnus, Corylus, Betula, Sorbus* and *Ilex* trees present in or close to the investigation area. At least two generations of *Quercus* are found, whereas the number of *Fagus* generations is more obscure (fig. 5).

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Brown-coloured hypha analysis

Total length measurements

Two main types of fungal hyphae are present in terrestrial soils: pale or almost transparent hyphae, and brown-coloured hyphae. Pigmentation by melanine and other substances protect the brown-coloured hyphae against breakdown (Gray and Williams 1975), and only this type of mycelia is found in samples prepared for pollen analysis.

Müller (1878) noticed that brown-coloured hyphae were more frequent in mor (raw humus) than in mull (lumbricid humus), and this difference in growth has been considered a characteristic feature distinguishing mull and mor (Müller 1878, Wilde 1954). Meyer (1959) found that the number of mycelia in lumbricid humus and raw humus do not show much difference when measured by the dilution plate method and expressed per gram of organic matter. Jensen (1963), using the same technique, found that per gram of dry soil, raw humus contains 3-4 times as many mycelia as does lumbricid humus, but per gram organic matter, the number of fungi was slightly higher in lumbricid humus than in raw humus. Nagel-de Boois and Jansen (1967) also found a higher mycelia content in raw humus than in lumbricid humus and explained the relation by differences in mycelium breakdown, not by differences in fungal activity in lumbricid- and raw humus. Waid (1960) has shown that nylon gauze after long exposure in soil contained more brown hyphae than gauze exposed for only a short time, and brown-coloured hyphae may form 80-90% of the mycelial population after one year.

The abundance of pigmented hyphae in acid soils, compared to neutral soils, may to some degree be due to the slower breakdown rate and longer life-span of the hyphae in the acid soils (Andersen, in print). Measurements of hypha fragment length may thus give valuable information about soil ecology and serve to distinguish between soil stages. Fungal hypha activity has been investigated for various reasons, and most experiments are concerned with the frequency of living mycelia and their growth during a relatively short observation period. Only little is known about the breakdown of mycelia in soil according to Nagel-de Boois and Jansen (1967), and even less is known about time-transgressive variations in hypha content.

Table 13. Relative and total length of brown coloured hypha fragments at various levels in sections 365:l and 365:2. Brackets indicate uncertain values.

Section 365:1

Soil stage	level	Hypha frequency relative to 100APcorr.	m g⁻¹ (matrix)	m g⁻¹ (organic matter)	m cm⁻³ (matrix)	m cm⁻²year⁻¹
Raw humus	0–1	2586	91	98	13	6.5
	2–3	2773	170	185	24	7.9
	5–6	2432	360	388	47	6.7
	10–11	2475	630	688	142	9.5
	15–16	2918	523	598	141	5.0
	20–21	2081	582	714	185	6.2
	21–22	2076	438	631	163	6.2
Arthropod humus	22–23	432	172	383	97	2.0
	23–24	907	219	522	130	2.6
	24–25	928	328	801	199	1.3
	25–26	276	72	290	60	0.8
	30–31	117	130	362	86	0.3
Lumbricid humus	35–36	76	34	294	36	0.4[x] 0.3[xx]
	39–40	67	15	259	20	
	42–44	23	2	78	3	
	46–48	45	2	117	3	
Section 365:2						
Raw humus	0–1	1200	155	169	27	6.9
	3–4	6905	190	211	39	3.9
	6–7.5	3489	261	355	70	3.1
Arthropod humus	9–10	2068	113	538	81	3.6
	12–13.5	2518	102	569	74	2.9
	15–16.5	818	122	1135	112	4.5
	18–19.5	318	69	2532	86	3.4
Lubricid humus	21–22.5	232	14	1380	22	1.7[x] 0.8[xx]
	25.5–27	382	2.8	277	4	
	36–37.5	–	(0.4)	(11)	(0.6)	

[x] Maximum value as pollen extinction may appear

[xx] Calculation based on the same pollen concentration as at 30–31 cm in section 365:1 and 18-19.5 cm in section 365:2

Analysis of brown-coloured hyphae in podzols may well contribute to knowledge of the latter topic, as living mycelia occur mainly in the leaf litter layer, decreasing in frequency even in the leaf fragmentation layer, with 95% of the hyphae found in the soil already dead (Nagel-de Boois and Jansen 1971). In addition, brown-coloured hyphae are very resistent to decay when fossilized.

The hypha length, expressed on several calculation bases, is shown on table 13.

Relative hypha length. The hypha length has been expressed as 'area coverage' relative to l00 APcorr. The hypha frequency was highest in the raw humus stage at both sections, and decreasing values were measured from the arthropod humus to the lumbricid humus stage. The section 365:1 values seem in general to be lower than those from section 365:2.

Metres x g(matrix)$^{-1}$. About 2-30 m were found in the lumbricid humus at both sections, with the smallest values at the bottom. The arthropod humus contains about 70-l20 m in section 365:2, whereas double that length was found in section 365:l, and the same relation was valid for the raw humus. The results are highly influenced by the content of inorganic matter, as dry density of this fraction is about l0 times higher than the density of organic matter.

Metres x g(organic matter)$^{-1}$ In the lumbricid and arthropod humus, the hypha length was much higher in section 365:2 than in section 365:l, whereas the opposite relation was seen in the raw humus. These calculations are corrected for variations in the content of inorganic matter, but the content of secondary humic matter may influence the results seriously.

Metres x cm(matrix)$^{-3}$. The values from the lumbricid humus and arthropod humus in section 365:l resemble their respective values in section 365:2. In section 365:l the hypha length was about l00-200 m in the lower part of the raw humus, with decreasing values upwards. The same trend was seen in section 365:2, but the absolute values were smaller.

These results show the difficulty of expressing the hypha concentration so that comparable results can be obtained from different levels in the same section, or from different sections. Hence, for correlation purposes, much caution is needed.

Metres x cm^{-2}year^{-1}. The hypha length measurements calculated on a volumetric basis have been converted to metres per cm^{-2}year^{-1}. The sediment accumulation curves are independent of matrix composition, as they were based on historically dated changes in pollen stratigraphy and constant pollen influx. The hypha content was measured as the net growth of the brown-coloured mycelia but, as breakdown of this type of mycelia was considered to be negligible, the results are possibly equal to gross production.

The lumbricid humus stage. Values cannot be calculated due to bioturbation of pollen. Results based on constant pollen influx at l1800 APcorr. cm^{-2}year^{-1} in section 365:l and 15l80 APcorr. cm^{-2}year^{-1} at section 365:2

may give hints as to the maximum hypha productivity. The destruction of pollen was not supposed to be serious at 35-36 cm in section 365:1 (see fig. 22), whereas this process may influence the calculations at 21.0-22.5 cm in section 365:2 (fig. 23). Taking pollen destruction into consideration, less than 1 m brown-coloured hypha was produced every year per square centimetre in a *Tilia*-dominated forest on brown earth.

The arthropod humus stage. At section 365:1 the annual hypha productivity equals the values obtained in the uppermost lumbricid humus and increases upwards. A *Tilia* forest, with a few *Corylus* and *Quercus,* dominated the vegetation during this soil stage and the increasing brown hypha productivity possibly reflects progressing soil deterioration. At the time of arthropod humus formation in section 365:2, the forest was dominated by a mixed *Fagus-Quercus* vegetation. Leaves from *Fagus* and *Quercus* disintegrate more slowly than *Tilia* leaves in woodland soils (Heath et al. 1965) and the higher productivity of brown-coloured hyphae found in this section, relative to the same stage in section 365:1, is supposed to depend mainly on differences in litter composition.

The raw humus stage. A distinct increase in annual hypha growth was found at the transition from arthropod humus to raw humus at section 365:1, contemporaneous with a change in forest composition from a *Tilia* to a *Betula-Fagus-Quercus* vegetation. The sudden change in leaf litter composition after the felling of the *Tilia* forest about AD 1650 was probably responsible for the distinct increase in hypha productivity. Change in the forest composition was very slight at the time of transition to raw humus in section 365:2, and no drastic change in annual hypha growth was observed. The forest composition has been more or less identical at the two sites during the raw humus stage, and so has the annual hypha growth.

It is concluded that forest composition has strongly influenced the annual growth of brown-coloured hyphae. The rate of litter decomposition is possibly another important factor. Litter decomposition was quickest in brown earth and slower in podzoloids and podzols.

Because the hypha growth depends in part on litter composition, the annual productivity is of less importance as a tool for diagnosis of soil stages.

