Forests at Løvenholm, Djursland, Denmark, at present and in the past

By SVEND TH. ANDERSEN

With a Contribution by H.J.B. Birks

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Synopsis

The Løvenholm-Fjeld forests constitute a large woodland complex in Djursland. The natural woodlands formerly formed a marginal area between dense settlements and consist to-day of *Fagus sylvatica* and *Quercus petraea* growing on sandy tills and sands. Geological substrate, soils, present vegetation and vegetational history were studied in a research area in Eldrup Forest. The soils are predominantly podzols. The ecology of canopy trees, reproductive tree layer and ground vegetation were studied. Four plant communities were distinguished. Holocene vegetational development was studied in small kettle-holes and soil sections. Traces of the cultivation of *Cannabis sativa* were found in an adjacent peat bog. Four natural forest communities occurred on dry soils in the past, and human exploitation in three periods. The decline of *Tilia cordata*, *Corylus avellana*, *Hedera helix* and *Viscum album*, and the history of *Quercus petraea* are discussed. Former aquatic and wet-ground plant communities are described.

KEY WORDS: Ecology - podzols - *Fagus sylvatica* - *Quercus petraea* - tree rejuvenation - *Ilex aquifolium* - forest communities - Holocene - vegetional history - local scale - Pollen corrosion - soil development - human exploitation of forest - *Cannabis sativa* - *Tilia cordata* - *Corylus avellana* - *Hedera helix* - *Viscum album* - *Plantago lanceolata* - *Fagopyrum esculentum* - *Centaurea cyanus*.

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Contents

The Løvenholm and the Fjeld forests in Djursland

The Løvenholm and Fjeld forests today form a large woodland complex occupying 4000 ha in northern Djursland, East Jutland (Figs. 1 and 4), and constituting the largest woodland area on the Djursland peninsula. Other large woodlands in northern Djursland are the Mejlgård forests, and the forests around Sostrup.

The woodland area in Djursland was considerably smaller in the late 18th century than today, and the Løvenholm-Fjeld forests consisted at that time of smaller woodlands separated by cultivated areas, and bogs and heaths (Estrup 1943, Figs. 2 and 3). Today much of the formerly unwooded land in the Løvenholm-Fjeld area is covered by plantations, mainly of *Picea*. The ancient woodlands still preserve their original names (Tårup Skov, Hvidbakke Skov, Eldrup Skov, Løvenholm Østerskov, Løvenholm Storskov, Højholt Skov, Troldkrat, Auning Skov, Fjeld Skov, Klemstrup Skov and Bøjstrup Skov, Fig. 4). Several bogs occur on lowlying areas (Sømose, Gjesing Mose, Elsborg Mose, Stadsborg Mose, Figs. 3 and 4).

Geology

The northern part of the Djursland peninsula is glacigenous landscape delimited towards west and south by deep valleys, today partly filled by Holo-

Fig. 1. Location map. 1 = Løvenholm.

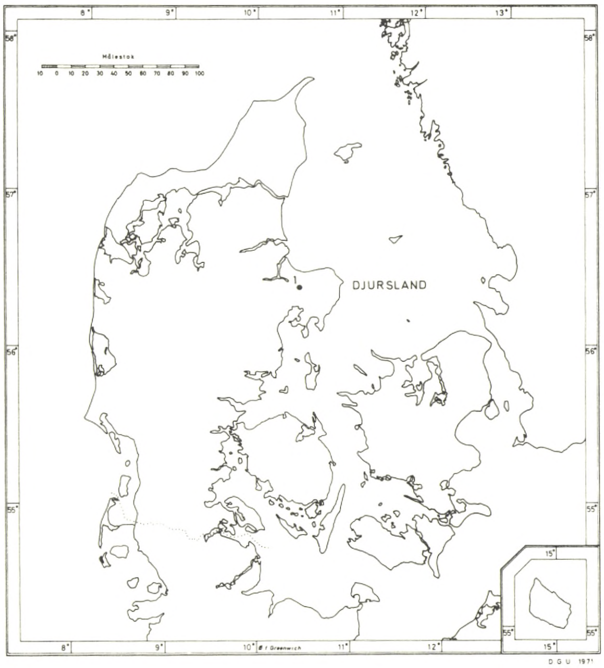


Fig. 3. Woodlands, bogs and villages in the Løvenholm-Fjeld area 1791. From the map of Det Kongelige Danske Videnskabernes Selskab (see Fig. 2, next page).

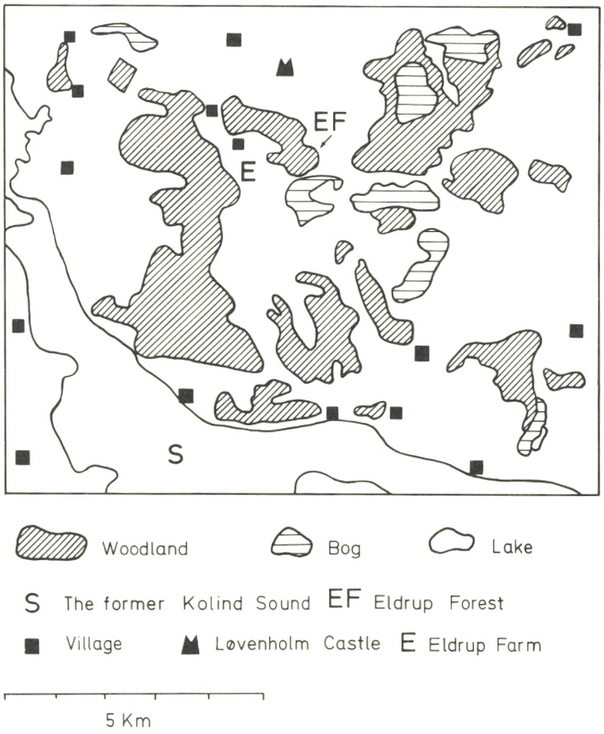


Fig. 2. Djursland. Det Kongelige Danske Videnskabernes Selskab, 1791.

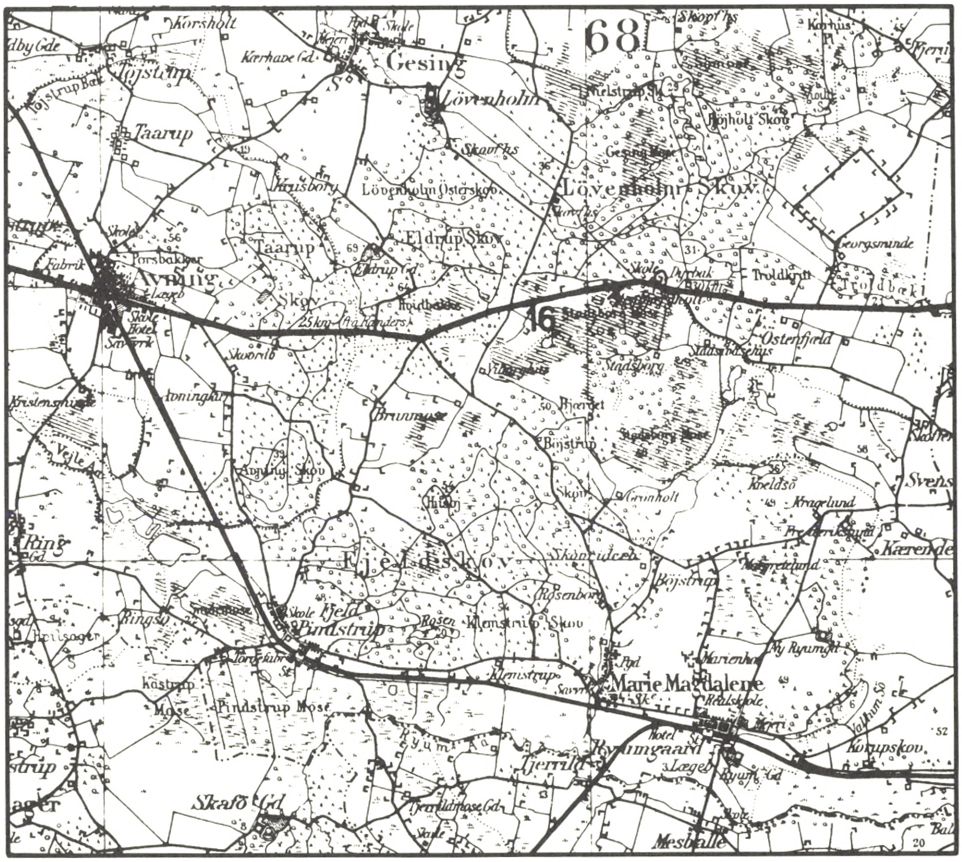


Fig. 4. The present Løvenholm-Fjeld Forests. Det Danske Geodætiske Institut, 1:100000.

cene sediments (Fig. 5). The Pre-Quaternary substrate is Danian limestone, the altitude of which varies from nearly 20m above sea-level in the east to 20m below sea-level at Løvenholm.

The glacial landscape in northern Djursland forms two high ridge systems, up to 70m above sea-level, which are orientated NW-SE (Milthers 1948, Fig. 5). The Løvenholm-Fjeld forests are situated on the southwestern ridge system.

The deep valleys delimiting northern Djursland were invaded by the sea in the early Holocene (A. Jessen 1920). A water level at 3m above the present sea level was reached in middle Atlantic time (Troels-Smith 1942), and from that time, or somewhat earlier, northern Djursland was an island isolated by a narrow sund which was connected with the Kattegat in the northwest and in the east (Fig. 5). The sea receded in early and middle Subboreal time (Iversen 1941, Troels-Smith 1942), and deep freshwater peat formed in the valleys, except for the deepest parts which were filled by a large freshwater lake, Kolind Sund, which was dried out artificially 1874-83 (A. Jessen 1920, Villumsen & Andersen 1976, Fig. 2).

Settlements

The former Kolind Sound was densely inhabited in Atlantic time; however, there are few finds of Mesolithic age in the Løvenholm area. Prehistoric barrows are numerous in northern Djursland, except for the area around Løvenholm, which is nearly void of such barrows (Fig. 5) and was apparently nearly uninhabited in prehistoric time.

