Reconstruction of recent forest dynamics based on pollen analysis and micromorphological studies of young acid forest soils under Scots pine plantations

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SUMMARY

Reconstructions of vegetation development of forest ecosystems have traditionally drawn on pollen samples of thick mor-humus profiles. In The Netherlands, however, well developed acid forest soils are scarce, especially under Scots pine (*Pinus sylvestris*). Scots pines have been planted from AD 1800 onwards, since when an acid soil profile has developed. This paper aims to show that pollen analysis of young acid forest soils not only can be used for the reconstruction of vegetation development in forests but also, combined with micromorphological observations, reveals information about forest dynamics in terms of litter production, decomposition processes and soil development. For that purpose four sites were selected in Scots pine stands, planted between AD 1900 and AD 1940 on drift sand deposits. At each site samples for pollen analysis were obtained from the entire organic layer and the top of the mineral soil. The pollen records of young acid forest soils show a shift in pollen assemblages, caused by a change from an open heath landscape towards a closed canopy after forest plantation. Micromorphological observations by thin sections of the undisturbed acid soil profile enhanced the interpretations of the pollen records. Micromorphological studies of these forest soils revealed the presence of non-burrowing soil animals and the preservation of pollen grains in the excrements of these soil animals. The absence of soil mixing animals and the pollen preservation in soils results in a pollen stratification, representing the recent local vegetation development. Furthermore, the pollen concentration curves show the stabilization periods of drift sand. The incidental increase of the pollen concentrations in the mineral soil indicates alternations of active sand drifting and stabilization periods, while the continuous increase of pollen concentrations towards the top of the mineral soil points to the final stabilization of the drift sand by Scots pine and the development of an AE-horizon.

Key-words: acid forest soils, drift sand deposits, micromorphology, pollen analysis, Scots pine plantations.

INTRODUCTION

Studies of pollen sequences from acid forest soils have been widely applied in reconstructions of former vegetation development of forest ecosystems and in tracing past human management practices. If forest soils have been developed under a closed forest canopy, pollen analysis of soil horizons provides information about the regional vegetation dynamics, but mainly about the local dynamics (Iversen, 1964; Andersen 1970). Many vegetation dynamic investigations have traditionally been carried out on mor-humus profiles of old-growth sites, developed on podzols (Aaby 1983; Andersen 1984; Bradshaw & Miller 1988; Mitchell 1990), which proved to be a good tool for studying vegetation development. The acid conditions in these profiles preserve the pollen, while the absence of biological activity in mor-humus profiles ensures a clear pollen stratification (Aaby 1983).

In The Netherlands, however, studies of pollen sequences from acid soils formed under forest canopies are scarce. In particular, this applies to studies of soils developed under Scots pine (*Pinus sylvestris*), and may be connected with the young age of these forests and the thinness of their soils. From AD 1800 onwards Scots pine trees were planted on large areas of heath and drift sand areas in the Netherlands. Reafforestations with Scots pine have resulted in the development of an acid forest soil, consisting of an accumulation of lowly decomposing organic matter over drift sand deposits or ploughed podzols.

In ecosystems there is an intimate relationship between vegetation, soil development and humus forms (Green *et al.* 1993). In particular in coniferous forests on poor sandy substrates, such as drift sand, soil organic matter dynamics are closely related to the vegetation (Emmer 1995). The aim of this paper is to show that pollen records of young acid forest soils, completed with micromorphological observations, provide important information about the local forest dynamics of Scots pine plantations. The pollen records not only show the vegetation development after pine plantation, but also reveal aspects of pedological processes. This viewpoint is illustrated by the pollen analysis and micromorphological observations of four acid forest soils on drift sand deposits.

MATERIALS AND METHODS

Study area

The study was carried out in drift sand areas in the eastern part of the province of Noord-Brabant, The Netherlands (Fig. 1). The climate in the area is humid temperate with mean July and January temperatures of 19°C and 4°C, respectively, and mean annual precipitation of 700 mm. All sites were chosen in Scots pine (*Pinus sylvestris*) forests planted on heath and sand drifts between AD 1900 and AD 1940. The understorey of most sites is poor in herbaceous species; *Dechampsia flexuosa* is the dominant species, occasionally with mosses and ferns. In the studied area, grazing domestic animals were absent.

Locally heathlands and small sized sand drifts already occurred during the Bronze Age when indigenous deciduous forests on dry sandy soils (cover sands) were destroyed by human disturbance. After the Middle Ages the expansion of agriculture caused a high demand for organic manure from the forests and heathlands, resulting in intense wind erosion of the cover sand and the formation of drift sand over wide areas. From the second half of the 18th century onwards, after the introduction of inorganic
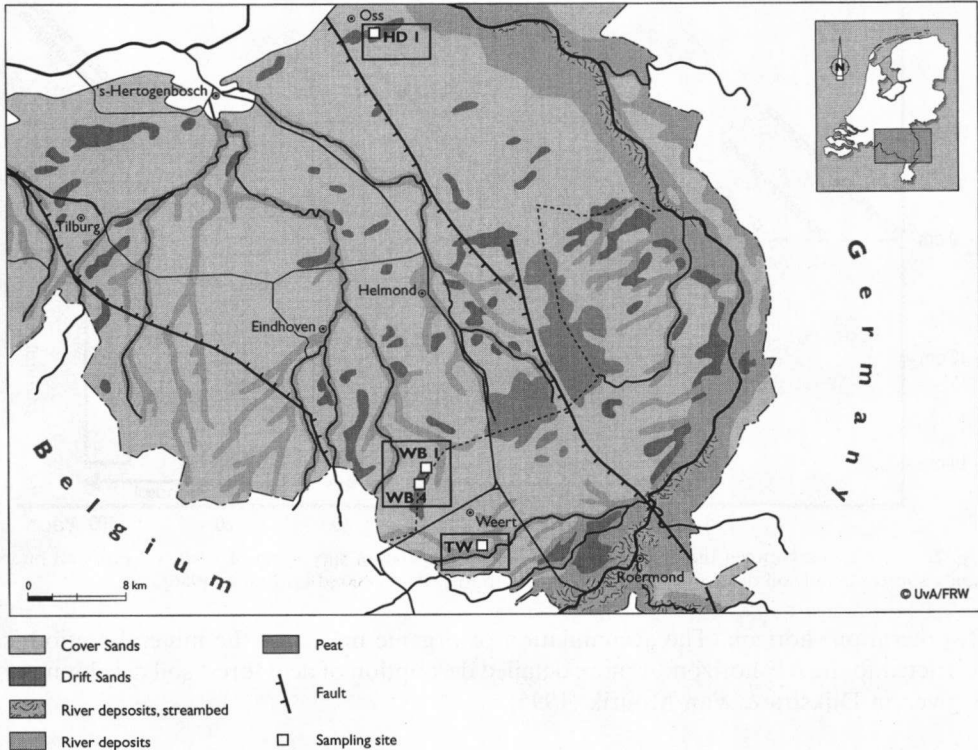
Fig. 1. Geological map of eastern part of the province of Noord-Brabant (The Netherlands), including the location of the sampling sites. Based on the General Geological Map of The Netherlands, Geological Survey of The Netherlands (1975).