Relative size distribution of hypha fragments

The brown-coloured hyphae found in acid forest soils are comminuted into fragments of varying lengths, and it has been assumed that the fragmentation was due to the activity of various soil animals (Andersen 1979, 1982; Müller

1878). Macroarthropods are responsible for the initial comminution and microarthropods, particularly oribatids, bite the hyphae into still smaller fragments (Andersen 1979). Andersen (1982) measured hypha fragments in faecal pellets from various soil animals and compared the results with measurements from soil samples. Hypha fragments produced by macroarthropods contain about 10% short fragments (less than 21 μm), whereas the fragments produced by oribatids contain 45% or more of short fragments. Intermediate frequencies of the short fragments indicate various degrees of oribatid influence. Macroarthropods, such as isopods and diplopods, feed mainly in the litter layer and the topmost soil layer. Microarthropods, like oribatids, occur to a considerable depth in brown earth, whereas they are found mainly in the topmost centimetres in podzoloids and podzols (Bocock and Heath 1967, Haarløv 1960, Weis-Fogh 1947-1948). Analysis of hypha fragments in the faecal pellets of oribatids has shown that these animals mainly produces fragments shorter than 35 μm (Andersen 1979). Analysis of hypha-fragment length may thus be used to detect former soil-animal assemblages characteristic for different types of soil stages.

The technique of analysing hypha fragments and the statistical treatment of these data were much influenced by the pioneer work of S. Th. Andersen, Geol. Surv. Denm., who generously offered me valuable help and fruitful criticism.

Hypha comminution by arthropods is illustrated by the distribution of fragment-length frequencies in four samples from section 365:1 (fig. 28). Fragments shorter than about 55 μm dominate in all the samples, and the distributions were strongly skewed. Fragments longer than 200 μm occur regularly and were obviously transported down by burrowing animals, most likely large lumbricids.

The relative frequencies of the hypha size classes are shown in fig. 29. The classes 21-35 μm, 55-61 μm and 61 μm were compared with the class 1-21 μm. At section 365:1, the frequency of the 21-35 μm class shows a weak correlation with the 1-21 μm class ($r = 0.18$), whereas the fragments longer than 35 μm were negatively correlated with the short fragment class ($r = -0.81$ and -0.80). The microarthropod fauna thus bite hyphae longer than 21 μm and produce fragments shorter than 35 μm, with the result that the 1-21 μm class increases, the 21-35 μm class remains stable, and fragments longer than 35 μm decrease in frequency. Similar results were found by Andersen (1979). At section 365:2, the 1-21 μm class was negatively correlated with all the other classes ($r = -0.71$, -0.98, and -0.83) indicating advanced fragmentation of most hyphae. For reasons of comparison, the A–(C + D) values were also calculated from this section.

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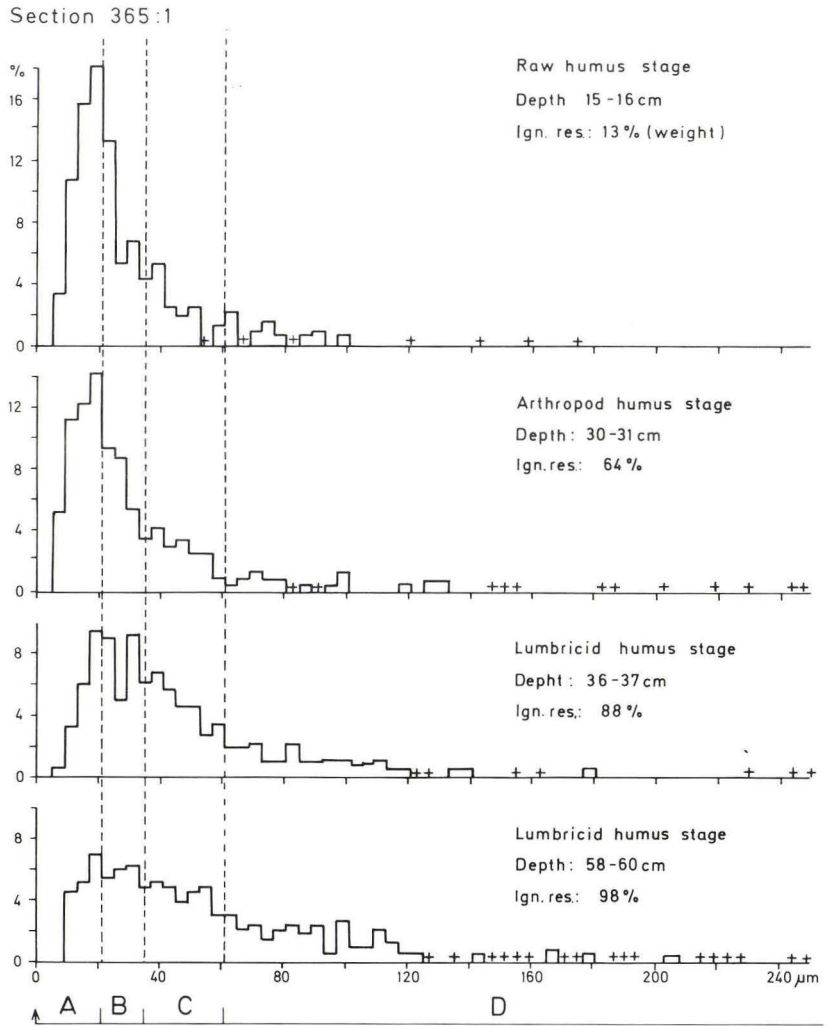
Fig. 28. Length distribution of hypha fragments at selected levels in section 365:1. Values below 0.5% are indicated by $+$. Length categories according to Andersen (1979).

The lumbricid humus stage. Hypha fragments longer than 61 μm were frequent in all samples in section 365:1, whereas short fragments were rare (fig. 29). It is assumed that the hyphae were comminuted in the litter layer mainly by macroarthropods and, after incorporation in the mineral soil, by lumbricids. In section 365:2 the relative frequency of short hypha fragments was considerably higher, indicating a thorough comminution by a rich

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Hypha fragment length

Section 365:1
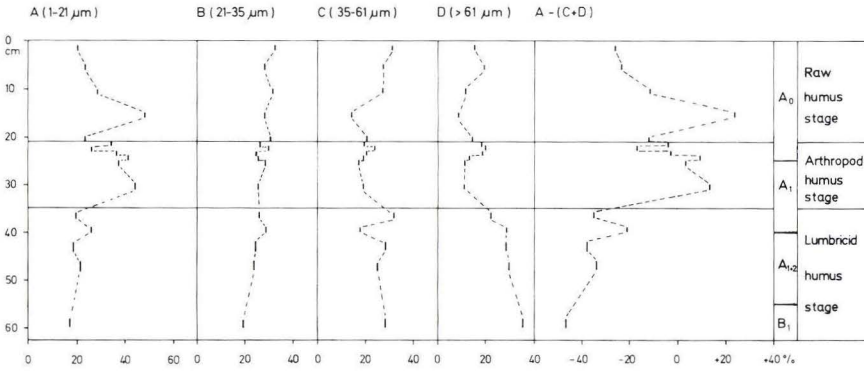
Section 365:2
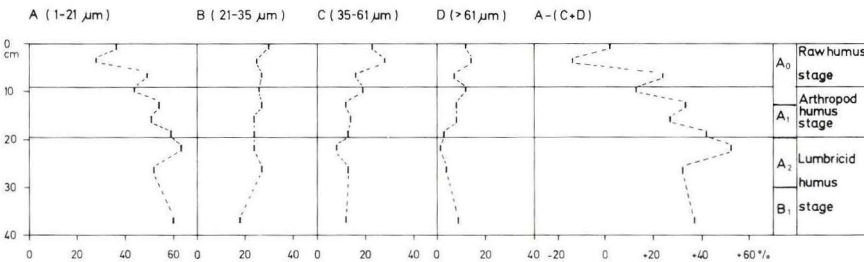
Fig. 29. Diagram showing the relative frequency of hypha fragment length categories from sections 365:1 and 365:2. Categories according to Andersen (1979).

microarthropod fauna after burrowing. The fragment size distribution in section 365:2 resembles the values found in most profiles by Andersen (1979, 1982). He also observed variations in hypha length classes in the lumbricid humus and supposed that low oribatid activity at some sites had been due to wind exposure and hence desiccation. This explanation is possibly inapplicable to the Draved Forest sites, as section 365:1 with a low microarthropod activity was located in a small sheltered depression, whereas section 365:2 is found on higher levelled ground. Instead, the low microarthropod activity at section 365:1 was possibly caused by moist soil conditions - as indicated by the herb flora, eg. Lamiaceae cf. *Ajuga repens,* and the lithology, showing gley horizons (p. 36). The oribatids were not hampered at the drier section 365:2 site.