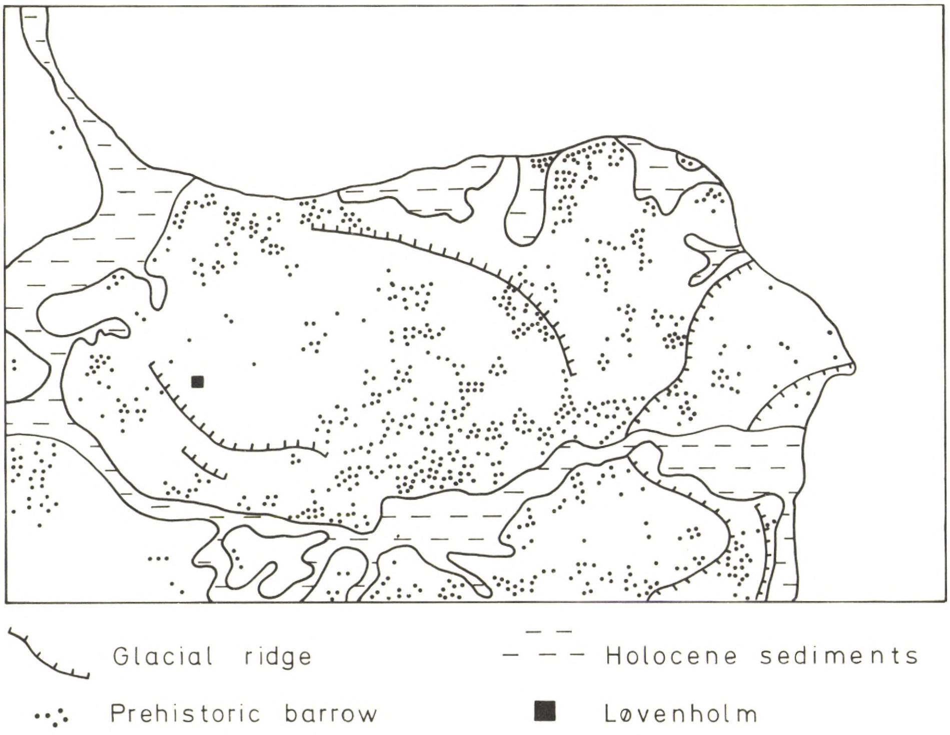


Fig. 5. Geological and archaeological features in Northern Djursland. Based on Milthers 1948 and Brøndsted 1957-60.

Villages occur today around the Løvenholm-Fjeld area (Fig. 3). Only two villages occurred inside that area, Krusborg and Eldrup, the latter of which was mentioned in records from 1271 (*Castrum Almaethorp*, Trap 1963). Later, the village Eldrup disappeared and only one farm, Eldrupgård, exists today.

The Eldrup Farm and the woodlands around it (Eldrup Skov, Hvidbakke Skov) belonged to the Stenalt Estate 1683-1930. The farm and the woodlands were aquired by the Løvenholm Estate 1930. The present farmhouse was built in 1874 at a position southeast of the original location shown on the map from 1791 (Fig. 9).

The Løvenholm Estate (originally Gjesingholm) was first mentioned in 1445 (Trap 1963), and the castle was built in the 1570s. The woodlands, Løvenholm Østerskov and Løvenholm Storskov originally belonged to the estate. Besides Hvidbakke Skov and Eldrup Skov, Auning Skov and Tårup Skov were aquired recently by the estate, and considerable plantations were established.

The woodlands around Løvenholm thus were thinly populated in prehistoric and Medieval time forming apparently a marginal area between densely populated settlements. Later they came into the possesion of the large estates. In the 17th and 18th centuries these woodlands were rather heavily exploited, and grazing by cattle and horses was intensive until 1805, when a law forbidding grazing was passed (Estrup 1943). Since then, the woodlands have been re-established and forestry exploitation initiated.

Climate

Climate data have been collected at Løvenholm at a station at 28m altitude (Det Danske Meteorologiske Institut 1966-74). Average temperatures for 1960-69 were 14.9°C for July and -0.6°C for January, the average precipitation was 651mm, and average days with snow cover 41 (data from Det Danske Meteorologiske Institut 1966-74). These figures are quite normal for Denmark. The dominant wind directions in Djursland are west and southwest in the summer (June-August, 25-33 and 20%) and southwest and west in the autumn (October to November, 25 and 20%, Frydendahl 1971).

Quercus petraea in the forests in Djursland

Fagus sylvatica predominates in the natural woodlands in northern Djursland. These woodlands are, however, especially noticeable because of the occurrence of *Quercus petraea*. The species is common in the Løvenholm-Fjeld forests, Ramten Forest, and the Mejlgård forests near the north coast of Djursland (Ødum 1968). The Løvenholm-Fjeld forests are also noticeable because of the absence of *Quercus robur*. The occurrences of *Quercus petraea* in northern Djursland are isolated from the occurrences in middle and West Jutland, East Jutland being otherwize void of the species (Fig. 6).

Quercus petraea occurs in middle and West Jutland in pure stands or mixed with *Quercus robur* (Gram, Jørgensen & Køie 1944). The individuals there are mostly scrubby, having been coppiced for centuries. *Quercus petraea* occurs in northern Djursland as pure tree stands or more or less mixed with *Fagus sylvatica*. These woodlands are therefore unique in Denmark.

The research area in Eldrup Forest

Because of the unique status of the Løvenholm Forests it was decided to establish a research area with the special purpose of studying the ecology and history of the *Quercus petraea* woodlands. Negotiations were initiated between the late Johs. Iversen, State Geologist, and the Løvenholm Foundation, which at present owns the estate. In 1969 the Løvenholm Foundation and the Geological Survey of Denmark agreed to establish such a research area, an agreement which was financially supported by the Carlsberg Foundation.

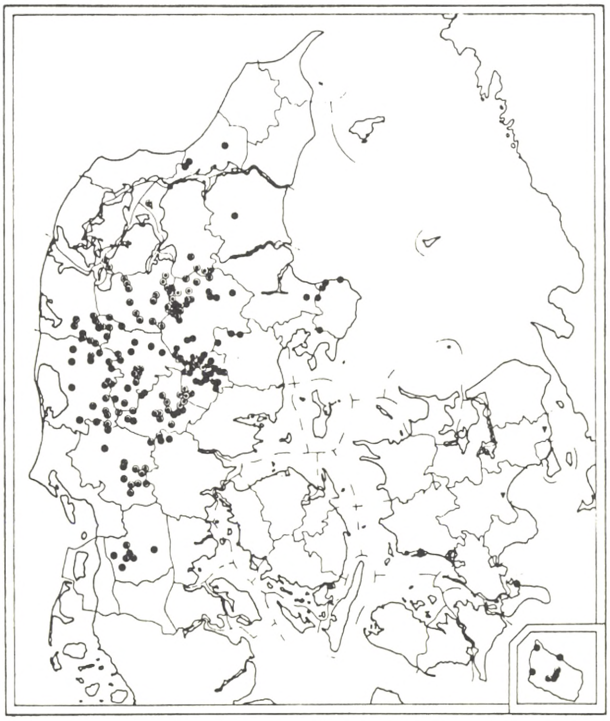


Fig. 6. The distribution of *Quercus petraea* in Denmark. ●, herbarium specimen; ⊙, other information. From Ødum 1968.

An area in the easternmost part of Eldrup Forest was selected, the area being the largest yet preserved woodland with stands of *Fagus sylvatica* and *Quercus petraea* (Figs. 7 and 8). The area comprises 9.7ha and is now left undisturbed except for measures with a scientific purpose. The area is delimited towards west and south by *Picea* plantations and towards north and east by an earth bank which formerly marked the boundary between Eldrup Forest and the Løvenholm fields. Here an area with a *Picea* plantation was left outside the research area.

In 1969 an enclosure was erected in the central part of the research area in order to protect tree rejunevation and ground vegetation from deer-browsing. As browsing formerly had favoured the spontaneous rejuvenation by *Fagus* and *Picea*, at the cost of *Quercus*, the entire generation of small trees

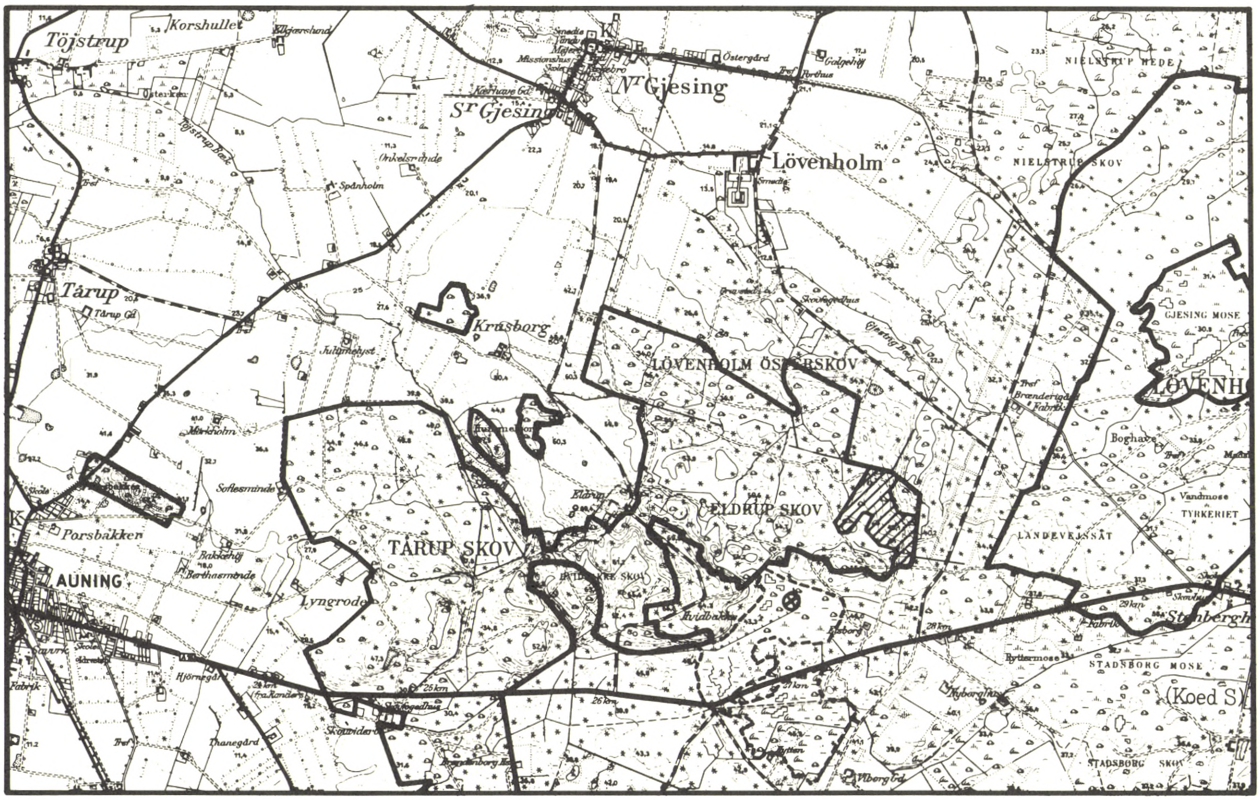


Fig. 7. Present and former woodlands around Løvenholm. Hatched: The research area in Eldrup Forest. ---, Elsborg Bog, ⊗, Section 1972 and 1974. Based on Det Danske Geodætiske Institut 1:25000. For scale see Fig. 9.

was removed before the establishment of the deer fence. Furthermore, in order to study the influence of light on fully exposed vegetation, a small artificial clearing was established by the felling of four *Quercus* trees. No other measures have been taken since, except for removal of self-sown *Picea*.

The studies in the research area in Eldrup Forest have been concerned with the geological substrate, the soils, the present vegetation and its response to the environment, and the past changes in vegetation and soil. Based on these studies, future trends of vegetational change will be followed.

The field work in Eldrup Forest was carried out by the author assisted by staff members of the Geological Survey, not least by Mr. H. Bahnson. Initially a coordinate system was established within the enclosure (Fig. 8). The surface was levelled, soil profiles were measured, and hollows with peat and gyttja layers were cored. The trees were mapped and measured, and the vegetation on the ground analyzed.

The properties of the soils were analyzed, and trends in vegetational history and soil evolution were investigated by analyses of pollen and other microfossils.