fertilizer, large quantities of organic manure from heathlands and forests became redundant. As a result, heathlands were reclaimed and partly transformed into arable lands. On heathlands that were not suitable for cereals, trees were planted for economical reasons (Buis 1993). Trees were also planted to reduce sand drifts. Scots pine was the most planted tree on the dry poor sandy substrates, because at that time pine was the only tree that could survive under poor growing conditions. Besides, its seed was available in large quantities (Fanta 1986).

At all sites investigated the acid forest soil has an organic layer, developed after plantation of Scots pine. The organic layer can be classified as mor-moder type of humus form (Green *et al.* 1993). The organic layer has different horizons. Each horizon represents increasing amounts of decomposed organic matter, from top to bottom in the organic layer. The L(litter)-horizon does not show decomposition of organic matter, while in the F(fermentation)-horizon organic matter is slightly decomposed; individual tissue fragments can still be recognized. In the H(humus)-horizon, which is absent or very thin at the sites, organic matter is completely decomposed.

Figure 2 shows the stages of soil development from a halpic arenosol towards a cambic arenosol (FAO 1988) in drift sand deposits. The mineral section of the soils is formed in acid drift sand deposits (C-horizon). Acidic soil conditions result in leaching of iron and aluminium, and the development of a light grey coloured E(eluviation)-horizon. The increasing brown colour below the mineral E-horizon points to a
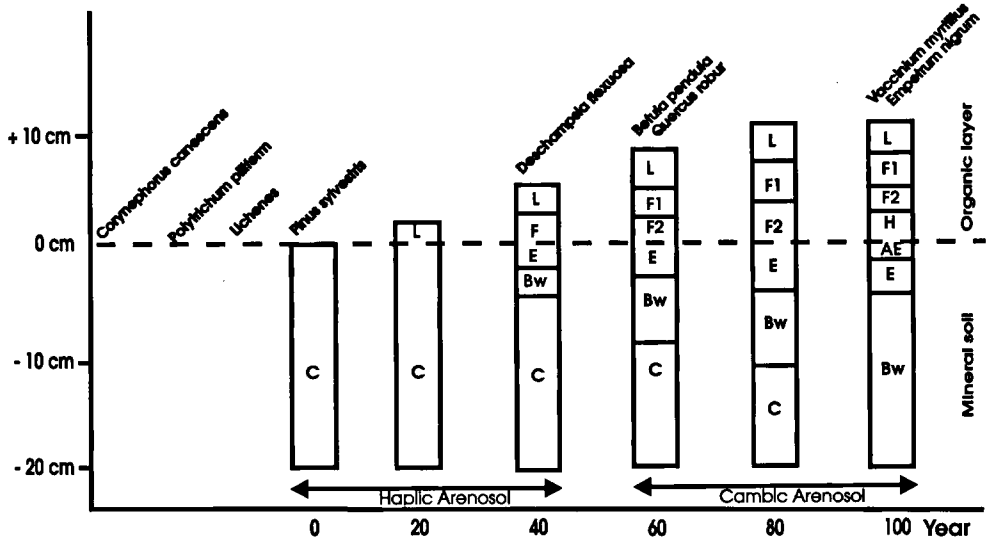
Fig. 2. The relation between the present-day spontaneous vegetation succession of *Pinus sylvestris* on poor sandy substrate and soil development in drift sand deposits. Partly based on Fanta (1986).

Bw(alteration)-horizon. The accumulation of organic matter in the mineral section is restricted to the AE-horizon. A more detailed description of acid forest soil development is given in Dijkstra & Van Mourik (1995).

Methods

At each site samples for pollen analysis were obtained to a depth of 15 cm below the surface, including the entire organic layer and the top of the mineral soil. The samples were taken from a clean pit wall by cutting horizontal slices at 15 mm intervals.

Pollen was extracted from 3 cm^3 organic and 1 cm^3 mineral subsamples respectively. A known number of *Lycopodium* spores was added for the determination of pollen concentrations (Stockmarr 1971). The samples were prepared according to the standard method for soil material (Moore *et al.* 1991). Extra was the purification of the samples under short ultrasonication. Like prolonged acetolysis, prolonged ultrasonication will damage the pollen grains.

The samples were boiled for 10 minutes in 10% NaOH to break up the organic material, followed by sieving (250 µm-mesh sieve) and washing three times in H$_2$O. The tablets with *Lycopodium* spores were separately dissolved in 10% HCl and added after sieving. To remove the silica, HF was added for 24 to 48 hours (cold treatment) depending on the content of silica in the samples. The samples were subsequently dehydrated in glacial acetic acid and acetolysed, using a mixture of sulfic acid and acetic anhydride (ratio 1:9 by volume). To get rid of the finest organic material, the pollen samples were purified under ultrasonication (max. 1 minute) using a 10 µm-mesh sieve. The residue was mounted in glycerin jelly.

Counts were made at a magnification of × 400 following equally spaced traverses over entire coverslip areas to prevent the effect of unevenness of pollen distribution in the slides. Counts comprised to a minimum of 300 pollen and spores in the organic samples. Some mineral samples had a very low pollen concentration or were even sterile. In mineral samples it was therefore impossible to obtain the minimum amount of 300

pollen grains per count. Here the minimum was 150 pollen. Identification of pollen and spore types was based on the key of Moore et al. (1991).