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The arthropod humus stage. The frequency of short fragments in section 365:1 was much higher than found in the lumbricid humus and resembles the frequency in section 365:2. Hence, oribatid activity has been considerable in the topmost centimetres of the soils in this stage.

The raw humus stage. In both sections the frequency of short hypha fragments shows great variation, but the upper samples contain fewer short fragments than those below. This presumably indicates that microarthropods living near the soil surface have not yet sufficed to comminute all the long fragments produced by the macroarthropods (Andersen 1982). The higher productivity of brown-coloured hyphae may also cause a higher proportion of longer hypha fragments.

Various levels of microarthropod influence can be found in the raw humus stage but, in general, the hyphae were less comminuted than those in arthropod humus.

Thus, the size distribution of hypha fragments may serve to distinguish different soil stages in podzols, but as fauna composition and frequency obviously varies within the same stages, the delineation of the stages cannot be based on hypha fragment criteria alone.

Discussion

Pollen diagrams from forest humus soils

Pollen diagrams from podzols are generally assumed to provide valuable information on the vegetational history near the investigation site. While the pollen assemblage stratigraphy in the humus layer is considered to reflect actual vegetational changes in the past, opinion varies as to the explanation of pollen stratigraphy from mineral soils. Munaut (1967) and Guillet (1972) assert that pollen grains are enveloped in humus aggregates from which they are released by microbial aggregate-decomposition and, then, subjected to downwash and microbial attack. Dimbleby (1957) assumes that the vertical pollen-distribution pattern in terrestrial soils is influenced by the length of time the pollen has been in the soil, owing to the gradual downward movement caused by percolating water. Neither theories take into account the mixing activity of the soil fauna.

It can be assumed that pollen concentration is related to mobile humic matter, if the burial of pollen is to be explained by percolating water and recapturing in other aggregates. The pollen concentration values calculated from the two sections in Draved Forest do not support this theory (see figs. 18, 19, and plate 4). Although the present observations do not support the theory of pollen burial with water transport, there seem to be indications that both burying and downwash of pollen grains may have occurred in some cases (Havinga 1974).

According to Havinga (1963), a homogeneous brown earth preceeds the podzol. During the brown earth stage the pollen assemblages become homogeneous, with differentiation occuring at the subsequent podzoloid and podzol stages when the depth and intensity of the bioturbation gradually decreases.

Similar results were obtained by Andersen (1979), who analysed the pollen sequence in a raw humus deposit and compared the pollen stratigraphy with synchronous diagrams from arthropod humus and lumbricid humus. Because the standard deviation due to elapsed time was known in the raw humus, the effect of mixing on the pollen curves in the other sections could be simulated. The recalculated curves from the raw humus closely resemble

the arthropod and lumbricid humus curves. These calculations definitely show that the incorporation of pollen in mineral soils, and the later modification of the pollen assemblage, can be explained by mixing during burial by soil fauna.

The present study shows a homogeneous pollen assemblage in the lumbricid humus at both sections 365:1 and 365:2, despite considerable variations in pollen concentration (table 8). Only at the transition to arthropod humus do the pollen assemblages begin to differentiate. Thus, the data from Draved Forest confirm the results obtained by Andersen (1979), Havinga (1963), Stockmarr (1975) and others.

Deterioration and destruction of pollen is serious at pH above 5.0-5.5 (Dimbleby 1957). The vegetation growing on the neutral brown earth is accordingly not reflected in pollen diagrams from mineral soil, which only contain pollen grains buried during more acidotrophic soil stages. The duration of the acidotrophic lumbricid humus stage is difficult to calculate, because pollen destruction is rather strong. A minimum time has been estimated from the pollen concentration values in section 365:1 and 365:2. The total number of arboreal pollen present in the lumbricid humus at section 365:1 has been calculated to 3.38×10^6 APcorr.cm^{-2}. If the APcorr. deposition rate equals present day values (11000 APcorr.cm^{-2}year^{-1}), the pollen preserved in the lumbricid humus represents about 300 years pollen influx. In section 365:2 about 100 years pollen influx has been preserved. This is not to say, however, that the pollen assemblages represent the mean pollen composition during the calculated periods, because some grains have possibly persisted for a longer period whereas others have decayed quickly.

The influence of stemflow on pollen representation has been discussed by Keatinge (1982). High percentages of *Tilia* pollen have been reported by various authors (Heim 1966, Guillet 1970, Keatinge 1982). Keatinge suggest that the high values are the result of concentration by stemflow, and that this interpretation is supported by neighbouring profiles with low *Tilia* proportions. Keatinge (op. cit.) mentioned a profile with 20% *Tilia,* which was within 20 m and 100 m of profiles with 4-8% and 2-3% *Tilia* respectively. Thus, according to Keatinge, profiles with 'abnormally' high percentages of *Tilia,* like sections 365:1 and 365:2, must have been situated close to the precise location of a tree trunk, which was responsible for the stemflow.

The present investigation does not support this theory, as synchronous pollen assemblages show only small differences, and it is not likely that trees have grown on the excavation sites in the past, according the soil stratigraphy. Obviously, stemflow may have a serious influence on the pollen assemblages in mineral soils, but the demonstration of stemflow should be based on other criteria than differences in *Tilia* pollen percentages at

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distances above 20-30 m. The pollen source area is very limited in forested areas, and even within 7 m significant differences at about 10% are registered (table 9). Therefore much greater differences in pollen representation may be expected with increasing distance between profiles.

Problems in dating forest humus soils

The humus present in a podzol has a complex origin: living roots,litter fall and the remains of the flora and fauna constitute the humus layer. The living roots penetrating older humus layers cause a metachronous accumulation of organic matter. During humus decay, mobile humic matter is formed and redeposited at lower levels. Thus the organic matter present at a given level consists of autochthonous and allochthonous fractions, each of which contain metachronous material in the covering humus layer. The mineral section of the podsol profile mainly contain allocthonous humus . The continuing passage of humic acids through podzol profiles rejuvenate the C-14 activity of humus in lower horizons and radiocarbon dates obtained from entire samples accordingly give mean values for the age of carbon in flux. This 'mean residence age' (Tamm and Östlund 1960) for surviving carbon is normally regarded as a minimum age (Cruickshank and Cruickshank 1981) which is supposed to be highly unreliable and of interest only in providing hints about the ages of the pollen assemblages (Stockmarr 1975).

Humus and charcoal from the same layer have been radiocarbon dated in Draved Forest to verify whether the humus was younger than the charcoal. The datings show that the humus was 3-400 years younger than the charcoal, which was dated to 1040 ± 100 BP (Iversen 1969). For more detailed dating purposes, radiocarbon dates of humus are of little help, and one must focus on other methods for dating terrestial soils.

Humus layers have been dated from their pollen assemblages by using historically well-defined changes in the vegetation. Often the introduction of foreign species, such as *Picea* in Denmark, is well-documented in many areas. S. Th. Andersen (unpublished data) successfully dated the top of a humus deposit found below a bank for which the construction date was documented. The pollen assemblage in the upper humus layer was then correlated with pollen spectra from neighbouring sites.

A time scale using pollen influx calculations has been constructed by Dabrowski (1971) for an Eemian site in Poland. He used modern pollen influx measurements to calculate the annual sediment accumulation rate. Because of the inaccuracy of the estimate, he preferred to call the time units palynochrones. Hicks (1974) used a similar technique to construct a time

scale for a peat deposit in northern Finland, but emphasized that the modern influx estimates must be made in the same area and from the same vegetation type for the method to be at all plausible.

The pollen influx dating method may also be applied to podzols if the criteria mentioned on p. 64 are satisfactorily fulfilled. Depending on the standard deviation of the measured mean pollen influx the dating method is supposed to be fairly accurate within a time range of about 1000 years. Beyond this scale, the dating method is of importance only to indicate larger time units.

A combination of different dating methods, as in the present study, allows a construction of an accumulation curve which reaches far back in time.

The history of *Tilia* in Draved Forest

Today *Tilia* is almost absent from the eastern part of Draved Forest, including forest part 365, whereas it has survived in the western area, as a dominant tree species together with *Fagus, Quercus* and *Alnus* in forest part 386, a 3 ha area left in natural state (see fig. 1).