Field observations were related to the coordinate system: a grid with forty-one east-west lines at 10m intervals, marked by letters, and twenty-nine north-south, marked by numbers. The intersections were marked in the field by plastic tubes. There were 670 main points in the coordinate system. All samplings refer to these main points.

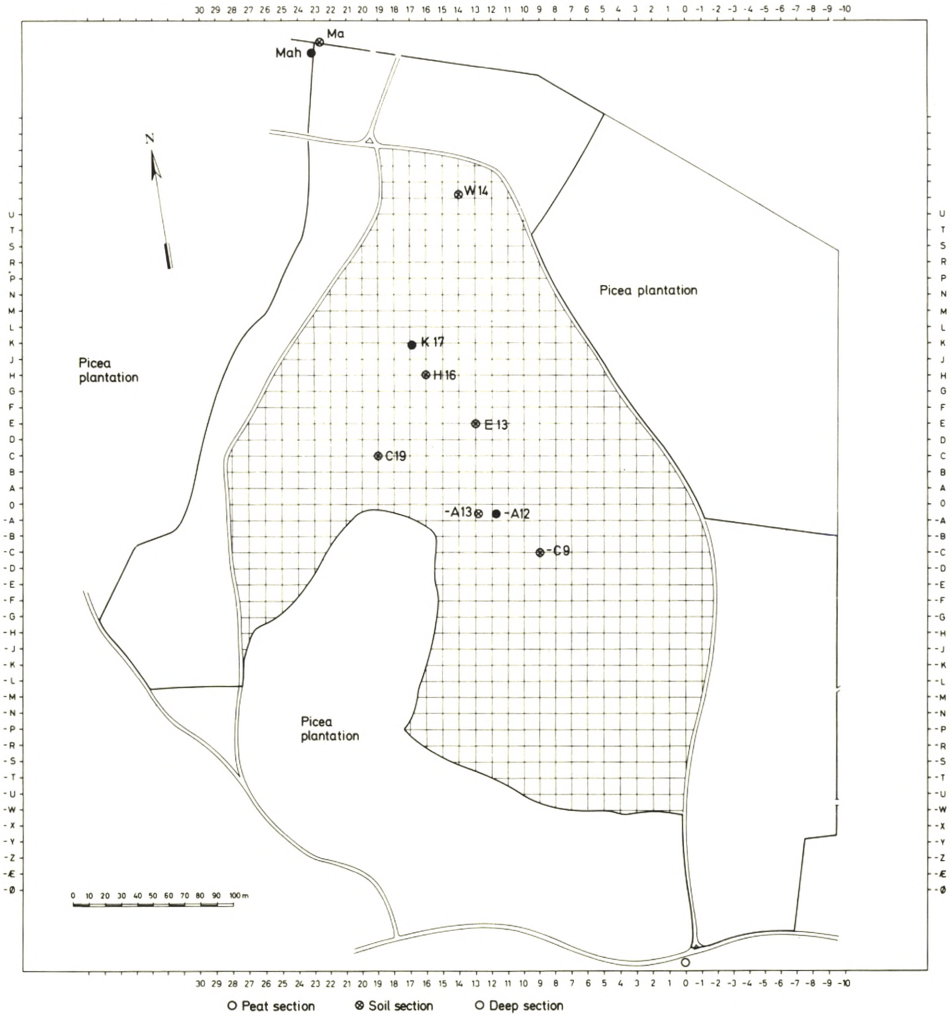


Fig. 8. Map of the research area and the enclosure (cross-hatched) in Eldrup Forest. A deep boring, and wet hollows (*Molinia* hollow: -A 12, *Glyceria* hollow: K 17, Matrikel hollow: Mah) and soil sections studied by pollen analysis are indicated.

Geological substrate and soils in the research area in Eldrup Forest

Field methods

Soil profiles

Soil horizons were described and measured in 1973 and 1974 at each main point by means of a soil auger with a half-cylindric opening 50 cm long and 2cm wide. If necessary, two or more consecutive cores were extracted from the same bore-hole at increasing depth. Samples in vertical sequence for laboratory analysis were secured in excavations and stored in plastic bags. Depth was measured from the top of the mineral soil, or the consolidated humus if a humus layer was present, excluding loose leaf litter. The corings in the peat areas are described on pp. 86-88.

Leaf litter

The depth of the unconsolidated leaf litter was measured at all main points July 1978. The dead leaves are distributed by winds in the autumn, and the litter had been compressed by snow in the winter.

Laboratory methods

Texture of the mineral soils

Mechanical analysis was performed at the Department of General Geology at the Geological Survey of Denmark. The content of mineral particles larger than 0.06mm was determined by dry sieving and that of particles smaller than 0.06mm by the hydrometer method (Dansk Standardiseringsråd 1978). The results are given as weight percentages of dry soil, excluding particles larger than 2mm.

Fe and Al in the soil profiles

Geochemical analysis was performed at the Geochemical Department of the Geological Survey. Total Fe and Al were determined on samples ignited at 1100°C and dissolved in 20% HCL, by atomic absorption spectrophotometry.

Organic content in the soil profiles

Organic content was determined as loss on ignition of the dry sample at 1100°C. Organic carbon was determined after combustion in an induction furnace by absorption in ascarite.

pH in the soil profiles

pH was measured on dried samples soaked in distilled water, using a glass electrode.

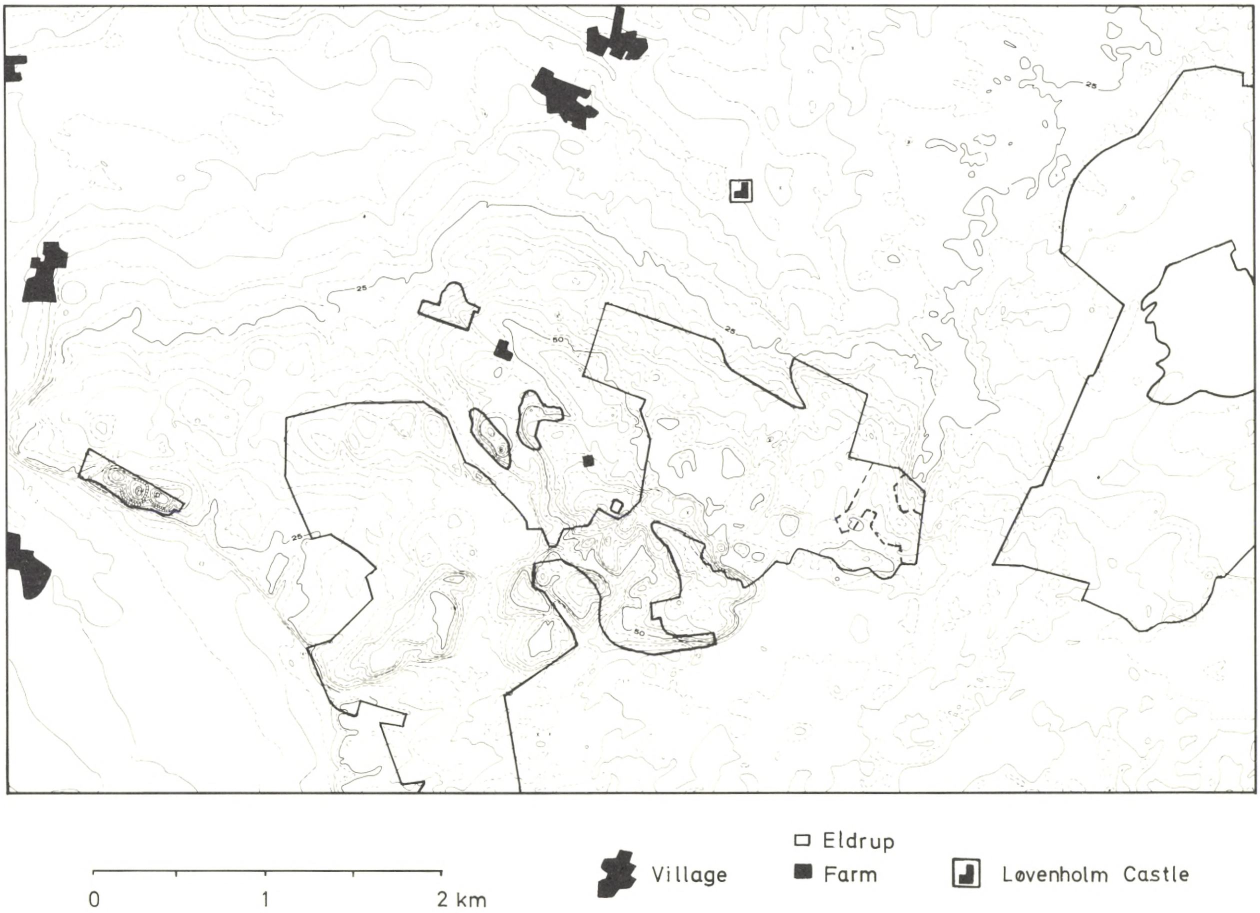


Fig. 9. Surface topography and the former woodlands around Løvenholm. Based on Det Danske Geodætiske Institut 1:25000 (Copyright). Contour intervals 2.5m.

Surface relief

The woodlands Hvidbakke Skov, Løvenholm Storskov and Eldrup Skov are situated on one of the glacigenous ridges in the southwestern part of northern Djursland (Fig. 9). The ridge forms the highest part of that area, reaching 70m altitude at Hvidbakke. The surface of the ridge is rugged with many kettle holes and erosion gullies.

Eldrup Skov and Løvenholm Østerskov occupy the northeastern slope of the high ridge. The detailed topography of the enclosure in Eldrup Forest is shown in Fig. 10. The northwestern part of the enclosure is a plateau which falls gently from 47 to 43m in altitude and rises to 51 m in the southwesternmost part. It is crossed south to northeast by a gully, 1-2m deep. A small kettle-hole with gyttja occupies a central part of the gully, and several shallow depressions occur in the northwestern area. The southeastern part has rather steep slopes facing north and east and dropping from 49 to 38m in altitude. There are two hollows in this area which are partly filled by peat and gyttja.