The results of the counts were worked into pollen diagrams (Figs 3–6) with the help of the computer program Tilia, version 1.09 (Grimm 1991). Only pollen and spore taxa that are represented by at least 1% of the pollen sum were plotted in the pollen diagrams. Besides the most important pollen types, these diagrams show the total actual pollen concentration (pollen grains/cm^3) and the soil profile.

In many pollen studies the pollen sum of relative pollen diagrams include pollen types with regional values only, to minimize the effects of local pollen taxa with a high pollen input (Janssen 1981). In this study the calculation sum included all pollen and fern spores in a given sample. Figure 7 shows that the fluctuations of the pollen curves are identical, whether the local pollen types (Ericaceae, Pinus and Gramineae) were excluded (Fig. 7A) or included (Fig. 7B) in the pollen sum. A pollen sum based on regional values only exaggerates the values for regional species (Fig. 7A). From this it is concluded that removal of the local species from the pollen sum is not necessary, when in the first place analysis is used to study the pedological processes in young acid humus profiles. In such soil profiles the pollen records are not only the result of pollen sedimentation, but infiltration and concentration of pollen also influence the pollen record. As a result the distinction between local and regional pollen in soil profiles is very diffuse.

From the same sampling pit samples for micromorphology were also obtained. Undisturbed soil samples for micromorphology were taken with help to Kubiena tins (8*6*4 cm). Thin sections were produced according to the technique described by Jongerius & Heintzberger (1975). The samples were air-dried and impregnated with polyester resin. The thin sections were polished to a thickness of about 20 µm. The micromorphological descriptions of the organic layers and the mineral section were made according to Brewer (1976) and Bal (1974), using a magnification factor of × 25.

RESULTS

Pollen diagrams

The results of pollen analysis are given in the diagrams of sites Herperduin 1 (HD1), Tungeler Wallen (TW), Weerter Bergen 1 (WB1) and Weerter Bergen 4 (WB4) (Figs 3–6). The pollen diagrams are divided into two pollen zones based on different pollen composition. The pollen assemblage of the lower pollen zone (I) at the sites WB1, WB4 and TW is characterized by pollen of a species-poor vegetation, mainly dominated by pollen of Ericaceae. The lower pollen zone (I) of site HD1, on the contrary, shows decreasing amounts of Ericaceae pollen and high amounts of Gramineae and other herbs. The upper pollen zone (II) of all pollen diagrams is dominated by high percentages of Pinus. In the top of the upper pollen zone (II) of sites WB4, TW and HD1 the amounts of Gramineae and other herbs slightly increase, whereas the amounts of Pinus decrease.

The total pollen concentration curves (Figs 3–6) show the vertical distribution patterns of the various pollen types in the acid forest soils. The vertical pollen distribution in soils is determined by a combination of factors, namely pollen deposition, preservation conditions of pollen in the soil profile and downward transport of pollen through the profile (Dimbleby 1985). Pollen deposition, on its term, is
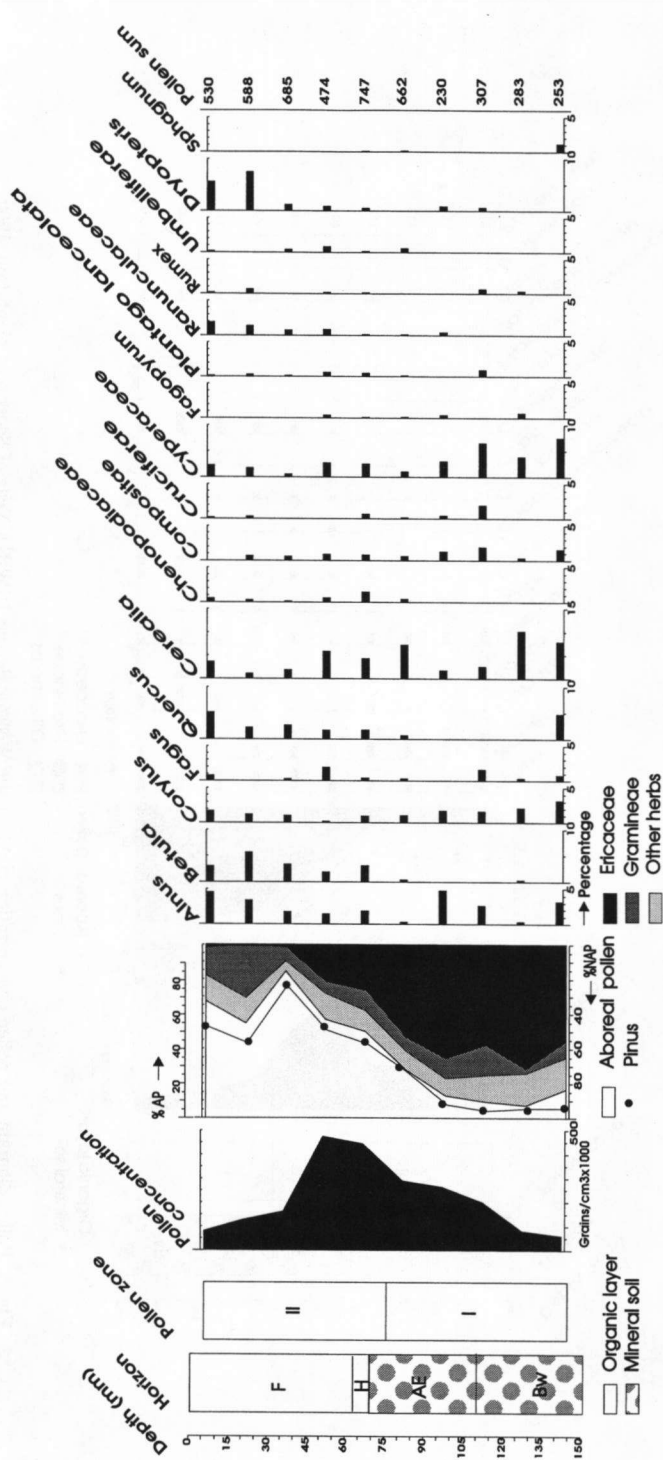
Fig. 3. Pollen diagram and pollen concentration curve of site Herperduin 1 (HD1). Year of Scots pine plantation: 1927.