Pollen-diagrams from podzols have outlined the history of *Tilia* in Draved Forest on acid soils. Most diagrams show that *Tilia,* with *Corylus* as pioneer, was the climax forest on oligotrophic brown earth during the Holocene climatic optimum (Iversen 1964, 1969, and unpublished). Peasants were active in the western part of the forest in the Subboreal , and selective exploitation of the trees and farming, reinforced by natural soil degradation ,
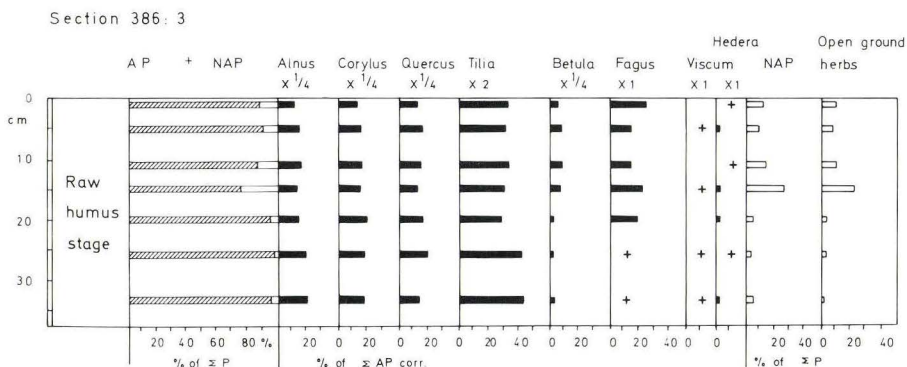
Fig. 30. Pollen percentage diagram from Draved Forest, part 386. Correction factors partly according to Andersen (1970,1978a). The diagram shows that the present forest vegetation has remained almost unchanged for a very long period and that *Viscum* appeared regularly in the vegetation until recently. *Picea* pollen grains were found at 5 and 1 cm. Values below 0.5% are indicated by + . (Recalculated from Iversen, 1958).

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diminished the extent of the *Tilia* forest. The pollen diagrams, show without exception that *Tilia* was of no importance on well-drained acid soils in this part of the forest during the Subatlantic.

Only a single pollen diagram (fig. 30) illuminates the forest development on moist, fertile brown earth (Iversen 1958). The sampling site is located near the edge of an extended podzol area only a few metres from a present-day mixed *Tilia-Quercus-Alnus* forest. The podzol area is covered with a *Quercus-Fagus* vegetation. In the transitional zone a fine *Tilia-Fagus* forest occurs. The pollen diagram thus reflects both the vegetation on podzol and on fertile brown earth. The outstanding feature of the diagram is the fact that the forest composition was essentially the same throughout, except that *Fagus* immigrated in the middle of the sequence and expanded at the expense of *Quercus.* The normal rapid disapperence of *Tilia* was not found.

The interference of Man in the area covered by the pollen diagram was not very intensive and was restricted to the podzolized soil (Iversen 1964). It thus appears that the composition of the forest on moist, fertile brown earth was surprisingly stable throughout the long period registered in the diagram.

Because of human activity, the *Tilia* forest seems to have been confined fairly early to the moist ground in the western part of the forest, whereas it was possibly more common on dry ground to the east where exploitation may have been less extensive. The pollen-diagrams from forest part 365 show that the expansion of *Fagus* was rather slow in local forest pollen zones C and D and, indeed, *Tilia* seems to have competed altogether as successfully as *Fagus* on oligotrophic brown earth and even on more acid soils in the Middle Ages. *Tilia* growing on podzolic soil has also been demonstrated by Swedish pollen diagrams (Berglund 1962), and *Tilia* also grows on fairly acid soils today (Rackham 1980). The sudden decrease in the *Tilia* curve about AD 1650 was artificial, and it was not until that time that *Fagus* became an important constituent in the area.

Although the present-day soil conditions have become unfavourable for the re-establishment of *Tilia* in forest part 365, the pollen analytical investigations clearly show that the fatal blow for the *Tilia* forest was dealt by the peasants, destroying the *Tilia* forest and favouring *Fagus* and *Quercus,* and thereby accelerating soil leaching.

The appearence of *Viscum album* in Draved Forest and its climatological significance

The pioneer work on the thermosphere of *Hedera helix, Ilex aquifolium* and *Viscum album* by Iversen (1944) has been widely accepted by scientists, and these pollen types have been used since as pollen indicators for determining

past thermal climates. The two species mentioned first are autophytes with an occurrence which is not supposed to be restricted by the quantity or quality of the substrate, and they are relatively common within the destribution area. *Viscum album,* on the contrary, is an autotrophic parasite restricted by the distribution pattern of its hosts. In Scandinavia, *Viscum* grows only on deciduous trees and most often on *Tilia, Populus,* and *Malus* species (Walldén 1961). Of these, *Tilia* in particular has become rare, with a discontinous distribution, a fact which possibly reduces *Viscum*'s migrating ability. *Viscum* is a rare species in Scandinavia and the British Isles, expunged from many places by Man. Hence, it is rather uncertain whether the distribution of *Viscum* is determined solely by climatic parameters, or whether it is affected by shortage of substrate or human exploitation as well. The thermal-limit curve given by Iversen (op. sit.) for *Viscum* may therefore be more uncertain than those given for *Hedera* and *Ilex*.

Today the Draved Forest area is outside the thermosphere of *Viscum* (Iversen op.cit.), with July temperatures from about 15.4°C (Løgumkloster) to 15.8°C (Tønder); and January temperatures at about 0.3–0,4°C (fig. 31).

Viscum flowers in March, or even earlier after mild winters, long before the leaves of the host come out. This is favourable for dispersal of the pollen grains which are probably produced in small quantities since *Viscum* is insect-pollinated. This is advantageous to pollen analysis, as the danger of long-distance transport of pollen is greatly reduced among insect pollinators. Regular finds of fossil *Viscum* pollen therefore imply that the species was present in the area.

The pollen spectra from section 365:1 and 365:2 show that *Viscum* did grow on *Tilia* inside the investigation area. It was continously represented from the time reprecented by the oldest spectra investigated to the 17'th century. Because of the close relationship in the pollen diagrams between the sudden decrease in *Tilia* pollen frequency and the disappearence of *Viscum* pollen, it is supposed that the felling of the *Tilia* forest, and not changes in the climate, caused the extinction of *Viscum* from the area. As mentioned, *Tilia* is still growing in the western part of Draved Forest and the pollen diagram, fig. 30, shows that *Viscum* was a part of the vegetation until recent time, as its pollen was found regularly from the lowermost sample until 5 cm below surface. The profile has not been dated, but the 5 cm level dates after the introduction of *Picea* plantations. Today *Viscum* is absent from the area.

The Iversen pollen diagram and the present investigation show that *Viscum* occurred regularly on *Tilia* in Draved Forest at least until about AD 1650, and later in restricted areas. Draved Forest was accordingly located inside the thermosphere of *Viscum* until recently. The regular appeerence in the Draved Forest area until AD 1650 shows that *Viscum* was able to tolerate

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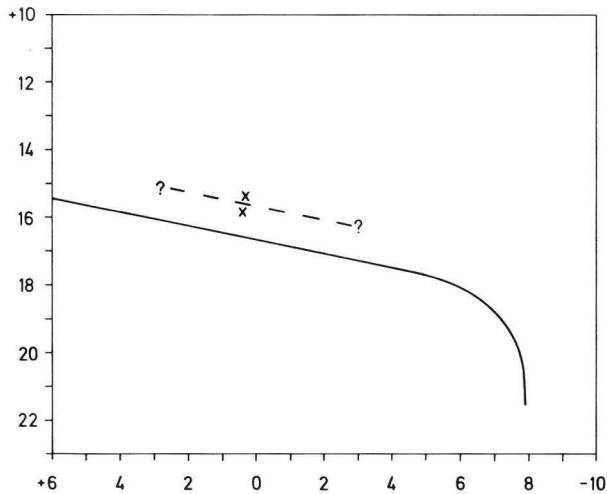
Fig. 31. The thermal limit of *Viscum album* (after Iversen 1944) with the thermal position of two meteorological stations near (4 and 10 km) Draved Forest. The thermosphere of *Viscum* is supposed to include areas with lower summer temperatures than assumed by Iversen. A tentative limit is indicated by a dashed line. Abscissa: Mean temperature of coldest month (°C). Ordinate: Mean temperature of warmest month (°C).

the climate in the 16'th and 17'th century. This period belongs to the so-called 'Little ice age', because of low summer and winter temperatures, which are known to have been lower than in our century (Lamb 1966, 1980). *Viscum* is not very sensitive to cold winter temperatures, whereas changes in summer warmth may have a serious effect (Iversen 1944). The thermosphere limit as outlined by Iversen may in general be correct but the present investigations show that areas with lower summer temperatures must be included in the thermosphere for *Viscum* (fig. 31).