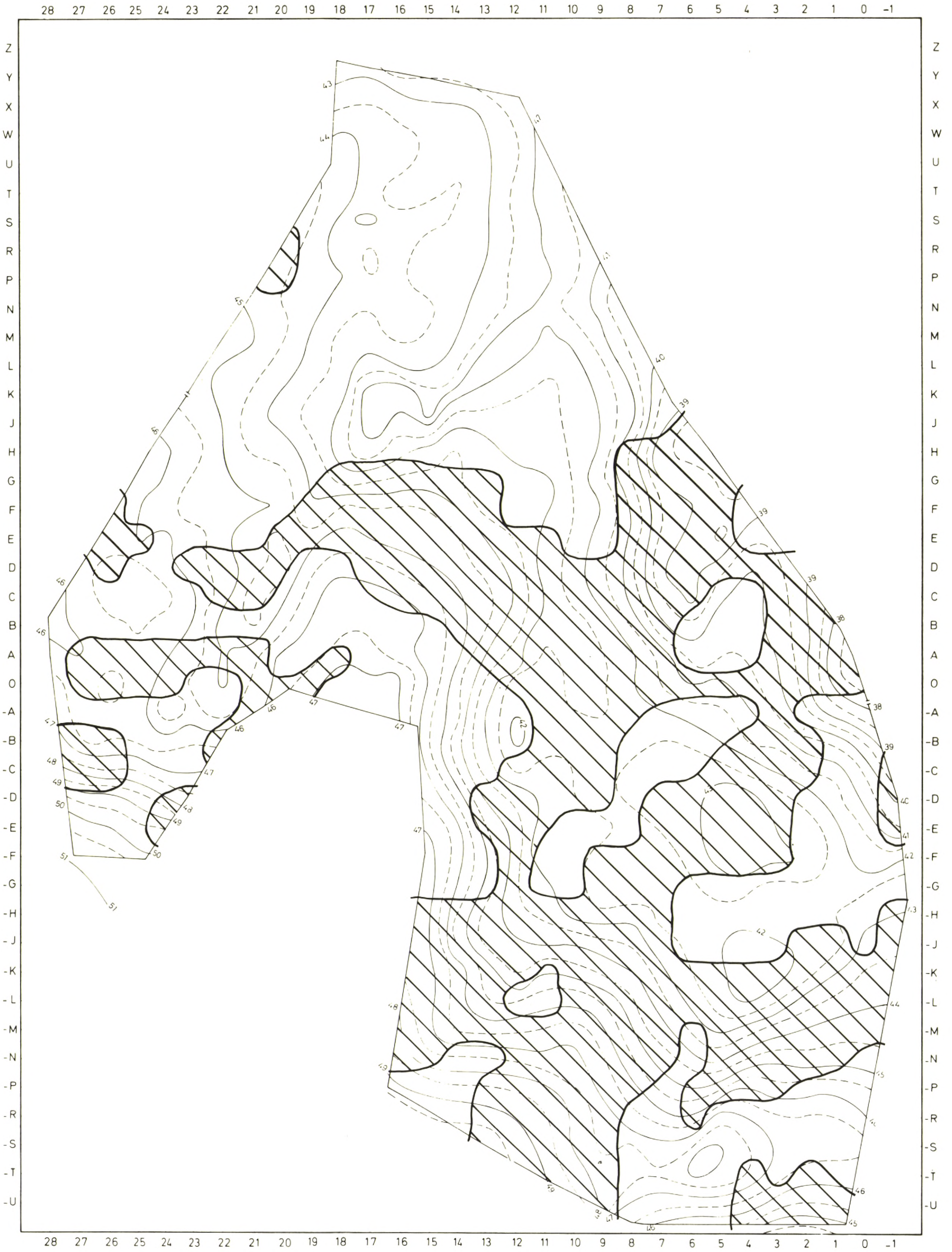


Fig. 10. Surface topography and the distribution of sorted sand in the enclosure in Eldrup Forest.

Mineral soils

Two kinds of mineral deposits were encountered, unsorted sandy till and sorted sand. The till was distinguished from the sand by the presence of pebbles and rocks during the field work. Particles smaller than 2mm typically contained about 80% sand, 15% silt and 4% clay (Fig. 11). Particles 0.2-0.3mm in diameter predominated in the sorted sand; there were about 5% silt and 1% clay particles (Fig. 11).

The sorted sand was superposed on the till, its depth varying from about 10cm to more than lm. It occurs in irregular areas which tend to be orientated southwest-northeast, and are unrelated to the present topography (Fig. 10). It can be suggested that the sand was deposited in water collected on a wasting ice sheet with an irregular horizontal surface, and that the present topography arose at the melting of the ice. The gully mentioned above was probably formed by the drainage of water collected on the ice.

The surface of the till is slightly rugged with many small depressions, whereas the sand surface is smooth.

The content of silt and clay particles in the sandy till tends to increase with depth. Two examples are shown in Fig. 12. In section W14, the clay content increases to nearly 20%, and, in section C19, the silt content to 30-40%, below 50cm depth.

The content of silt and clay particles in the A and

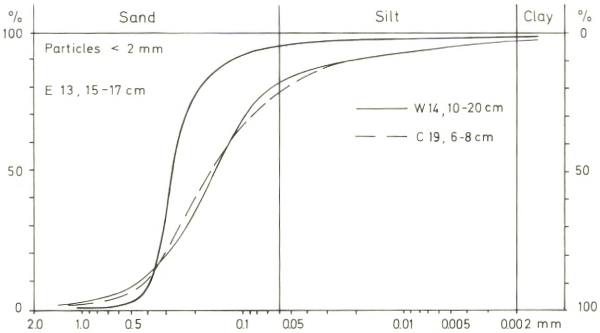


Fig. 11. Grain size distribution in sorted sand (E 13) and sandy till (W 14, C 19).

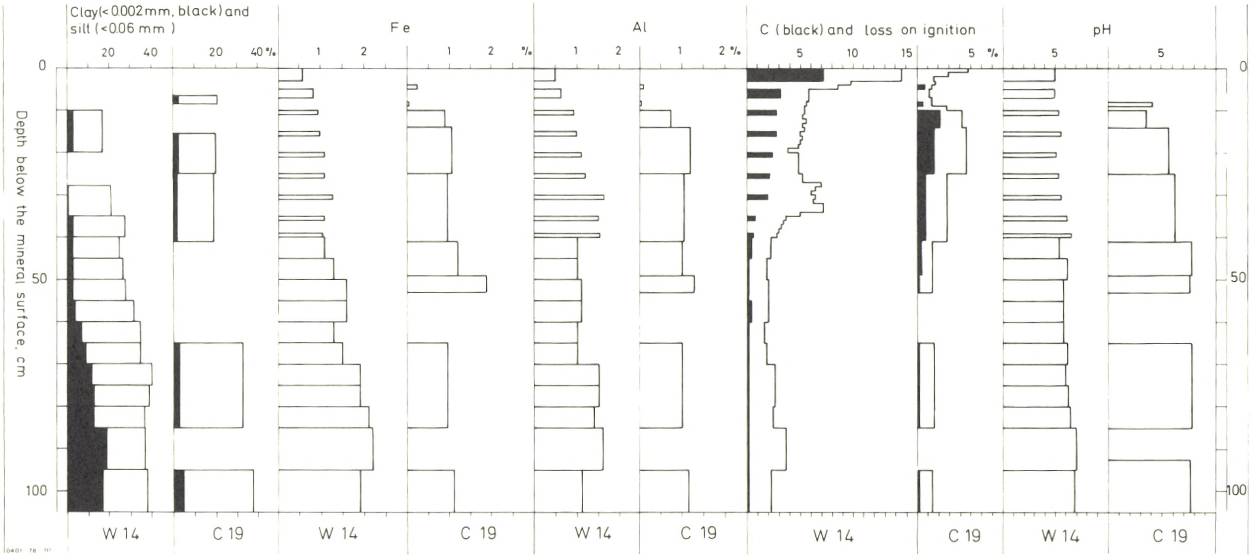


Fig. 12. Clay and silt particles, total iron and aluminium, organic carbon, loss on ignition, and pH, in brown earth (W 14) and podzol (C 19) on sandy till (from Andersen 1979a).

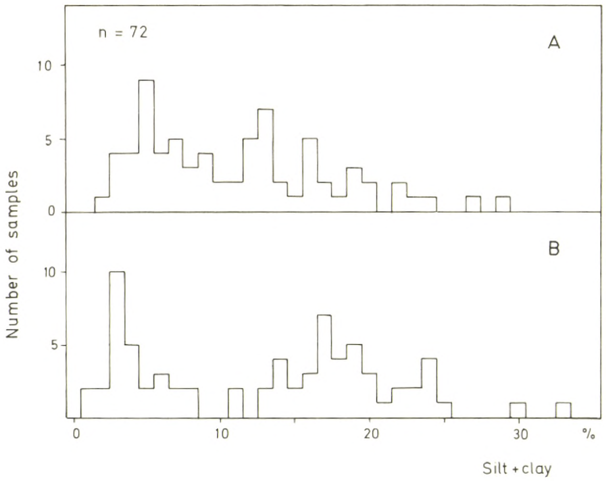


Fig. 13. Silt and clay particles (<0.06 mm) in samples from the A and B horizons of 72 podzol profiles from the enclosure.

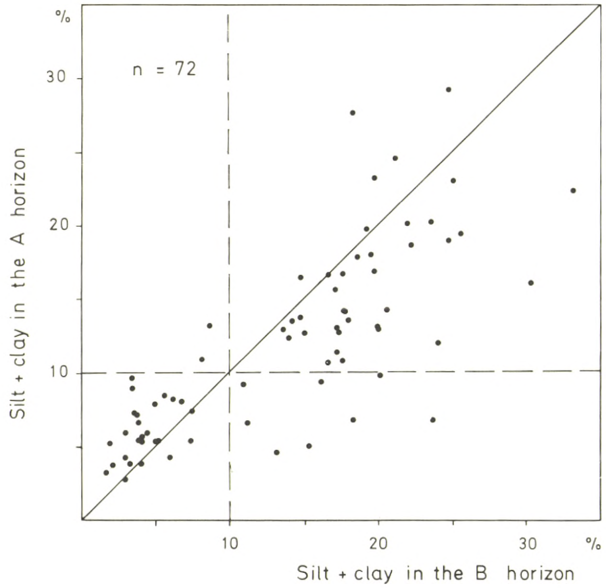


Fig. 14. Silt and clay particles in the A and B horizons of 72 podzol profiles. The dashed lines indicate the upper limits for sorted sand in the B horizon.

TABLE 1. Boring at the southernmost limit of the research area in Eldrup Forest. (DGU 70 180). Descriptions by H. Bahnson. Surface at 48m altitude.

0.0– 2.0 m	Sorted sand
2.0– 3.0 m	Sorted sandy silt
3.0–10.6 m	Brown weathered till (without lime)
10.6–18.6 m	Grey till (with lime)
18.6–20.0 m	Sorted gravel
20.0–52.0 m	Sorted layers of sand, silt and gravel
52.0–56.0 m	Stony gravel (boring stopped at 56 m)

B-horizons of podzols was measured in 72 sections (along the B, C, D and E-lines). Till and sorted sand appeared clearly distinguished in the samples from the B-horizons (Fig. 13). The till samples contained 11-35%, and the sand samples 1-8%, silt and clay particles. Till and sand were less well distinguished in the samples from the A-horizons.

The sections with sand in the B-horizon usually had higher silt and clay content in the A-horizon than in the B-horizon (Fig. 14). This probably indicates decreased transport velocity in the original depositional environment. The sections with till in the B-horizon usually had decreased silt and clay in the A-horizon (Fig. 14). In some of these cases, a sand layer was superposed on the till; in the other cases sand was apparently mixed into the uppermost part of the till.

Lime is absent from the mineral soil in the research area.

A boring carried out by the Geological Survey at the southern limit of the research area penetrated to 56m depth (Fig. 8, Table 1). The uppermost sorted sand and silt layers, 3m deep, correspond to the sand layer mentioned above and were probably deposited in stagnant water on top of a glacier. The till was 16m deep and contained 20-50% silt and 10-20% clay. Hence, the content of fine particles is somewhat larger than that of the superficial till in the research area. The uppermost 7m of the till was weathered and devoid of lime. Sorted gravel, sand and silt occurred beneath the till.

Fig. 15. The depth of the leaf litter in the enclosure.