Fig. 4. Pollen diagram and pollen concentration curve of site Tungeler Wallen (TW). Year of Scots pine plantation: around 1945.
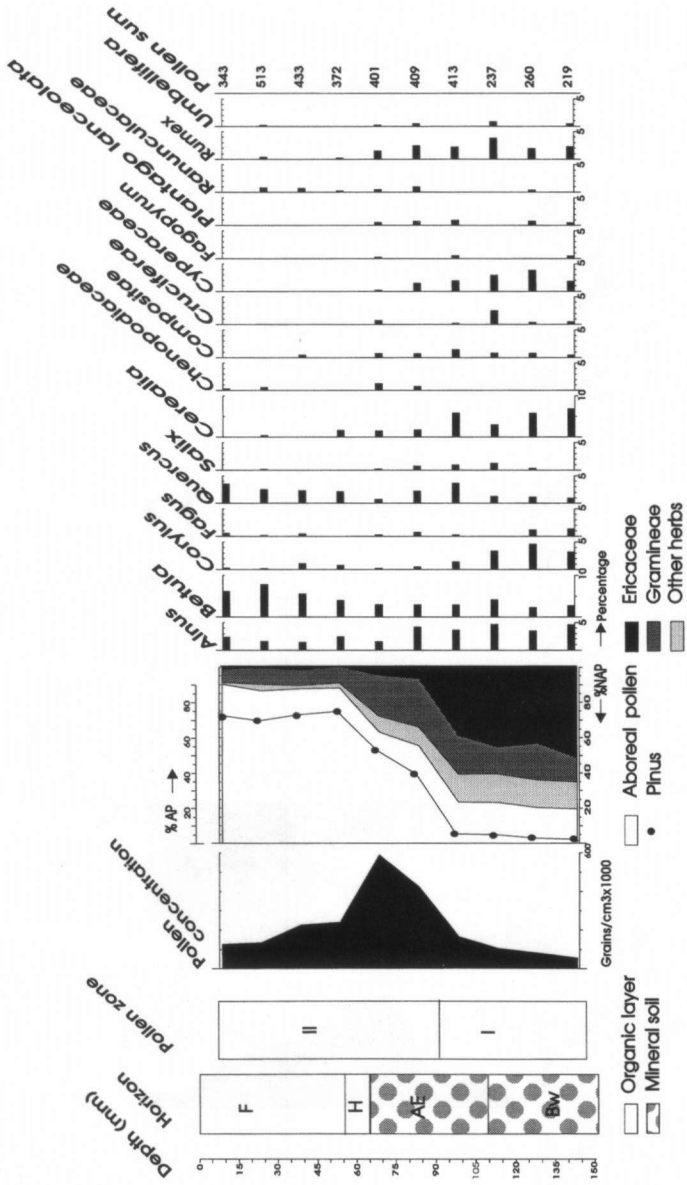
Fig. 5. Pollen diagram and pollen concentration curve of site Weerter Bergen 1 (WB1). Year of Scots pine plantation: 1900.
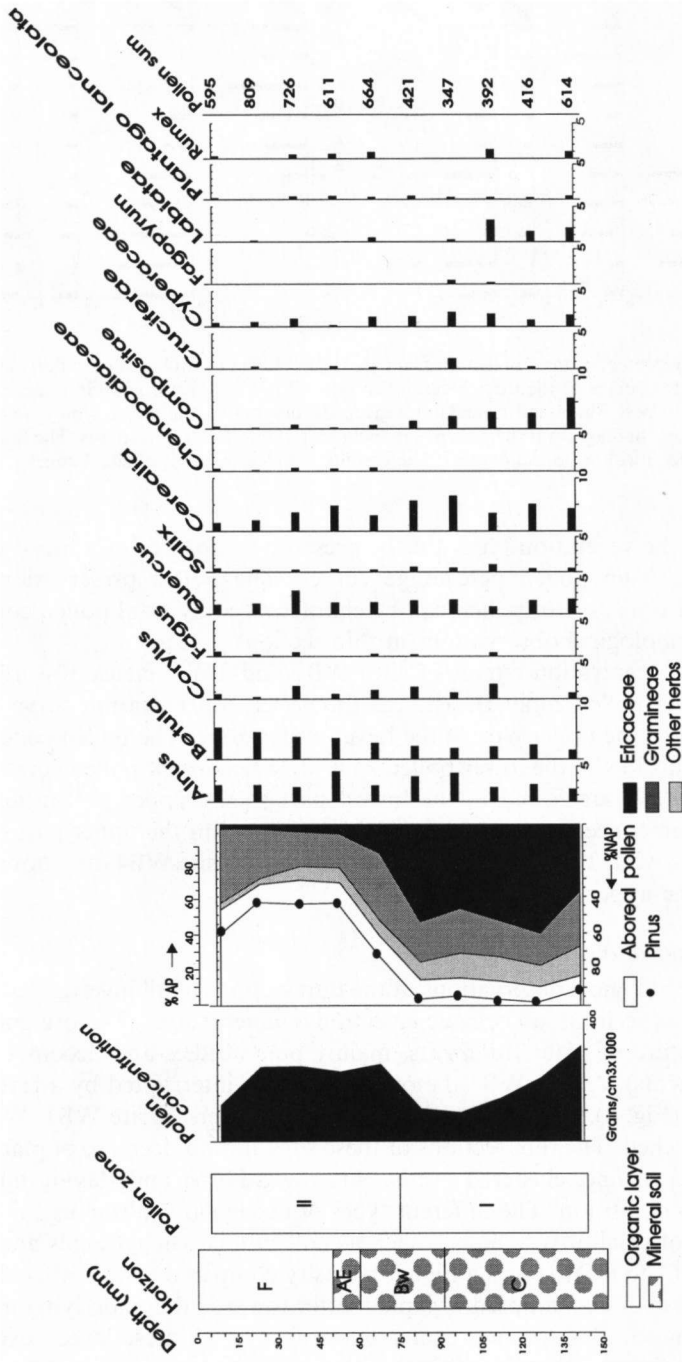
Fig. 6. Pollen diagram and pollen concentration curve of site Weerter Bergen 4 (WB4). Year of Scots pine plantation: 1930.
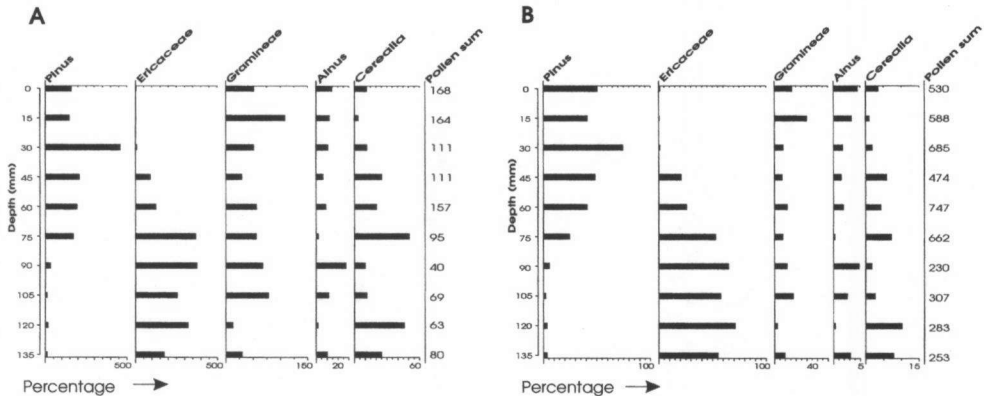
Fig. 7. Shortened representation of pollen diagram Tungeler Wallen (TW) based on different pollen sums. In diagram **A** and **B** the curves of the three local pollen types Pinus, Ericaceae and Gramineae, and two most abundant regional types, Alnus and Cerealia are given. In diagram **A** the pollen sum is only based on the regional pollen types. In diagram **B** the pollen sum includes all pollen and fern spores. The fluctuations of the pollen curves are identical in both diagrams. The complete pollen diagram of site Tungeler Wallen (TW) is given in Fig. 5.