Viscum has been a valuable fodder plant, as proved by Troels-Smith (1960) and Iversen (1973) and its lower pollen representation in early Subboreal is partly explained by exploitation of trees hosting *Viscum* to alleviate food scarcity (Troels-Smith 1960). This possibly holds true for the early agricultural phases, but the practice may have changed in more recent times as indicated from the section 365:1 pollen diagram. The human interference reflected in the forest zones B, C, and D does not seem to have had any serious influence on the representation of *Viscum* in the forest vegetation. It was still growing on the *Tilia* trees and there does not seem to have been any selective demand for *Viscum*.

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Soil genesis, forest composition, and human activity

In assessing the importance of soil genesis in the development of habitat conditions, one needs to know the succession of soil types in the past and the space of time of each stage. The former may be illuminated by the study of actual soil processes and microfossil analysis (e.g. Andersen 1979), but palaeoecological investigations provide little knowledge about the space of time, because of low dating accuracy. Hints about soil maturity in early Holocene sediments have been elucidated by Havinga (1963) from studies of buried soils which have retained their visible profile characteristics relatively unchanged. Homogeneous forest profiles were present in a variety of forest types in the Preboreal and the Boreal. In some cases bleached soils had succeeded the homogeneous profiles, showing that retrogressive soil development can proceed fairly quickly under natural conditions on very poor soils.
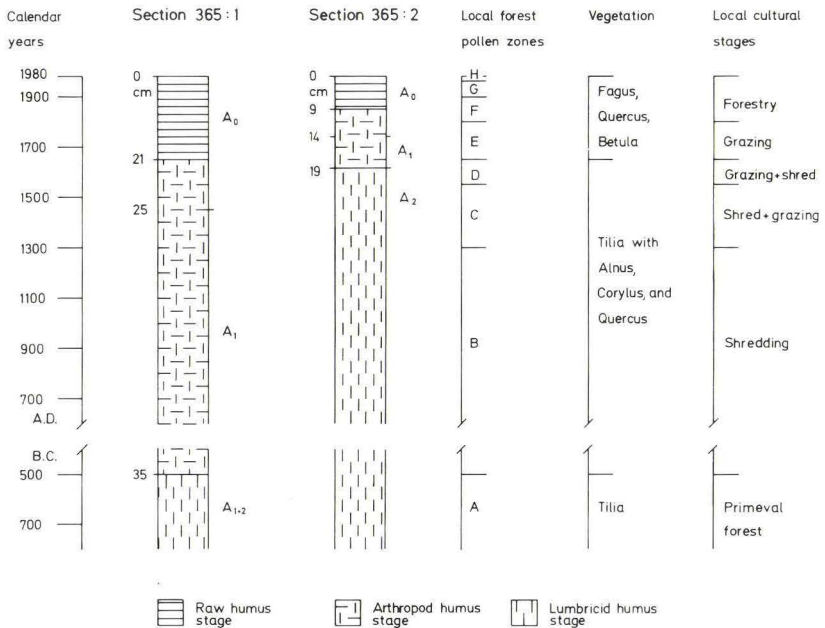
Fig. 32. Schematic illustration of soil development at section 365:1 and 365:2 in relation to vegetation and human activity. The figure shows that the soil development at the two sites was similar but out of phase from Late Subboreal to about AD 1850. The arthropod humus stage lasted for about 2000 years at section 365:1 and only about 200 years at the other site.

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In general, pedogenesis is considered to be a slow process in natural-state ecosystems, as illustrated by forest part 365(fig. 32). In section 365:1, brown earth has prevailed until the Subboreal on glaciofluviatile sand with a low clay content. At that time, soil acidity was sufficiently high to prevent pollen destruction. Leaching of the soil proceeded slowly in accordance with the retrogressive development of the forest vegetation. *Tilia* possibly played an essential part in maintaining a pedological equilibrium in the primeval forest, as also indicated by Dimbleby (1965).

Considering the investigation area as a whole, the western part - with a relatively high ground water table, as appears from the shallow gley horizons - first came into a critical state where even small environmental variations were able to affect the humus formation. There is a close relationship between the first signs of human activity in the Subboreal to be registered in the pollen diagrams, and the change from lumbricid humus to arthropod humus in section 365:1. Reduced water transpiration becauce of leaf-hay gathering may have elevated the water table slightly - sufficiently, at any rate, to hamper biological activity - thereby provoking a change in humus formation, a change which was possible only because the maturity of the brown earth had already reached a critical threshold.

The water table in the eastern area was possibly more deeply located; the gley horizons are here found at a greater depth and are weakly developed. The soils maintained a high biological activity until late Medieval Time, AD 1600-1650 (fig. 32).

Variations in litter fall rates are not supposed to have influenced the pedogenesis in the investigated area, as found by Andersen (1979, 1982).

The peasants managed the forest very extensively during pre-historical times, and the forest composition changed only little. This possibly explains why the arthropod stage lasted for more than 2000 years at section 365:1, and lumbricid humus was still present in the eastern part of the investigation area. The climax vegetation still maintained a type of pedological equilibrium as well, although it had changed to a certain extent since the time of primeval forest.

Soil degradation accelerated in the Middle Ages when the forest was more intensely exploited and oligotrophic brown earth appeared at section 365:2.

The sudden change from a mixed *Tilia* forest to a *Fagus-Quercus-Betula* forest, about AD 1650, was quite different from the previous slow forest succession, and a contemporanous change in humus formation was registered. Soil degradation may be accelerated by forest clearances (Iversen 1964), but the change in litter composition possibly has a more pronounced effect on leaching and soil fauna composition, as *Quercus* and *Betula* leaves are much more acid than *Tilia* leaves; *Fagus* leaves also disintegrate less rapidly

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than *Tilia* leaves in woodland soil (Heath et. al. 1965). *Quercus* leaves also are less palatable to earthworms than are *Tilia* leaves (Heath et. al. op. cit.). The changes from lumbricid to arthropod humus at section 365:2, and from arthropod to raw humus at section 365:1, thus coincides with the change in forest community caused by human disturbance. Similar relationships were demonstrated by Andersen (1982).

The effect of litter composition on soil maturity speed is illustrated by the quantity of pollen accumulated during the arthropod humus stage at the two sites (fig. 32). While the stage lasted for more than 2000 years in a *Tilia* community (section 365:1), the same stage was completed in about 200-250 years in a *Fagus-Quercus-Betula* forest, despite a higher clay content in the soil (section 365:2). The abandonment of cattle-grazing, after the construction of a fence in the year 1784, may also have facilitated the soil degradation (Andersen 1979, Linnermark 1960).

Without Man's interference the soil genesis would possibly have been delayed. In the previous interglacial epochs, the anthropogenic factor was negligible, and interglacial regional pollen diagrams demonstrate very clealy that soil and forest development was generally very slow (Andersen 1965).

Acknowledgements

Dansk sammendrag

I Draved skov, ca. l0 km nord for Tønder, findes uforstyrrede humusaflejringer, der er velegnede til geobotaniske studier. I den østlige del af skoven udvalgtes et lille undersøgelsesområde (36x30m) til belysning af vegetationsudvikling, jordbundsudvikling og menneskelig aktivitet.

Området består af gammel bøge-egeskov med en sparsom undervegetation af arter, som er almindelig på næringsfattig, humusrig jordbund. Jorden er podsoleret og består af sandede eller lerede sedimenter, aflejret i Saale istiden. Over disse aflejringer findes et tyndt lag flyvesand, afsat i slutningen af Weichsel istiden.

De øvre jordlag er kortlagt på grundlag af 270 boringer og materiale er indsamlet fra to profiler med en indbyrdes afstand på 7 m. Den ringe afstand er valgt for at kunne fastlægge synkrone niveauer i de to profiler, og for bl.a. at kunne studere jordbundsudviklingen og pollensammensætningen inden for et område, som med sikkerhed har båret den samme vegetation og været udsat for den samme menneskelige påvirkning. Profil 365:l ligger i en lille lavning og humustykkelsen er stor, ca. 25 cm. Sandede sedimenter findes til mere end 2 m dybde. Profil 365:2 ligger lidt højere og på jævnt terræn. Humuslaget er væsentligt tyndere, ca. l0 cm, og underlaget består af sandede aflejringer til ca. 0.5-l m dybde. Herunder følger siltet moræneler. Der er udviklet et tydeligt blegsandslag og en meget kraftig al-horisont.