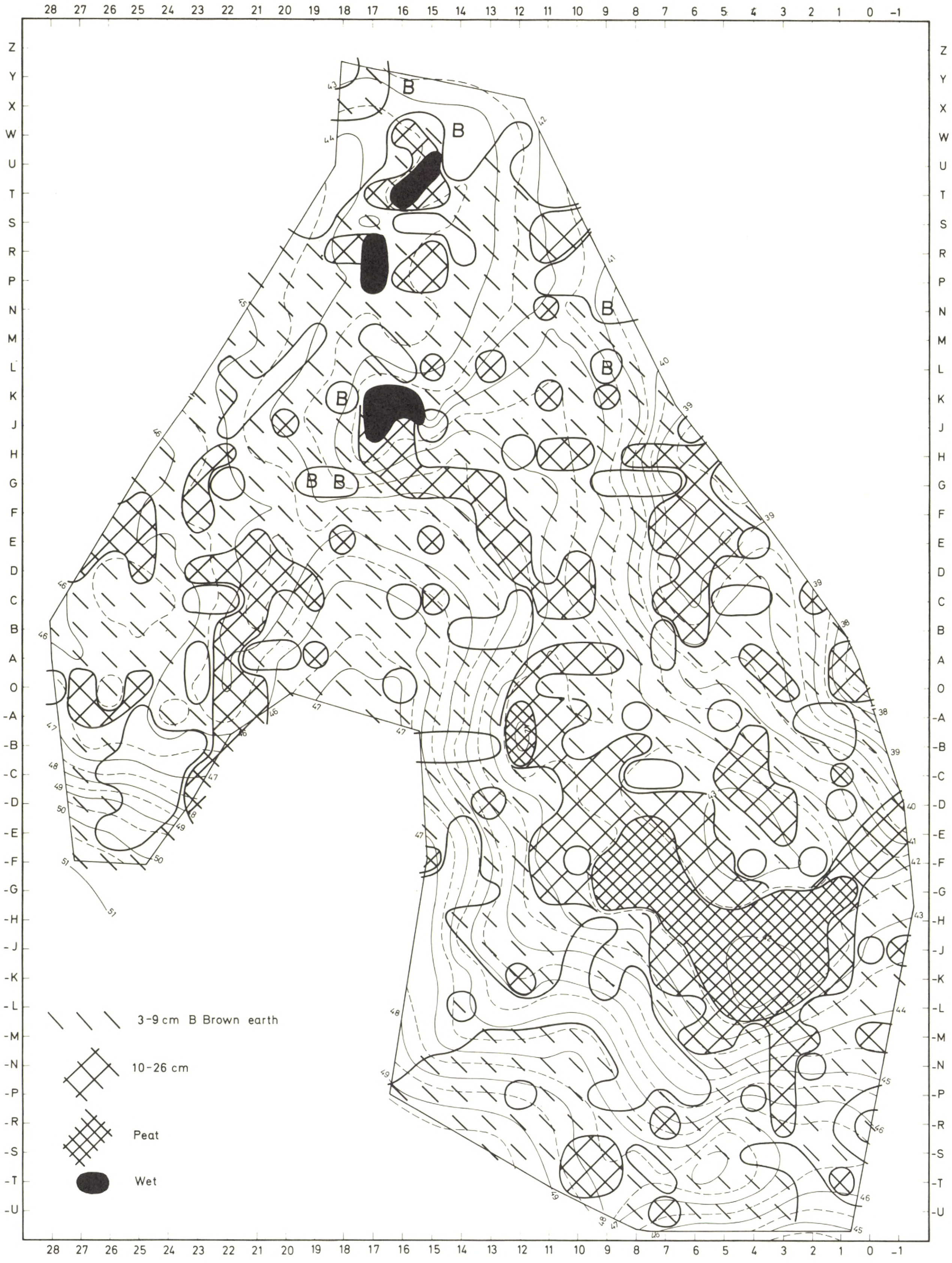


Fig. 16. The depth of the humus layer in the enclosure. B: Sections with brown earth, M: *Molinia* hollow; G: *Glyceria* hollow.

Leaf litter and humus layers

The depth of the leaf litter varied 0-10cm (Fig. 15). The dead leaves tend to accumulate on the lower parts of the large slopes facing east and northeast, which are sheltered from the predominantly westerly and southwesterly winds (p. 9), in shallow depressions, and in dense field vegetation. Wind exposure thus mainly determines the depth of the litter layer, in accordance with Watt (1931) and Ovington (1953).

The mineral soil is mostly covered by a humus layer of varying depth outside the hollows with peat and the wet hollows (Fig. 16). A humus layer was absent in some areas.

The humus layer is up to 26cm deep. The topmost part of the humus was light brown and brittle, and the lower part brown and greasy (Table 2).

Andersen (1979a, 1983) found that accumulation of shallow humus layers on level ground began 130 years ago. Most of the shallow humus is presumably of a similar age. A considerably earlier age (4000 years) was found for humus layers occurring between the hollows in the southeastern part of the enclosure. The humus layers which are older than 130 years are more than 20cm deep. In four sections, the highest humus accumulation rates were found on sites sheltered from wind (Andersen 1983).

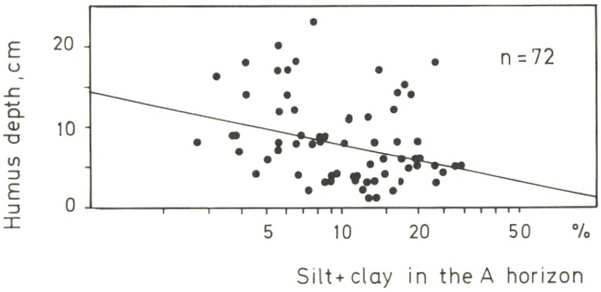


Fig. 17. The depth of the humus layer and the content of silt and clay particles in the A horizon of 72 podzol profiles.

Generally, the humus layer tends to be shallow on the highest parts of the slopes and deeper on the lower parts (Fig. 16). The depth of humus layers less than 20cm deep is correlated with the depth of the litter layer (n=618, r=0.110, P=0.006). The depth of the litter, and, hence, wind exposure, thus determine the depth of the young humus layers.

The depth of the young humus layers was compared with the content of silt and clay particles of the topmost mineral soil at the 72 sections mentioned above (Fig. 17). The humus depth was negatively correlated to the natural logarithm of the percentage of silt and clay (n=72, r=0.315, P=0.007). The reason for this relationship is somewhat difficult to evaluate. One may assume that the biological decomposition of the litter is stimulated by moisture and is, accordingly, slowest on those soils with the coarsest texture.

It appears that the depth of the young humus layer is generally determined by leaf-litter depth, which depends on wind exposure, and by the silt and clay content of the mineral soil beneath the humus layer.

Soil types

Podzols

Podzols (spodosols in the nomenclature of FAO 1968) prevail in the research area. A leached horizon (A), a rust coloured eluvial horizon (B), and untransformed subsoil (C), could be distinguished beneath the humus layer (Plate I, Table 2).

The vertical variation in total iron and aluminium content, and in the loss on ignition, in the mineral soil of two podzols on till and one on sand

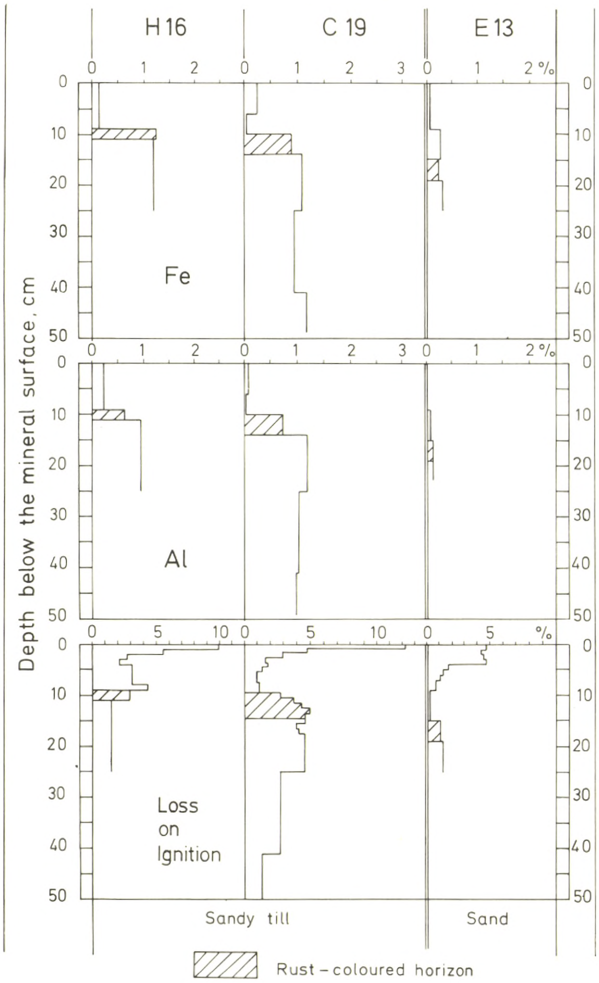


Fig. 18. Total iron and aluminium, and the loss on ignition, in the mineral soil of 3 podzol profiles on sandy till (H 16 and C 19) and sorted sand (E 13).

TABLE 2. Descriptions of four soil sections on podzols.

H16	A_0	0– 8 cm	Light-brown, brittle humus
	A_0	8– 21 cm	Dark-brown humus
	A_0	21– 27 cm	Blackish-brown greasy humus
	A_{1+2}	27– 36 cm	Blackish-grey humic sandy till
	B_1	36– 38 cm	Rust-coloured sandy till
	B_2	38– cm	Yellow-grey sandy till
C19	A_0	0– 5 cm	Brown tough humus
	A_{1+2}	5– 15 cm	Grey Sandy till
	B_1	15– 19 cm	Rust-coloured sandy till
	B_2	19– 46 cm	Yellow sandy till
	C	46– 54 cm	Yellow-grey sandy till
	C	54– 58 cm	Yellow gravelly sand
	C	58–100 cm	Yellow-grey sandy till
	C	100– cm	Grey sandy till
–C9	A_0	0– 4 cm	Brown, brittle humus
	A_0	4– 22 cm	Blackish-brown, greasy humus
	A_{1+2}	22– 44 cm	Blackish-grey sandy till
	A_2	44– cm	Rust-coloured hard sandy till
E13	A_0	0– 1 cm	Light-brown brittle humus
	A_0	1– 8 cm	Blackish-brown greasy humus
	A_1	8– 12 cm	Blackish-grey humic sand
	A_2	12– 23 cm	Grey sand
	B_1	23– 27 cm	Rust-coloured sand
	B_2	27– cm	Yellow sand

are shown in Fig. 18. Iron and aluminium are typically low in the leached horizons (A) and increase suddenly in the eluvial horizons (B) of the tills, whereas these metals increase less pronouncedly in the section on sand. The loss on ignition, indicating organic matter, is typically high (5-10%) in the topmost centimeters (A_1-horizon) and decreases with depth in the leached soil (A_2-horizon). It increases in the B-horizon of two sections (C 19 and E 13), but does not increase in one of the till sections (H 16), which has high humus content in the A-horizon. Hence, the till sections are distinguished mainly by leaching of the iron and aluminium in the A-horizon, and the sand section is distinguished mainly by an increase of the humus content in the B-horizon.

The pH increases from about 4 in the A-horizon to 5-6 in the B-horizon (Fig. 12).