determined by the vegetation type and the presence or absence of a forest canopy, and can be derived from pollen percentage curves. The pollen preservation conditions and downward transport of pollen can be characterized by total pollen concentrations and micromorphological observations in thin sections.

The pollen concentration curves of sites WB1 and TW increase towards the upper part of the lower pollen zone (I), whereas the pollen concentration curve of site WB4 decreases towards the upper part of the lower pollen zone. The pollen concentration of site HD1 remains low in the lower pollen zone. The maximum pollen concentrations of sites WB1 and TW are found in the lowest part of the upper pollen zone (II). The maximum pollen concentrations of site HD1 are found in the upper part of the upper pollen zone (II), while the pollen concentration curve of site WB4 does not show a clear maximum in the upper pollen zone.

Micromorphological observations

The micromorphological observations of the thin sections of all investigated sites clearly show two distinct sections; an organic layer and a mineral layer. The organic layer of all sites has a mixture of plant fragments, mainly pine needles and decomposed organic matter (excrements). At site WB4 the organic layer is interrupted by a layer of mainly mineral grains (Fig. 8). The elements of the organic layers of site WB1, WB4 and TW are very well packed. The thin sections of these sites show a decrease of plant fragments and an increase of fine, clustered excrements towards the underlaying mineral layer, because of decomposition. The different types of excrements in the organic layer point to the activity of small invertebrates, such as collembola, enchytraeids and mites. The organic layer of site HD1 shows a higher porosity compared to the other sites (Fig. 9), while the increase of decomposed organic matter towards the underlying mineral layer is less pronounced. Besides fine excrements of invertebrates, larger excrements of unknown soil animals are observed.

Thin sections of sites WB1 and WB4 shows a sharp boundary between the organic mineral layer. The mineral layer of these sites consists of well-rounded and well-sorted
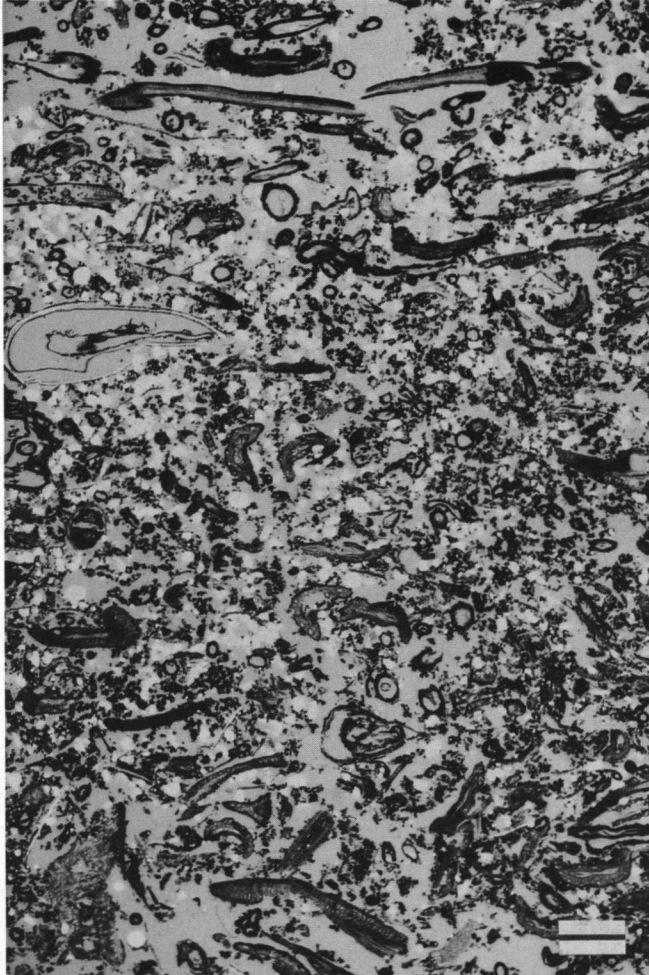
Fig. 8. The compact organic layer of site Weerter Bergen 4 (WB4) mixed with mineral grains. The photo shows the presence of pine needles, roots, small excrements and mineral grains. Bar: 1·1 mm.

quartz grains. Besides mineral grains, the mineral layer of WB1 contains small organic excrements. Organic excrements are absent from the mineral layer of site WB4. Thin sections of sites TW and HD1, on the contrary, show a gradual boundary between organic and mineral layer. The mineral layer of sites TW and HD1 is a mixture of well-rounded and well-sorted quartz grains and clustered organic excrements (Fig. 10).