Terminologi

Humusdannelse er intimt forbundet med jordbundsfaunaen, som sønderdeler og blander det organiske materiale. Den anvendte terminologi er baseret på dette forhold og humustypen er bestemt på grundlag af det primære indhold af planterester. Aflejringer, hvor regnorme har foretaget en væsentlig del af bearbejdelsen, kaldes lumbricid humus. Arthropod humus er betegnelsen på humustypen, hvor arthropoderne har foretaget en intensiv bearbejdelse af humusmaterialet og hvor nedbrydningen har været så omfattende, at kun særligt modstandsdygtigt materiale som pollen, svampehyfer og trækul er bevaret på deres oprindelige aflejringssted. Med tiltagende

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surhedsgrad mindskes den biologiske omsætning i jorden, og der dannes råhumus, hvori enkelte makroskopiske planterester er bevaret.

Humuslagets tykkelse

I undersøgelsesområdet varierer humuslagets tykkelse fra ca. 40 cm til mindre end l0 cm. Humuslaget er tykkere i lavninger end på jævnt terræn. Den nuværende overflade udviser derfor mindre højdeforskelle end den oprindelige mineraljordsoverflade. De tykkeste humuslag findes i den vestlige del af området. Terrænet er højest i den nordøstlige del og falder mod sydvest. Der er således ikke en tydelig relation mellem de generelle terrænforhold og humustykkelsen. Det antages derimod, at områdets hydrologi har haft en væsentlig indflydelse på humusdannelsen.

Er humusdannelsen samtidig?

I forbindelse med kortlægningen af de øvre jordlag registreredes en trækulhorisont i humusaflejringer med større mægtighed end l8 cm. Denne horisont er dateret til perioden ca. l300-l650. Trækulstøv er naturligvis også aflejret i områder som i dag har et tyndt humusdække, men her fandtes dengang muldjord og regnormenes aktivitet har bevirket, at en egentlig kulhorisont ikke kan erkendes idag.

Tilstedeværelsen af særdeles pollenrige aflejringer ('Pollenmor') viser, at humusakkumuleringen er begyndt for mere end 2500 år siden, hvor der idag findes tykke humuslag. Undersøgelserne viser således, at der indenfor et lille område kan være en forskel på mere end 2000 år mellem påbegyndt humusakkumulering.

Fysiske forhold

Glødetab og massefylde i tør tilstand er målt på indsamlede prøver fra profil 365:l og 365:2. Der er beregnet en formel for tør massefylde, som funktion af glødetabet. Ligeledes er gløderest volumen bestemt og udtrykt som funktion af gløderest vægten.

Mængden af KOH-opløseligt humus er bestemt og ud fra relationen mellem pollenkoncentrationen i råhumus og arthropod humus og mængden af opløseligt humus, kan det vises, at der er sket en betydelig nedsivning af opløseligt humus. Det organiske indhold i lumbricid og arthropod humus lagene består således næsten udelukkende af sekundært humus.

Pollenets bevaringsgrad

Pollenkornenes bevaringsgrad er analyseret for at undersøge, om de oprinde-
lige pollenspektre kan ændres, som følge af forskelle i de enkelte arters
pollenmodstandsdygtighed. Der er sondret mellem to typer af pollenskader,
korrosion og tynding. Korrosion er afgrænsede ødelæggelser af pollen
exinen, forårsaget af svampe- og bakterieangreb, hvorimod tynding formodes
at være en abiotisk iltning af pollenkornet. Tyndingsskader er diffuse og kan
involvere hele exinen eller dele heraf.

Korrosion og tynding er målt på pollen af el, birk, hassel og lind.
Resultaterne er vist på figur 22 og 23, samt tabel 3.

Korrosionsgraden er ringe i råhumus, stiger i arthropod humus og er
størst i lumbricid humus, hvor den biologiske aktivitet er mest omfattende.
Der er en signifikant forskel mellem korrosionsgraden i de tre humus stadier
(tabel 4). Tynding er ret almindelig i råhumus og stiger i arthropod humus og
lumbricid humus. Der er ligeledes ofte en signifikant forskel i tyndingsgrad
mellem humusstadierne (tabel 4). Det kemiske og biologiske miljø har
således været forskelligt i de undersøgte humusstadier.

En sammenligning af bevaringsgraden i det samme humusstadie i de to
profiler viser, at korrosionsgraden er ens i råhumus stadiet, hvorimod den
var større i arthropod humus og lumbricid humus stadierne i profil 365:2 end
i det andet profil. Det mikrobiologiske miljø må således have været mest
agressivt i de første humus stadier i profilet 365:2. Tyndingsgraden var den
samme i råhumus og arthropod humus stadierne, medens den var tydeligt
større i lumbricid humus stadiet i profil 365:2.

Sammenligning af synkrone pollenspektre, aflejret i forskellige humussta-
dier viser, at der ikke er forskelle i pollen sammensætningen, som følge af
forskellig pollenbevaringsgrad (tabel 6 og 7). I profil 365:2, indeholder
lumbricid humus laget dog ca. 7% mere lindepollen end i profil 365:l (tabel
7), men forskellen er af samme størrelsesorden, som registreret i prøver fra
råhumus. Her kan forskellen ikke være forårsaget af pollenets bevaringsgrad,
men må skyldes oprindelige forskelle i pollensammensætningen på de to
lokaliteter (tabel 9).

Det må således med rimelighed antages, at de pollenanalytiske data
afspejler den faktiske vegetationsudvikling, inden for det undersøgte område.

Beregning af sediment akkumulationskurver

På grundlag af statsskovvæsenets driftplaner vides det, at birk blev fældet i
l960/6l, at gran begyndte at blomstre omkring år l900 og at der blev foretaget
en omfattende foryngelse af eg omkring år l800. Denne foryngelse forudsatte

en rydning, som tydeligt registreres i pollendiagrammerne, ligesom de to øvrige begivenheder. På grundlag af disse tre historiske oplysninger er der konstrueret sediment akkumulationskurver tilbage til ca. år 1750. Alderen på ældre aflejringer er beregnet ud fra pollenkoncentrationen, idet det antages, at influx af pollen har været konstant i tid og af samme størrelsesorden, som beregnet for perioden 1750-1980.

Pollendiagrammer

Tre typer diagrammer er vist (tavle 1-4), procent-, influx- og koncentrations-diagrammer.

Procent-diagrammerne (tavle 1-2). På grundlag af spektrene i diagram 365:1 er der opstillet otte lokale pollenzoner, som hver er beskrevet.

En sammenligning af synkrone pollenzoner, E-H, viser, at de fleste pollentyper er ens repræsenteret i de to profiler, dog har lind og bøg højere værdier, og eg lavere værdier i profil 365:2 end i profil 365:1 (tabel 9). Forskellen er ca. 10% og skyldes oprindelige forskelle i pollensammensæt-ningen.

Influx-diagrammerne (tavle 3). I perioden 1750-1980 faldt der årligt pr. cm² ca. 40-45000 pollen på skovbunden eller ca. 11-15000 APcorr.(d.v.s. omregnet til bøgepollen). Det påvises at influx af pollen er den samme på de to lokaliteter, beregnet både for hele 230 års perioden og for de enkelte pollenzoner, F-H. Derimod kan der være betydelig forskel mellem de to lokaliteter, indenfor mindre tidsafsnit (20-30 år).

Det kan ligeledes vises, at pollen influx har været konstant i tid, på hver af de to steder (tabel 12).

De enkelte pollenzoner er beskrevet og det kan konkluderes, at influx-diagrammerne ofte viser vegetationsændringer tydeligere end procent-dia-grammerne.

Koncentrations-diagrammerne (tavle 4). Pollenværdierne er udtrykt pr. g organisk stof, og hvert humus stadium er beskrevet for sig.

I den nedre del af arthropod humus laget i profil 365:1, findes et tydeligt minimum i kurverne for lind. Også hassel og el viser samme tendens, hvorimod pollenkurverne for eg, buske og urter, ikke viser noget minimum. Disse kurveforløb er helt forskellige fra procent-diagrammets kurveforløb (tabel 1). Derfor kan pollenkurvernes forløb i koncentrations-diagrammet ikke forklares som ændringer i matrix, men må enten være forårsaget af forskelle i pollenets bevaringsgrad eller ændringer i pollen influx. Det er tidligere vist, at den første mulighed må forkastes. Den eneste rimelige antagelse er derfor at der pr. tidsenhed er faldet færre træpollen, navnlig af

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lind og hassel end tidligere. Denne ændring er menneskeligt betinget, og skyldes at træerne, fortrinsvis lind, er blevet stynet og løvet brugt til foder. Der er anvendt en speciel form for styning, 'shredding', hvor en mindre del af træets top bevares, medens resten af træets grene og kviste afløves regelmæssigt.