As remarked above, the content of clay and silt particles of the mineral soil was somewhat higher in the A-horizons than in the B-horizons of the sections on sorted sand (Fig. 14). Hence, no illuviation of the fine particles can be demonstrated in these soils. In some of the till sections, an increase of the clay and silt particles with depth could be demonstrated (Fig. 14); a downward transport of fine particles cannot, therefore, be excluded in these cases.

The depth of the A-horizon varied from a few to more than 40cm. It was noticed that the leached horizon was deeper on sand than on till. Hence, the content of clay and silt particles measured at the 72 sections mentioned above was compared with the depth of the A-horizon.

It may be assumed that an increase in the silt and clay content with depth influences the depth of the A-horizon. The silt and clay content of the A-horizon was higher than that of the B-horizon at 31 sections and lower at 41 sections. The depth of the A-horizon was therefore compared with the silt and clay content of the A-horizon in these data sets separately (Fig. 19). The depth of the A-horizon was negatively correlated with the natural logarithm of the percentage of silt and clay particles in the A-horizon in both cases (n=31, r=0.448, P=0.011; n=41, r=0.531,=P<0.001). Hence the silt and clay content of the soil influences the depth of the A-horizon, which is less than 20cm on the till (silt and clay more than 10%), and more than 20cm on the sand (silt and clay less than 10%, Fig. 19).

Linnermark (1960) compared the depth of leaching with the depth of the humus layer and found significant correlations. However, as he compared depths of leaching at 0-4cm, 4-10cm and more than 10cm separately, the correlations found may not be valid. In the present investigation, the depth of leaching was slightly correlated with the depth of the humus layer (n=72, r=0.234, P=0.048).

The depth of the leached horizon thus is correlated with the silt and clay content of the topmost mineral soil, and with the depth of the superposed humus layer. Hence, a multiple regression equation was calculated

$x = 33.84 + 0.139y - 8.092 \log_n z$

where x is the depth of the A-horizon in cm, y is humus depth in cm, and z is the percentage of silt and clay in the A-horizon.

The variation in the depth of the A-horizon with the silt and clay content at varying humus depth is shown in Fig. 19. The variation due to differences in the silt and clay content is much larger than the variation due to differences in humus depth.

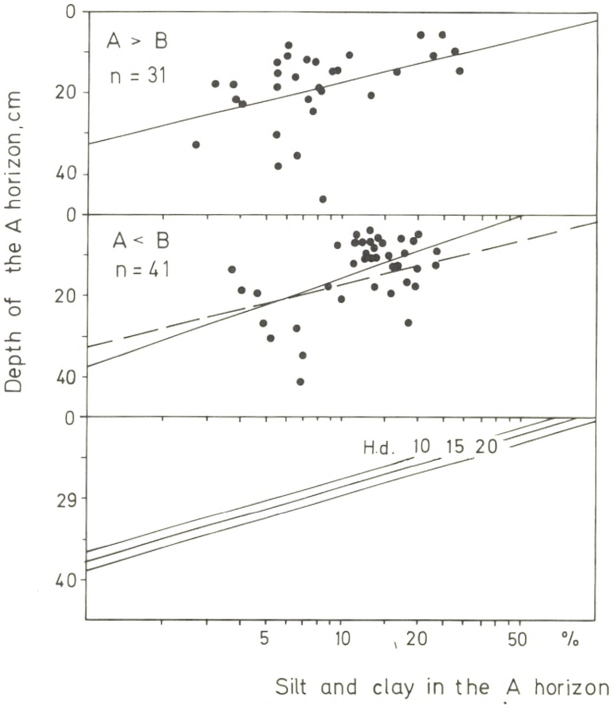


Fig. 19. The depth of the A horizon and the content of silt and clay particles in the A horizon of 72 podzol profiles (A>B, the silt and clay content of the A horizon higher than that of the B horizon; A<B, the silt and clay content of the A horizon lower than that of the B horizon), and depth of the A horizon at humus depth (A_0) 10, 15 and 30 cm, according to the equation on p. 21 (bottom). The dashed line shows the regression line for samples with A>B.

Petersen (1976) found that the leaching of iron and aluminium in podzols was due to the uptake of easily available compounds of those metals by water soluble compounds, and he postulated that the depth of the leached horizon will increase, as aluminium and iron are removed from the uppermost soil layers. Hence, the leaching will procede more slowly in a soil rich in fine particles than in a soil poor in fine particles.

Andersen (1979a) found that the podzolization in Eldrup Forest in general is likely to have initiated about 130 years ago on sites with a young humus layer. The decrease in the depth of the leached horizon with increasing silt and clay content is thus in accordance with the results of Petersen (1976).

Brown earths

Brown earths (luvisols in the nomenclature of FAO 1968) occurred at a few of the soil sections (Fig. 16). There was no distinctive humus layer at these sections, and the colour of the mineral soil changed gradually from blackish-grey to yellow at increasing depth (Plate II, Table 3). The sections with brown earth occurred on sandy till except for one case (G 18).

Andersen (1979a) compared a brown earth profile (W 14) with one of the podzol profiles on sandy till (C 19, Fig. 12). Iron and aluminium are present in the brown earth at the top of the mineral soil and increase slightly with depth, and the carbon content decreases with depth, in contrast to the podzol. pH is about 5 at the top of the brown earth and increases only slightly with depth, also contrasting with the podzol.

Iron and aluminium appear to be leached slightly from the topmost part of the brown earth, and there may be a slight accumulation of these metals, especially aluminium, at 10-40cm below the surface. A slight maximum in the loss on ignition at 25-35cm may reflect accumulated iron and aluminium compounds.

TABLE 3. Description of a soil section on brown earth.

W14	A	0– 5 cm	Blackish-grey humic sandy till
	A	5–10 cm	Blackish-yellow humic sandy till
	B	10–17 cm	Blackish-yellow sandy till
	B	17–28 cm	Slightly blackish-yellow sandy till
	B	28–35 cm	Yellow sandy till
	C	35–70 cm	Yellowish-grey sandy till
	C	70– cm	Yellow-grey clayey till

Hydromorphic soils

The general ground water table at Eldrup Forest is about 10m below the surface. Stagnant ground water occurs locally in five depressions in the enclosure.

The peat and gyttja deposits found in the three deep hollows will be described later. The two shallow depressions in the northernmost part of the enclosure (Fig. 16) contain a humic sandy deposit, 20-25cm deep and, beneath it, a rust-coloured mottled horizon indicating reducing conditions (gley horizon). A podzol-gley occurred in a shallow depression (-A 13, N 4, E 2, Table 48).

The present vegetation in the research area in Eldrup Forest and its environment

ARTIFICIAL INFLUENCES

The research area in Eldrup Forest shows no direct traces of tilling in prehistoric or historic times. The slightly pitted surface of the sandy till indicates that these areas have not been ploughed.

As Eldrup belonged to the Stenalt Estate up to 1930, no archives are present at Løvenholm. It has not been possible to consult archives elsewhere for information about the former management of Eldrup Forest.

Eldrup Forest was exploited and grazed by cattle and horses in the 17th and 18th centuries, as were most Danish woodlands at that time. The grazing was abandoned due to the Forest Protection Law of 1805. Since that time Eldrup Forest has been subjected to normal forestry management. The plantations which delimit the enclosure towards the south and northeast (Fig. 8) are second or third generation *Picea abies*. The present cultures derive from 1960.

Tree thinning

No extensive tree felling has occurred within the research area; however, tree thinning has been undertaken up to about 1960. In the 1940s some stumps of felled trees were removed for fuel. The recent removal of a few large trees is evidenced by disruptions of the tree canopy.

Deer browsing

The Løvenholm forests today support large populations of red deer and roe. Such populations often feed on cultivated areas outside the forest (Strandgaard 1972) and are, accordingly, artificially large. Tree saplings are one of their food sources in the winter (Strandgaard 1972).

The local hunting is insufficient for a reduction of the game.

The effect of browsing was evident in 1967. The ground flora was poorly developed, and clumps of tree reproduction consisted of self-sown *Fagus sylvatica* and *Picea abies*, whereas *Quercus petraea* was absent, and all specimens of *Ilex aquifolium* were less than lm tall. *Quercus* saplings and the *Ilex* shrubs thus evidently had been suppressed by the deer.

Removal of the reproductive tree layer

All young trees less than 10cm thick were removed in 1968. The saplings were cut just above the ground, but no measures for prevention of sprouting were taken. *Picea* saplings which have appeared since 1968 have been removed as well.

Fencing

With the purpose of excluding the effects of browsing on the ground vegetation and new tree saplings, the central part of the research area was fenced 1969. The fence is 3m tall, and the meshes of the fence are too small for the passage of deer and hares. The badger, which inhabits the area, has made passages beneath the fence, and individuals of red deer have jumped the fence a few times and have spent short periods inside.

Tree felling

Four large *Quercus* were felled in 1968 in order to establish a clearing where the ground vegetation is fully illuminated. Sprouting from the stumps was prevented by cutting of the sprouts as they appeared. Furthermore, two large specimens of *Picea abies*, about 100 years old, were removed.

Ditching

The two hollows in the southeastern part of the enclosure have been drained by ditches which are connected to a common ditch, by which water was drained towards northeast. The ditches were established by the middle of the 19th century (E. Due, personal communication), but have not been maintained since 1967.

FIELD METHODS

Trees

Trees more than 10cm and tree stumps more than 20cm thick were mapped 1969 and 1970. Tree heights and diameters were measured March 1971. For trees dividing into two or more trunks at below 1.3m, each trunk was measured separately. The tree heights were measured with a device constructed by J.A. Løvengreen (Løvengreen 1952). Ideally, the accuracy of the instrument is +0.5%. A major difficulty occurs in determining the highest point of the tree crown, when observing the tree from the ground. It was often necessary to study the tree crown from below at various directions and distances. It was also necessary to take care that the scaled rod used for the instrument was placed exactly under the point measured. In view of these difficulties, the accuracy of the height measurements is hardly less than ±1m. Tree diameters were measured at 1.3m above the ground with a steel caliper with an accuracy of lmm. Two measurements at right angles were taken for each tree trunk, and averaged.

Tree saplings

Tree saplings were counted July 1976 in the circular lm^2 plots used for field-vegetation analysis (see below). The saplings were at that time less than lm tall. In the artificial clearing, saplings were counted again July 1981 in lm^2 plots, and all saplings taller than lm were counted in April 1981.

Field vegetation

The field vegetation was analyzed in circular lm^2 plots at each main point of the coordinate system. The point method of Levy & Madden (1933) was used in a modified form developed for vegetation analysis in Draved Forest by the late Johs. Iversen. Levy and Madden's point method has been widely utilized in field layer analysis, and its various statistical aspects have been discussed by Goodall (1952). Levy & Madden (1933) showed that point scores correspond well to cover degrees. In Iversen's modification of the point method, a steel rod 3.5mm thick is placed vertically at 10 points within the circular plot (eight at eight radii, and two near the centre) and all live plant parts touching the rod are identified to species and scored. Hence, plants rooted outside the sample plot may be included in the analysis. Tree saplings were excluded and tree seedlings were included. Plant species present within the plot but not scored with the rod were included in the analysis with a score 1. The point scores for each species thus can vary from 1 to 10, and will be mentioned as cover points. An advantage is that the cover degrees are equally large and can be used statistically in a simple way.