DISCUSSION

Vegetation development based on pollen analysis

The pollen assemblage of the lower pollen zone (I) of the sites TW, WB1, and WB4 (Figs 4–6) reflects the initial heath vegetation, growing at the sampling sites or in the surroundings before the plantation of the pine trees. The species-poor nature of heathlands was probably caused by high grazing pressure, which prevented the
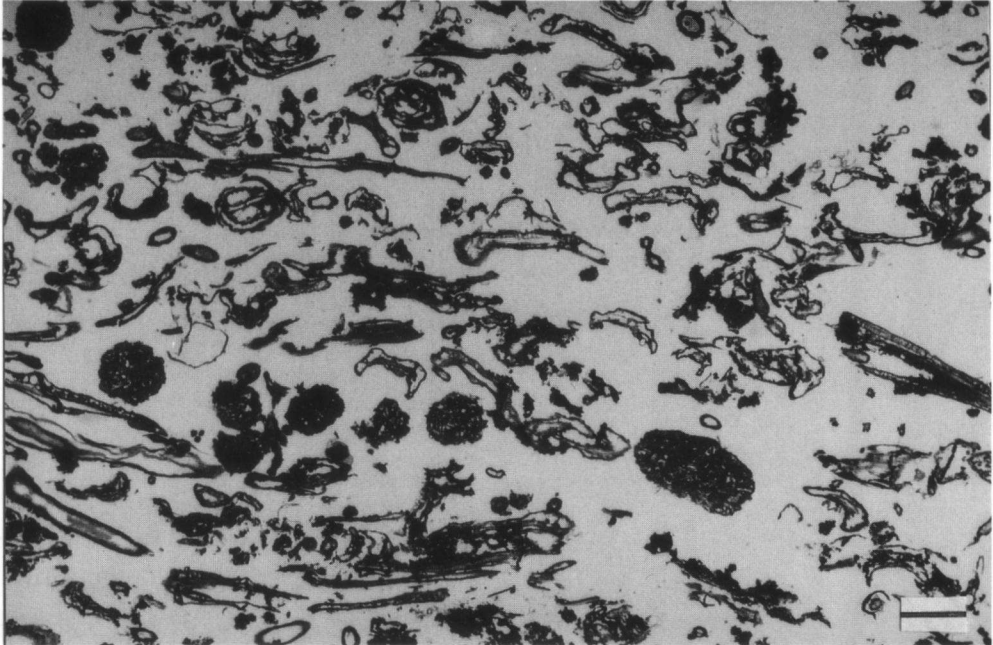
Fig. 9. The organic layer of site Herperduin 1 (HD1), showing the high porosity of the organic layer and the absence of small excrements. The round to ovoid excrements of an unknown soil animal dominate the photograph. Bar: 1·1 mm.

expansion of herbaceous taxa (Mitchell 1990). The low amounts of Ericaceae pollen and higher amounts of Gramineae and other herbs of site HD1 (Fig. 3) were probably caused by diminished human influence. Heath only maintains, if enrichment of the soil with organic material is avoided by fire culture, sod cutting and grazing. After the introduction of artificial fertilizer, large quantities of organic manure were no longer needed. As a result, the poor drift sand deposits were enriched with nutrients and the growing conditions for herbaceous species improved. The appearance of pollen types such as Cerealia and *Fagopyrum* indicates the presence of cultivated areas in the neighbourhood of heathlands. Heathlands often were surrounded by arable lands of which organic manure was needed.

The percentages of non-arboreal pollen (NAP) exceed the percentages of arboreal pollen (AP) in the lower pollen zone of all diagrams. This is probably not the result of differences in pollen deterioration (Havinga 1984), because of the low amount of all arboreal pollen in this zone. The low percentages of AP in the lower pollen zone of the diagrams show the absence of a (closed) forest canopy at the sites and stresses the open character of the heath landscape. The open character of the heath landscape will allow a greater representation of regional pollen (Bradshaw 1981).

The pollen assemblage of the lower pollen zone points to the absence of a forest canopy, yet low percentages of AP occur in this zone. The presence of low percentages is explained by effective pollen dispersal of some tree species. *Pinus* pollen (WB1 and TW) are supplied by distance transport. Usually, the percentages of *Pinus* pollen in drift sand deposits do not exceed 5% (Kalis 1984; Van Mourik & Dijkstra 1995). Like *Pinus*, *Betula* has an effective pollen dispersal (Mitchell 1988) and has not necessarily been
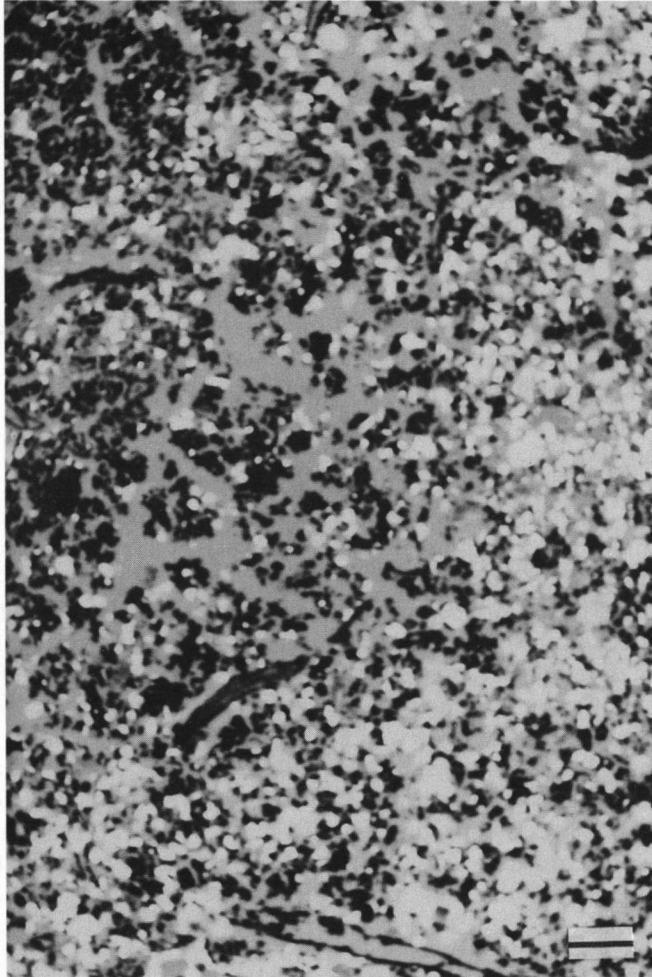
Fig. 10. Organic fine material and excrements in the mineral section of site Tungeler Wallen (TW), forming the AE-horizon. Bar: 0·9 mm.