Vegetationsudvikling

Vegetationsudviklingen er beskrevet på grundlag af de tre typer diagrammer.

I Subboreal tid fandtes lindeskov med enkelte el, hassel og eg. I slutningen af perioden begyndte man at anvende området til indsamling af løvfoder. Bønderne stynede urskovens træer direkte, uden forudgående afbrænding eller fældning. Denne driftform anvendtes i mere end 2000 år og resulterede ikke i nogen væsentlig ændring i skovens artssammensætning. I middelalderen, omkring år 1300, fældes eg og i lysningerne blomstrede vedbend og røn, hvorimod lysforholdene forblev ringe på skovbunden. I slutningen af middelalderen og frem til ca. år 1650, er skoven væsentlig mere lysåben og urtefloret mere tæt end tidligere. Et ret stort indhold af kulstøv i humuslagene vidner om, at brande forekom i denne periode. Sikkert har man afbrændt den visne vegetation, for at gøde jorden. Historiske kilder beretter, at skoven på den tid anvendtes til græsning, som først er blevet intensiv i den følgende periode.

Omkring år 1650 ændres skovbilledet fuldstændigt. Lind fældes og erstattes af ege-bøgeskov. Løvhøstningen har mistet sin betydning og skovens udnyttelse er nu næsten udelukkende baseret på græsning. Oldentræerne eg og bøg får derfor øget betydning. Birk, der tidligere var værdiløs som løvfoder og derfor blev holdt i ave, får nu lov til at vokse op og blomstre, fordi der ikke længere foretages en intensiv pleje af skoven. Den store bestand af græssende kreaturer har sandsynligvis hæmmet urternes blomstringsmuligheder.

I 1785 hegnes store dele af skoven og græsning forbydes, således at en rationel skovdrift baseret på gavntræproduktion kan etableres. Skoven er siden forblevet ege-bøgeskov, med enkelte birk. Der er foretaget fældninger omkring år 1800, 1840, 1900, 1922-37 og sidst i 1960/61.

Svampehyfe undersøgelser

Total længde. Brunfarvede svampehyfer er meget modstandsdygtige overfor nedbrydning. Målinger af hyfemængden i forskellig dybde kan give vigtige oplysninger om jordbundsøkologi og omsætningsforhold, idet undersøgelser har vist at mængden af brunfarvede hyfer i nogen grad er afhængig af det organiske stofs omsætningshastighed og hyfernes livslængde.

Den totale hyfelængde er udtrykt på forskelligt beregningsgrundlag og angivet i tabel 13.

Udtrykt som m cm^{-2} $år^{-1}$ produceres der mindre end 1 m i lumbricid humus stadiet. Hyfeproduktionen stiger gradvist i arthropod humus stadiet og når 2-2,5 m i den yngste del. Hyfeproduktionen er noget højere i profil 365:2 end i det andet profil. Mængden af brune hyfer er ca. 6 m i råhumus stadiet og således betydeligt større end i de foregående stadier.

Det påvises at skovsammensætningen har stor betydning for den årlige produktion af brunfarvede svampehyfer. Nedbrydningshastigheden er en anden vigtig faktor.

Relativ størrelsesfordeling. Hyfer sønderdeles i større og mindre fragmenter af jordbundsfaunaen. Makroarthropoderne foretager den første fragmentering og mikroarthropoderne sørger for den efterfølgende findeling. Undersøgelser af hyfernes størrelsesfordeling i ekskrementer har vist, at denne er karakteristisk for de enkelte dyregrupper. Analyser af fragmentfordelingen kan derfor give vigtige oplysninger om det tidligere dyreliv i de enkelte humus stadier.

Lange hyfefragmenter forekom almindeligt i lumbricid humus stadiet. Korte fragmenter var sjældne i profil 365:1, medens de hyppigt fandtes i profil 365:2. Denne forskel skyldes antagelig, at mikroarhtropoderne var hæmmet af høj fugtighed i det lavtliggende profil 365:1, medens dette ikke var tilfældet i det højereliggende profil 365:2.

Arthropod humus stadiet er karakteriseret ved et stort indhold af korte hyfer. Mikroarthropod aktiviteten har således været betydelig i dette stadium.

Mængden af korte hyfer varierer en del i råhumus stadiet, men er generelt betydeligt lavere end i det foregående stadium.

Hyfefragmenternes størrelsesfordeling er relateret til humus stadierne og derfor vigtige for en diagnose af disse. Faunasammensætningen har tilsyneladende varieret en del inden for de enkelte humus stadier og derfor kan deres afgrænsning ikke baseres alene på hyfefragmentkriterier.

Diskussion

Problemerne ved pollenanalytiske undersøgelser i jordbundsprofiler diskuteres, ligesom vanskelighederne ved at bestemme alderen på de undersøgte humuslag omtales. Forskellige dateringsmetoder diskuteres.

Lindeskovens historie i Draved skov belyses ud fra pollendiagrammer i forskellige dele af skoven. Det påpeges, at ændringer i bondens udnyttelse af skoven var hovedårsagen til lindeskovens undergang. Klimatiske eller jordbundsmæssige forhold har næppe haft betydning, som tidligere antaget.

Mistelten betragtes normalt som en god klimaindikator, der kun forekommer, når sommer- og vintertemperaturerne er tilstrækkelig høje. Draved skov ligger således udenfor misteltenens temperaturområde i dag.

Misteltenen fandtes flere steder i skoven indtil midten af 1600-tallet og et enkelt sted endnu senere. Planten har således kunnet tåle klimaforholdene i 15-1700-tallet, den periode, som ofte benævnes 'den lille istid' på grund af kolde sommer- og vintertemperaturer. Det påpeges at misteltenen tåler lavere sommertemperaturer end hidtil antaget. Den er derfor næppe så god en klimaindikator, som tidligere antaget. Dens forsvinden i nordvest Europa er sandsynligvis tæt forbundet med lindeskovens udryddelse.

Undersøgelserne viser, at der en nøje sammenhæng mellem vegetation, jordbundsudvikling og menneskelig aktivitet. Den først registrerede menneskelige forstyrrelse i slutningen af Subboreal tid, bevirker en moderat jordbundsforringelse, bl.a. med øget jordfugtighed i lavtliggende områder, og arthropod humus aflejres (se figur 32). Ændringerne i skovens sammensætning er ubetydelige i de følgende 2000 år og jordbundsudviklingen er særdeles langsom. Først da udnyttelsen af skoven ændrer karakter fra løvhøstning og moderat græsning til intensiv græsning og lindeskoven derfor fældes, sker der en markant forringelse af jordbunden. Bøgens og egens blade og kviste er surere end lindens og lader sig vanskeligere omsætte. Derfor sker der hurtigt en udvaskning af næringsstoffer og de sidste dele af området podsoleres.

Vegetationens betydning for den hastighed hvormed jordbundsudviklingen forløber, illustreres af arthropod humus stadiets varighed. I lindeskov varede stadiet mere end 2000 år, medens det samme stadium blev gennemløbet på omkring 200 år i bøge-ege-birkeskov.