The analyses of the field layer were performed July 1976. Additional plots were analyzed at 5m intervals in the cleared area, and this analysis was repeated in August 1981. Mosses were very scarce in 1976 and were not recorded. They were recorded in the analyses from the clearing 1981.

Tree seedlings were analyzed again in July 1977. Frequencies and cover points were recorded for each sample plot.

Frequencies of saplings and cover points in the lm^2 sample plots will be referred to as densities. The plant names follow *Flora Europaea* (1964-1980). *Dryopteris carthusiana* includes *D.assimilis*, which occurred at 1 plot. *Dryopteris dilatata* occurred outside the plots.

Light

The tree canopy is dense throughout the fenced research area. Some disruptions exist due to recent felling of single trees, and in the cleared area. The *Picea* plantations bordering the enclosure were 5-10m tall, when the ground vegetation was recorded in 1976. The sample plots along these borders thus received light from the side. It is very difficult to measure light intensities at such sites, because the illumination varies throughout the day and the growing season, according to the position of the sun and variations in the cloud cover. Instead, plots with less than 50% crown cover were mapped 1981, and such plots and their neighbour plots to the east, northeast, north, northwest and west were recorded as "light" plots. The "light" plots are not fully illuminated, as they are in shade through a part of the day. All other plots were shaded throughout the day.

Plots with light were scored as 1 and plots without as 0.

Surface soil

Soil samples for geochemical analysis were collected in July 1978, 1979 and 1980 at 40 selected sample points. The root systems of saplings and the field vegetation are mainly concentrated in the topmost part of the soil. Hence, three subsamples at 0-6cm depth were extracted at each point with a half-cylindrical stainless-steel auger, and mixed. The samples were stored in plastic bags in a refrigerator.

LABORATORY METHODS

Laboratory analyses were carried out at the Department of General Geology (water content), the Geobotanical Department (organic matter), and the Geochemical Department (pH, geochemical elements) at the Geological Survey of Denmark.

Water content in the surface soil

The volume and the weight of 20 naturally moist samples, taken in July 1979 after three weeks without rainfall, were measured; the samples were dried at 110°C, and weighed again. The water lost by drying was calculated as percentages of the volume of the samples.

Organic matter in the surface soil

The content of organic matter was determined as loss on ignition at 550°C.

pH in the surface soil

Soil samples used for pH measurements were dried at 50°C, and homogenized. 10mg sample were shaken with 25ml boiled distilled water for 20 minutes before the measurement, which was performed with a glass electrode.

Samples which had been dried before soaking with water had higher pH than naturally moist samples treated similarly, mainly because carbon

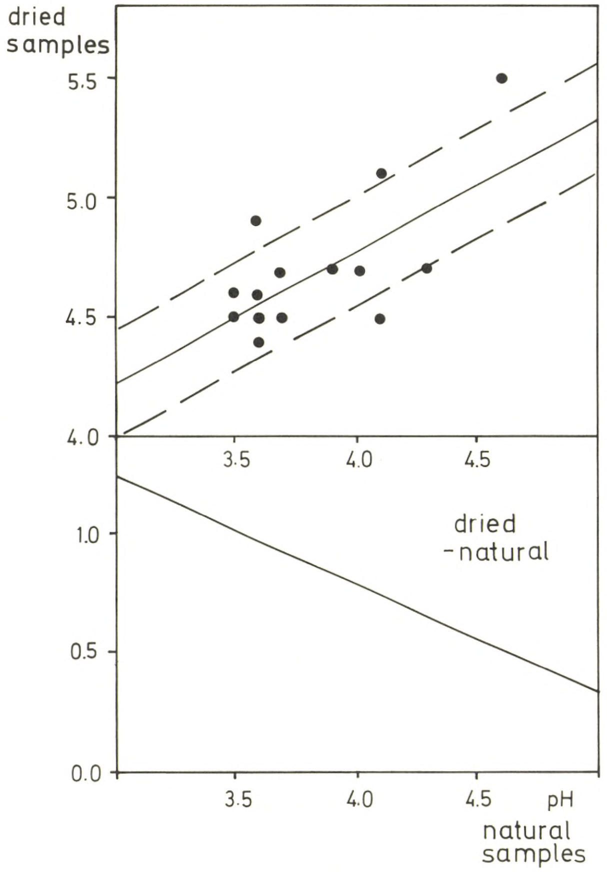


Fig. 20. pH measured in dried samples soaked in water and the pH of naturally moist samples soaked in water (n = 20, top), and the difference between dried and naturally moist samples (botton). The dashed lines indicate ± s.

dioxide dissolved in the soil water was expelled on drying. pH was measured in 20 naturally moist samples shaken with water as described above, and again after drying. The pH measurements were correlated ($r=0.653$, $P=0.002$, Fig. 20). The regression line in Fig. 20 shows that pH measured in a naturally moist sample with pH 3.5 increased by 1.0, and pH on a naturally moist sample with pH 4.5 increased by 0.5, after drying. The difference between moist and dried samples is probably negligible at pH higher than 5.5, due to increased buffering capacity.

The carbon dioxide content of the soil water can be supposed to vary considerably throughout the growing season. Ellenberg (1939) thus found that pH measured in naturally moist samples shaken with water varied considerably. At low pH values, pH measured in dried samples is, therefore, likely to vary less than pH measured on naturally moist samples, and is better suited for comparisons than pH measured on moist samples.

Køie (1951) observed that the pH-ranges found by Olsen (1921) for various plants from *Fagus* forest with acid soils were lower than the ranges found by himself for the same species in *Quercus* copses, and concluded that these species occur at higher soil acidity in *Fagus* forest than in *Quercus* forest. As the measurements by Olsen (1921) were performed on naturally moist samples, and those by Køie (1951) on dried samples, the differences noticed by Køie are rather more likely due to the difference in pretreatment of the samples. It is, accordingly, important to consider the pre-treatment of soil samples with low pH, when pH-values are compared.

Geochemical elements in the surface soil

Extractable elements were determined according to the methods used by Hansen (1976). All samples were dried at 110°C and homogenized.

Ca, Mg, K, Na, and Mn. 2g of the dried sample were shaken with 50ml ln ammoniumacetate (pH 7) for 2 hours, and left overnight. The mixture was filtered (Whatman 541) and diluted with distilled water. Na and K were determined by flame emission, Ca, Mg and Mn by atomic absorption spectrophotometry.

Cu, Zn, Pb and Fe. 2g of the dried sample were shaken with 50ml EDTA-solution, and left overnight. The mixture was filtered, and the content of metals determined by atomic absorption spectrophotometry.

P. 2g of the dried sample were shaken with 50ml 0.2n NH_2SO_4 for 3 hours and filtered. P was determined by spectrophotometry.

Al. 2g of the dried sample were shaken with distilled water and left for 24 hours. The mixture was filtered on a membrane filter (pore diameter 0.45 um). Al was determined by atomic absorption spectrophotometry.

Geochemical elements were originally calculated as percentage of dry weight of the samples. As the bulk density of the soil samples varied greatly according to the content of mineral matter, weight percentages were re-calculated as weight per unit of volume, using Jeffrey's equation (Jeffrey 1970, cp. Huntley & Birks 1979)

$y=1.482-0.6786 \log_{10}x$

where y is the soil bulk density (gm cm^{-3}) and x is the percentage loss-in-dry-weight upon ignition.

STATISTICAL METHODS

Tests of significance

The following significance tests were used: normal distribution, chi-squared test; difference between grouped samples (homogeneity), variance ratio test; difference between paired observations, t-test; difference between two or more proportions (homogeneity), chi-squared-test; coefficient of correlation, t-test. Probability(P) is stated for a null hypothesis. Differences with P larger than 0.05 were considered insignificant.

$\bar{x}$ is used for the arithmetic mean and s for the estimated standard deviation of a sample. r is used for the coefficient of correlation (least squares) between paired observations.

Numerical methods

Principal components analysis (PCA)

An attempt was made to structure the ground vegetation analyses using principal components analysis (cp. Huntley & Birks 1979). As in the analysis performed by Huntley & Birks (1979), the large data set (670 plots, 35 species) necessitated the use of a centred R-mode PCA. The data were analyzed by H.J.B. Birks on the IBM 370/165 computer at the University of Cambridge, England, using the FORTRAN IV program PCA R MODE written by H.J.B. Birks.

Attemps were made to derive a structure of the 35 species by means of the loadings, and to detect principal directions of variation in plots by comparing plot scores with ecological variables (e.g. Bates 1975, Rackham 1980). Contrasting high and low scores on the principal components were used for a selection of plots for surface soil analysis.

TWINSPAN analysis (by H.J.B.Birks)

TWINSPAN (TWO-way INdicator SPecies ANalysis) is a polythetic divisive classificatory procedure developed by M.O. Hill and implemented in the FORTRAN IV computer program written by Hill (1979). It is designed for ecologists and phytosociologists with data on the occurrence of species in a large number of quadrats. TWINSPAN is a development of indicator-species analysis (Hill *et al.* 1975). It first constructs a classification of quadrats, and then uses this classification to obtain a classification of the species according to their observed preferences. The two classifications are then used together to derive an ordered two-way table that attempts to display the species' synecological relations as succintly as possible. The two-way table is constructed by identifying species differential to the quadrat groupings.

The basic procedure is as follows:

1. Classify the quadrats into a divisive hierarchy, dividing the first into 2 subsets, then 4, 8, 16, etc.
2. Convert the quadrat classification into an ordering of quadrats.
3. Construct attributes for the species such as "preferential to the left side of the major division" using the quadrat groups as a basis.

4. Classify the species in the same way as the quadrat, but with the difference that whereas the species are treated as attributes of the samples the species have attributes of the kind in 3.
5. Convert the species classification into an ordering of species.
6. Print out the resulting ordered two-way table. The construction of the dichotomy in stage 1 is done as follows:
1. Ordinate the quadrats using the method of correspondence analysis or reciprocal averaging (Hill 1973, 1974), a method related to principal components analysis. This ordination inditifies a major "direction of variation" within the data and is called the "primary" ordination.
2. Divide the ordination at its middle to derive a crude dichotomy of the quadrats.
3. Identify differential species that are preferential to one side or other of the crude dichotomy. These species are emphasised in order to polarise the quadrats. Assign a score of +1 to each differential species, and add the scores together for each quadrat.
4. Construct an improved or "refined" ordination (sensu Hill, 1979) using the scores of the differential species.
5. Divide the refined ordination at an appropriate point to derive the desired dichotomy.
6. Construct a third simplified or "indicator" ordination based on a few of the most highly preferential species. See whether the dichotomy suggested by the refined ordination is reproduced by a division of the indicator ordination.
7. Repeat the procedures l-6 on the two subsets to give four groups of quadrats, and so on until each group has no more than a chosen maximum number of quadrats.

The final output from TWINSPAN is a structured two-way table with the quadrats and species ordered and classified so as to display the major structure within the data. The emphasis of TWINSPAN is on differential species and on the production of a structured two-way table (Gauch, 1982). It thus has many similarities to the tabular approach of the Braun-Blanquet school of plant sociology (Müller-Dumbois & Ellenberg, 1974).

The TWINSPAN analysis of the 670 quadrats and 31 species from Eldrup Forest was implemented by the FORTRAN IV programme TWINSPAN written by M.O. Hill and modified by H.J.B. Birks and B. Huntley for use on the University of Cambridge IBM 370/165 computer.