growing around the sampling sites. Also the pollen representation of *Corylus* is considerable especially when growing in open conditions (Mitchell 1990), indicating the existence of *Corylus* near heathlands. *Corylus* was present in hedges around arable fields of the traditional villages.

The rising *Pinus* curve in the upper pollen zone (II) is attended by a decrease of the NAP. In the first place the decreasing NAP is caused by the development of a closed forest canopy. After the introduction of artificial fertilizer, large areas of heathland were no longer needed. The heath was reclaimed and the drift sand areas were stabilized by Scots pine (*Pinus sylvestris*) plantations. In a Scots pine plantation a closed canopy is reached within 20 years after plantation (De Vries *et al.* 1990). In the meantime the light intensity in the forest will be reduced. A low light intensity prohibits growth of herbaceous species and, therefore, the production of its pollen. Especially Ericaceae species are very sensitive to shade. Secondly, the acid conditions of the soil profile under Scots pine diminish the variety of herbaceous species in favour of grasses. Furthermore,

the closed canopy reduces the influx of regional pollen. Most pollen collected under a closed canopy originates from local sources (Andersen 1970). On the other hand, the enormous local pollen production of the pine trees suppresses the relative amount of herbaceous pollen grains in this zone.

The upper pollen zone of the diagrams WB4, TW and HD1 shows a slight decrease of *Pinus* pollen in favour of herbaceous species, indicating a more open forest canopy today. This is confirmed by vegetational surveys of the actual understorey at the sample sites. The closed understorey at sites WB4 and TW is dominated by grasses (*Dechampsia flexuosa*). The actual understorey of site HD1 also contains, besides grasses, ferns (*Dryopteris*), which are indicators of a higher light intensity. Van Dobben *et al.* (1994) showed that since 1985, the composition of the understorey has changed considerably for nearly all Scots pine stands of The Netherlands.

Usually the increase of grasses in forest ecosystems is explained by the effects of acid deposition. However, the change of a closed canopy Scots pine forest towards a more open canopy can also be connected to vegetational succession (Fig. 2). In nearly every Scots pine plantation, with trees of similar age a spontaneous rejuvenation of various tree species will occur (Kuper 1989). Without forest management the transformation towards a deciduous forest will be fast (Van der Werf 1991). In the upper pollen zone this process is indicated by increasing percentages of *Quercus*.

In spite of several limitations (Groenman-van Waateringe 1986), pollen records from drift sand deposits and the overlaying organic layer give a fairly correct reconstruction of the vegetation development just before and after the pine plantation. Our results are similar to the spontaneous vegetational succession of Scots pine on blown-out areas (Fanta 1986) (Fig. 2) and recent vegetation surveys in Scots pine forests (Van Dobben *et al.* 1994). The pollen assemblages of the pollen zones largely coincide with the soil horizons, formed after the plantation of Scots pine. In the lower zone Ericaceae dominate, indicating the stabilization of drift sand deposits with heath vegetation. The organic layer, formed by accumulation of litter after pine plantation, largely corresponds to the pine dominated upper pollen zone.

Vertical pollen distribution pattern and micromorphology

In general the preservation conditions of pollen in aerobic organic layers and mineral soils are low, as the result of oxidation (Havinga 1964). However, the pollen concentrations in the organic layers of all sites (Figs 3–6) are significantly higher, compared with the pollen concentrations in the mineral sections. Under special circumstances the organic layers have similar preservation conditions to that of peat deposits and free-draining soils such as podzols (Moore *et al.* 1991). A high content of slowly decomposing organic material results in an accumulation of partly decomposed acid litter, preserving pollen grains. These organic layers have a mor-humus profile. Mor-humus is found under vegetation producing litter of a high polyphenolic content (Davies *et al.* 1964) like under coniferous trees.

In general the highest pollen concentrations are found near the surface on which the pollen rain falls, declining with depth due to corrosion (Dimbleby 1985). In these environments, where the concentration of oxygen and the pH are sufficiently high, microbiological activities corrode the exine of pollen grains, thus causing this typically vertical pollen distribution pattern, which becomes more intense if soil mixing animals are absent. However, in organic layers with good pollen preservation conditions, like mor-humus profiles, the pollen concentrations increase with depth.
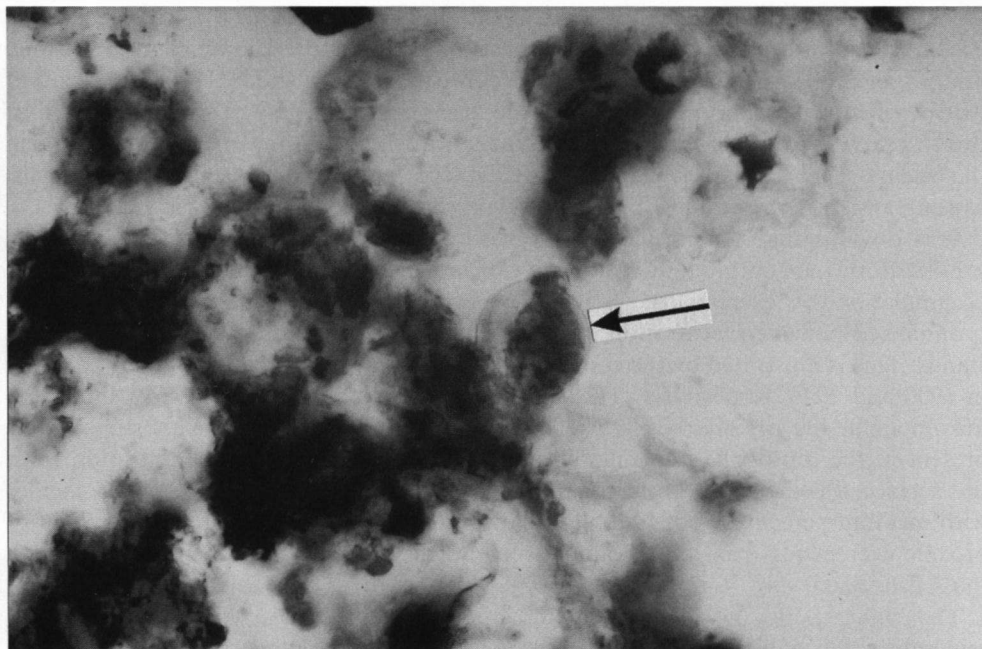
Fig. 11. Partly decomposed excrement, containing a pollen grain (pointer). The pollen type cannot be recognized, because of degradation of the pollen grains after ingestion by soil invertebrates. The diameter of the pollen grain is 20 μm.