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Section 365:1

LEVEL, cm

	0,5	1,5	2,5	3,5	4,5	5,5	6,5	7,5	8,5	9,5	10,5	11,5	12,5	13,5	14,5	15,5	16,5	17,5	18,5	19,5	20,5	21,5	22,5	23,5	24,5	25,5	26,5	27,5	28,5	29,5	30,5	31,5	32,5	33,5	34,5	35,5	36,5	37,5	39,5	43	47
SHRUBS																																									
Juniperus communis																																		0,1	0,2						
Viburnum opulus	0,4																																								
Sambucus racemosus			0,2	0,5		0,4																																			0,1
HERBS																																									
Pasture																																									
Plantago major																								0,2							0,2										
Polygonum persicaria																																							0,1		
Centaurea jacea-type						0,2																																			
Forest, shaded ground																																									
Prunella-type						0,2																																			
Ecology uncertain																																									
Brassicaceae				0,1		0,2	0,2	0,2				0,2	0,2		0,2		0,2	0,2		0,2		0,3		0,3		0,1															
Campunula												0,2	0,2	0,9	0,2																										
Caryophyllaceae				0,3																																					
Convolvulus arvensis															0,2	0,2				0,2																					
Fabaceae undiff.												0,2																					0,1								
Filipendula ulmaria				0,2	0,2	0,2			0,2		0,1					0,1			0,1			0,2																			
Galeopsis-type											0,2																														
Galium-type																	0,2				0,2									0,2											
Hypericum							0,2			0,1			0,2	0,2														0,2													
Lamiaceae undiff.													0,2																												
Lycopodium clavatum																												0,2													
Osmunda regalis																																							0,1		
Rhinanthus-type																																									
Rumex acetosa-type						0,2																						0,2													
Sphagnum		0,2	0,2	0,1		0,2				0,2	0,2			0,2			0,2		0,1	0,2				0,5	0,2									0,1	0,1					0,1	0,2
Stachys-type	0,2																			0,2		0,3						0,2	0,2												
Succisa pratensis																			0,2																						
Thalictrum																						0,2																			
Typha angustifolia-type						0,2																																			
Urtica dioeca				0,1		0,1											0,2					0,2																			

Pollen types not included in the percentage diagram (plate 1). Values are % of P.

APPENDIX 2

Section 365:2

LEVEL, cm

	0,5	1,5	2,5	3,5	4,5	5,5	6,5	8,5	9,5	10,5	11,5	13	14,5	16	17,5	19	20,5	22	23,5	25
SHRUBS																				
HERBS																				
Pasture																				
Plantago major												0,1								
Polygonum aviculare															0,1					
Spergula arvensis						0,2														
Trifolium cf. *pratense*							0,5													
Forest, open ground																				
Empetrum nigrum				0,2																
Ecology uncertain																				
Brassicaceae											0,1			0,2						
Convolvulus arvensis												0,1	0,1							
Dryopteris linneana											0,1			0,5		0,2				
Galium-type															0,1					
Humulus lupulus						0,2						0,1			0,1					
Hypericum					0,2				0,2					0,2						
Lamiaceae undiff.																	0,1			
Sphagnum	0,1		0,4	0,3		0,1			0,3		0,2			0,1						
Stachys type						0,1										0,1				
Succisa pratensis			0,1								0,1									
Urtica dioeca				0,2								0,1	0,1			0,1				

Pollen types not included in the percentage diagram (plate 2). Values are % af P.

Section 365:1   Pollen percentage diagram

TREES

SHRUBS   HERBS s.l.

Local

Exotic

Field & Pasture

Forest open ground

Forest shaded ground

Uncertain

Lithology

Soil genesis

TREES

SHRUBS + HERBS s.l.

Alnus Corylus Quercus Tilia

Ulmus Viscum Hedera Betula Fagus

Fraxinus Picea Pinus Carpinus Acer

TOTAL Sorbus Salix Frangula DIV.

TOTAL DIV., Field Rumex DIV., Pasture

TOTAL Calluna Poaceae anl.—D ≥8 µm Melampyrum Pteridium

Dryopteris Polypodium DIV.

TOTAL Myrica DIV.

Microscopic charcoal

AP × APcorr^{-1}

Local forest pollen zones

Local cultural stages

Calendar years

Moss pulster

Raw humus stage

Arthropod humus stage

Lumbricid humus stage

% of total pollen

0 20 40 60 80

% corrected tree pollen sum ; + < 0.5 %

0 20 0 20 0 20 0 20 40 60 0 20 40 60 80 0 0 0 0 0

% of total pollen and spores, + < 0.5 %

0 0 0 0 0   0 0 0 0   0 20 0 0 20 0   0 0 0   0 0

% of corrected tree pollen sum

0 500 1000 1500   1 2 3

Local forest pollen zones: H, G, F, E, D, C, B, A

Local cultural stages:
Forestry – stage
Grazing – stage
Grazing+shred?–stage
Shred+grazing?–stage
Shredding–stage
Primeval – forest–stage

Calendar years:
1975 A.D.
1970
1960
1950
1925
1900
1850
1800
1700
1600
1500
1300
600
0
400 B.C.

Anal. B. Aaby

LEGEND:
Slightly decomposed humus
Medium – –
Medium–strongly – –
Strongly – –
Sand
Charcoal
Stone

SHRUBS
I: Ilex aquifolium
P: Populus tremula
L: Lonicera periclymenum

FIELD
S: Secale cereale
H: Hordeum type
A: Avena type
F: Fagopyrum

PASTURE
P: Plantago lanceolata
A: Artemisia sp.
C: Chenopodiaceae
T: Trifolium cf. repens
Tp: Trifolium cf. pratense

FOREST, shaded
A: Anemone sp.
M: Mercurialis perennis
Aj: cf. Ajuga repens
S: Stellaria holostea

UNCERTAIN
V: Vaccinium sp.
C: Cyperaceae
L: Liguliflorae
P: Potentilla sp.
T: Tubiflorae
A: Apiaceae
R: Ranunculus sp.

PLATE 1
DGU II Rk. nr. 114

TREES

SHRUBS

HERBS s.l.

Local

Exotic

Field & Pasture

Forest open ground

Forest shaded ground

Uncertain

| Lithology | Soil genesis | TREES | SHRUBS + HERBS s.l. | Alnus | Corylus | Quercus | Tilia | Ulmus | Hedera Viscum | Betula | Fagus | Fraxinus | Picea | Pinus | Carpinus | Acer | TOTAL | Sorbus | Ilex | Salix | Frangula | DIV. | TOTAL | DIV., Field | Rumex | DIV., Pasture | TOTAL | Calluna | Poaceae ant.-D <8µm E | Melampyrum | Pteridium | DIV. | TOTAL | Dryopteris | Polypodium | Anemone | DIV. | TOTAL | Myrica | DIV. | Microscopic charcoal | AP×AP corr.⁻¹ | Local forest pollen zones | Local cultural stages | Calendar years |

Raw humus stage

Arthropod humus stage

Lumbricid humus stage

0 20 40 60 80   0 20   0 20   0 20 40   0 20 40 60 80

% of total pollen

% of corrected tree pollen sum, + <0,5 %

% of total pollen and spores, + <0,5 %

% of corrected tree pollen sum

0   500 1000

0404-82-02

Anal. B. Aaby

Local forest pollen zones: H, G, F, E, D

Local cultural stages: Forestry stage, Grazing stage, Grazing + shredding? stage

Calendar years: 1980, 1950, 1900, 1850, 1800, 1750, 1700, 1650

Lithology legend:
Slightly decomposed humus
Medium – –
Strongly – –
Sand and gravel

SHRUBS
P: Populus tremula
L: Lonicera periclymenum
J: Juniperus commune
S: Sambucus racemosus

FIELD
S: Secale cereale
H: Hordeum vulgare
F: Fagopyrum

PASTURE
P: Plantago lanceolata
A: Artemisia sp.
L: Liguliflorae
T: Trifolium cf. repens
C: Centaurea cyanus

FOREST, shaded
M: Mercurialis perennis
S: Stellaria holostea
I: Impatiens noli-tangere
T: Trientalis europaeus

UNCERTAIN
V: Vaccinium sp.
C: Cyperaceae
L: Liguliflorae
P: Potentilla sp.
T: Tubiflorae
A: Apiaceae
R: Ranunculus sp.
F: Filipendula ulmaria

PLATE 2
DGU II Rk. nr. 114

POLLEN INFLUX DIAGRAMS

PLATE 3
DGU II Rk. nr. 114

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POLLEN CONCENTRATION DIAGRAMS   g (organic matter)

Section 365:1

Column headers: AP · Alnus · Corylus · Quercus · Tilia · Betula · Fagus · NAP · Open ground herbs · Local forest pollen zones

Depth labels: 20, 30, 40, 50

Stage labels: Raw humus · Arthropod humus stage · Lumbricid humus stage

Zones: E, D, C, B, A

x 10⁶ grains

Section 365:2

Column headers: AP · Alnus · Corylus · Quercus · Tilia · Betula · Fagus · NAP · Open ground herbs · Local forest pollen zones

Depth labels: 12, 20, 30, 40

Stage labels: Arthropod humus stage · Lumbricid humus stage

Zones: E, D

Annotations: + 15 400 grains, + 4000 grains

x 10⁶ grains

Legend:
- ▨ P g (organic matter)⁻¹
- ■ AP corr. g (organic matter)⁻¹
- +< 20 000 grains
- ▯ x 10

PLATE 4
DGU II Rk. nr. 114

0404·82·05