Micromorphological observations in thin sections of the studied sites show that the differences in total pollen concentrations between the organic layer and the top of the mineral soil is not explained by hampered decomposition processes, but by the abundance of fine excrements in the organic layer. Closer observation of the excrements with a high magnification factor (× 650) demonstrates that pollen grains are present in these excrements (Fig. 11). From this it can be concluded that pollen grains are preserved inside excrements. Ponge (1991a,b) observed that the soil inhabiting animals in the organic layer under Scots pine (enchytraeids, collembola and mites) consume pollen grains with plant fragments. The ingestion of pollen grains may cause some degradation, particularly exine thinning and crumpling (Moore *et al.* 1991), but inside the excrements pollen grains are preserved by acid and anaerobic conditions (Currie 1961).

The vertical pollen distribution patterns of the sites TW and WB1 show the maximum pollen concentrations in the lowest parts of the organic layer and the top of the mineral soil (Figs 4 and 5). The maximum pollen concentrations of these sites coincide with high amounts of fine excrements, observed in thin sections. This vertical pollen pattern is best explained by pollen infiltration from the surface after the plantation of Scots pines. Mechanical transport of excrements is responsible for the displacement of pollen. The high stability of the excrement and the very slow decomposition of the excrements from fungal digestion causes an accumulation of these excrements and pollen in the lower part of the organic layers (Topp 1981). Compared to TW and WB1, the organic layers of sites HD1 and WB4 (Figs 3 and 6) show lower total pollen concentrations, caused by differences in composition of the organic layer. The lower concentrations of site WB4

are explained by the presence of sand in the organic layer (Fig. 8). At this site, the accumulation of organic matter was probably interrupted by a phase of sand drifting, diluting the pollen rain. In contrast, lower concentrations of site HD1 are the result of worse pollen preservation conditions in the organic layer. Study of the thin section of this site shows fewer fine excrements. A higher porosity, and some macro excrements in the organic layer of site HD1 (Fig. 9) prove the presence of larger soil-mixing animals, causing a higher oxidation of pollen and a more even vertical pollen distribution.

It is obvious that time influences the vertical pollen distribution pattern in a soil profile. Both the continuing development of an acid humus profile and the increased accumulation of excrements with pollen cause a deeper pollen infiltration and pronounced pollen concentration in the organic layers and mineral soils of old forest stands. This is illustrated by the concentration diagrams of sites WB1 and TW, planted in 1900 and 1945, respectively. The pollen concentration curve of site TW shows the maximum in the organic layer. The maximum pollen concentration of site WB1 is present in the top of the mineral soil, and points to a longer pollen infiltration from the surface. Furthermore, the maximum pollen concentration of site WB1 coincides with medium percentages of both *Pinus* and NAP. This is the result of infiltration of organic excrements from the organic layer into the underlaying mineral soil, forming the AE-horizon.

The higher pollen concentrations and abundance of organic fine material in the mineral section of site TW (Fig. 10) are not the result of pollen infiltration from the organic layer, because the percentages of *Pinus* are low compared to the percentages of NAP. Site TW probably was completely stabilized with heather before the plantation of Scots pines. This resulted in the development of an AE-horizon before pine plantation. In contrast, the increasing pollen concentrations with depth in the mineral soil of site WB4 indicate an earlier stabilization phase of the sandy deposits by vegetation. During stabilization of sand, the pollen rain was not diluted, but was concentrated in the vegetation layer. Pollen was stored together with the decomposed organic matter. The decreasing pollen concentrations towards the top of the mineral soil of this profile point to an increase of active sand drifting before Scots pine plantation. Probably the vegetation cover was destroyed again at this site after a (short) stabilization phase.

The pollen preservation conditions are low in the mineral soil. This is shown by the quick decreasing pollen concentrations in the lower part mineral soil of sites HD1, TW and WB1. These low pollen concentrations are not only determined by the poor preservation conditions, because of the absence of organic fine material. The low pollen concentrations also agree with the usually pollen-poor character of cover sand (Koster 1978), from which drift sand originates. A podzol was often developed in the top of the cover sand deposits. Podzols are relatively rich in pollen, compared to the underlaying C-horizon (cover sand). Deposition of pollen from the destroyed podzols together with the sand grains in drift sand deposits is negligible, because pollen grains were mechanically destroyed during eolian transport. Furthermore, the continuous sand drifting caused a dilution of the pollen.

Vertical transport of excrements with pollen can give misleading vegetation reconstructions at the sampling sites. The infiltration of younger pollen grains into older horizons differs from truly stratified deposits, like peat deposits. At any depth there is pollen of various ages, which would not be the case with stratified deposits (Dimbleby 1985). Nevertheless, the vertical pollen distribution curves of young acid forest soils can tell us something about the vegetational succession at the site if the abundance of

younger pollen swamps that of contemporary pollen, which is true for developing Scots pine stands on drift sand deposits.

ACKNOWLEDGEMENT

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