ECOLOGICAL VARIABLES

The vegetation in the enclosure in Eldrup Forest owes its present aspect to its history, to the interactions of the environment, and to mutual influences from the plants themselves. The mature trees originated in the past, and their present state results from growth conditions and artificial influences throughout an extended period. Their distribution and size can be compared with variations in soil and topography. The reproductive tree layer and the field vegetation were formerly influenced by a one-sided biotic factor, but have since the fencing had time to regenerate. The vegetational analyses can be compared with ecological variables such as light, litter depth, humus depth, root competition, water content and geochemical elements.

Climate

There are no measurements of the climate of the research area, but the data from the station at Løvenholm 1960-69 (p. 8) can be assumed to be fairly typical for the area. Thirty-three percent of the annual precipitation (651mm) fell during the growing season June-August. The rainfall was particularly low in the 1970's, especially 1975 and

1976, and the dry climate caused the wet hollows to dry out superficially during those summers.

Wind was recorded 1931-60 at stations northwest and east of Løvenholm (Udbyhøj and Fornæs, Frydendahl 1971). The wind directions were predominantly west and southwest during the growing season (45 and 53% of all wind directions at the two stations). The mean wind velocity was 4.8 and 3.8 m/sec (24 hours) in June-August. The wind velocities can thus be assumed to be more than 5 m/sec during the day in the growing season.

The wind speeds over the tree canopy are modified by variations in topography and the altitude of the tree canopy. The trunk space is fairly open, but wind forces near the ground may be modified considerably by the topography and the ground vegetation.

Surface relief

As was mentioned earlier, the ground surface in the enclosure generally slopes toward northeast; the northwestern part forms a rather even plateau falling from 47 to 43m in altitude, whereas the southeastern part contains rather steep slopes facing east, northeast and north, and dropping from about 49 to 38m. These slopes, accordingly, are sheltered from the predominant winds during the growing season. Surface relief was measured in gradient angles, with gradients less than 4° predominant in the northwest part and gradients of more than 4° in the southeast (Fig. 21).

Light

18% of the sample plots were recorded as light plots (Table 4). All other plots were fully shaded.

The tree saplings were still so small at the recording of the field vegetation in 1976 that their shadows on the field layer plants were insignificant.

The effect on the ground vegetation of exposure to full illumination in the artificial clearing will be discussed in a special chapter.

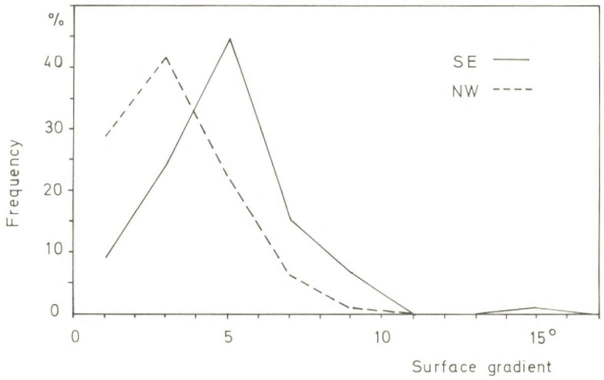


Fig. 21. The distribution of the 670 sample plots in relation to the surface gradient angle in the southeastern and the northwestern parts of the enclosure in Eldrup Forest.

Leaf litter

The depth of the leaf litter varies according to wind exposure (p. 19, Fig. 15). Holstener-Jørgensen (1958) found decreased water-retaining capability in soils with a shallow litter layer, due to decreased pore volume. The soil in the research area in Eldrup Forest have a lower clay content (less than 5%) than the soils investigated by that author and may not react in the same way to wind exposure. Sites with a shallow litter layer may, however, become more desiccated due to higher evaporation than sheltered sites, and afford less protection for tree fruits against predators (Watt 1919, Jarvis 1964) than sites with deep litter. A deep litter layer, on the other hand, may be unfavourable for some herbaceous plants due to its physical properties (Sydes & Grime 1981). Hence, the depth of the litter layer may influence the distribution and density of tree seedlings and herbaceous plants.

The depth of the litter layer varied 0-10cm (Fig. 22); the distribution is normal and the average is 3.3cm (Table 4).

Soil texture

The mineral soil in the enclosure is generally coarse-textured, with 80% sand in the sandy tills

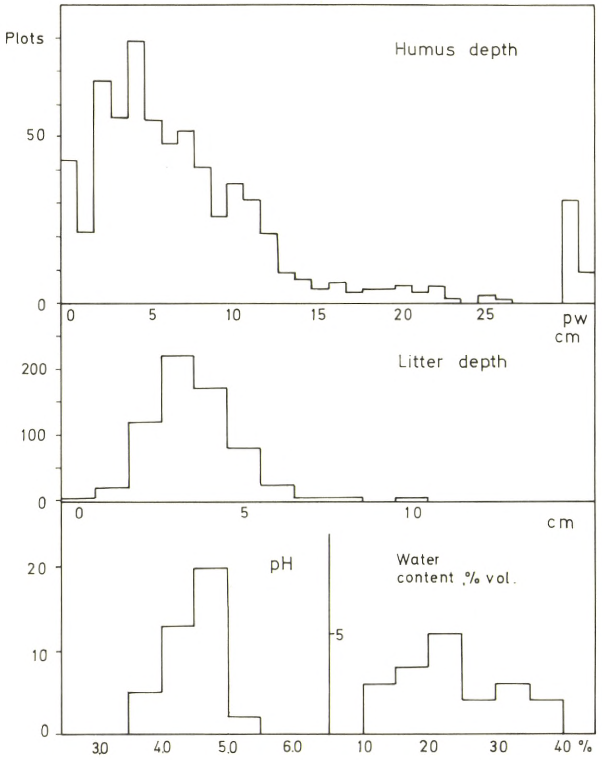


Fig. 22. The distribution of sample plots in relation to the depth of the humus layer (n = 670), litter depth (n = 670), pH (n = 40) and water content (n = 20). p, peat; w, wet sites.

and 95% sand in the sorted sands; clay particles constitute about 5% in the till and about 1% in the sands. Hence, the water-retaining capacity is low, and water drains away rather quickly from the topmost mineral soil.

Humus layer

The distribution of the 670 plots in relation to the depth of the humus layer is shown in Fig. 22. Plots with less than 10cm humus dominate, and there are 31 plots on peat, where the humus layer is more than 30cm deep, and 9 plots on wet sites. The distribution of the plots with less than 30cm humus is skewed (Table 4). The average humus depth is 7.5cm. In the calculations of correlations with humus depth, the plots on peat were scored as 30cm humus depth.

TABLE 4. Plot frequencies and averages for ecological variables.

	Plots	Frequency of plots	Average	Normal distribution
	(n)	(%)		(P)
Light	670	17.76		
Litter depth (cm)	670		3.31	0.087
Humus depth (cm)	630		7.49	<0.001
Fagus nearest tree	670	49.44		
Water content (vol%)	20		23.10	
pH	40		4.43	

Root competition

Fagus is usually considered to have a shallower, denser root system than *Quercus*, and the tree tends to form a dense mat of fine roots when growing on a humus layer. Root competition is therefore strong on sites near a *Fagus* tree, and the soil may dry out more quickly there than on sites near a *Quercus* or with no trees in the vicinity. An attempt was therefore made to correlate the species densities with plots where *Fagus* was the nearest tree within 10m. The frequency of the plots with *Fagus* as the nearest tree was 49% (Table 4).

Water content in the surface soil

Variations in the amount of water in the surface soil avaible to the plants throughout the year are difficult to measure. The water content of 20 samples from the topmost 6cm of the soil, collected July 1979, after three weeks without rainfall, varied from 10 to 38% of the volume of the moist soil. The sample distribution was approximately normal (Fig. 22), and the average was 23% (Table 4). The measurements give some indication of the tendency of the topmost soil layer to dry out.

Geochemical variables in the surface soil

Forty plots with contrasting high and low scores on the first three principal components of the PCA-analysis (p. 27) were selected for geochemical analysis. As the samples comprised the topmost 6cm of the soil, the samples from plots with less than 6cm humus consist of a mixture of mineral soil and humus, whereas the samples from plots with 6cm or more humus are pure humus. pH, organic content, and the extractable content of 11 chemical elements were determined.

pH varied from 3.6-5.5; the sample distribution was approximately normal (Fig. 22), and the average was 4.4 (Table 4).

TABLE 5. Correlations of geochemical variables to organic matter, mineral matter and pH in samples of the top soil (humus depth 0–>30 cm).

	Samples	Org. matter		Min. matter		pH	
	(n)	(r)	(P)	(r)	(P)	(r)	(P)
Fe	40	–0.639	<0.001	0.655	<0.001	0.392	<0.012
P	37	–0.220	0.190	0.428	0.008	0.700	<0.001
Ca	40	0.019	0.908	0.145	0.373	0.263	0.100
Mg	38	0.329	0.044	–0.117	0.483	0.046	0.784
K	40	0.414	0008	–0.170	0.294	–0.022	0.893
Na	38	–0.170	0.308	0.362	0.025	0.311	0.057
Mn	40	–0.251	0.118	0.299	0.061	0.652	<0.001
Cu	38	0.324	0.047	–0.196	0.237	0.118	0.482
Zn	40	–0.246	0.125	0.270	0.092	–0.099	0.542
Pb	40	0.185	0.254	–0.044	0.788	–0.130	0.424
Al	38	–0.434	0.007	0.431	0.007	0.149	0.371
pH	40	–0.525	<0.001	0.658	<0.001		

TABLE 6. Significance for correlations of geochemical variables (from Table 5).

	Organic matter	Mineral matter	pH
Fe	– – –	+ + +	+ +
P		+ +	+ + +
Ca			
Mg	+		
K	+ +		
Na		+	
Mn			+ + +
Cu	+		
Zn			
Pb			
Al	– –	+ +	
pH	– – –	+ + +	

+,–: P<5%; + +,– –: P<1%; + + +, – – –: P<0.1%

TABLE 7. Significant correlations (P<5%) of geochemical variables with pH in top soil samples with humus depth 0–1 cm.

	r	P
Mn	0.858	0.003
Zn	–0.749	0.020
P	0.711	0.032

Correlation of the geochemical variables

The content of the 11 chemical variables in the 40 samples of surface soil was compared with the content of organic and mineral matter, and with pH (Tables 5 and 6). Extractable Mg, K and Cu were correlated with organic matter, Fe, P, Na and Al with mineral matter, and Fe, P and Mn with pH. Samples with high mineral content also had the highest pH; these samples are thus particularly rich in extractable Fe, P, Na, Mn and Al.

The pH of the samples with no or very shallow humus (humus depth 0-lcm) varied considerably, from 4.2 to 5.5 (Fig. 24). Mn and P were positively, and Zn negatively, correlated with pH in these samples (Table 7). The samples with the highest pH were thus particularly rich in extractable Mn and P.

Correlation of the ecological variables

The correlations for six ecological variables are shown in Tables 8 and 9. Four of these: light, litter depth, humus depth, and *Fagus* nearest tree, were measured at all of the sample plots; pH at 40, and water content at 20 plots.

Light is independent of the other variables except for depth. The slight correlation with litter depth (P=0.013) may be due to the fact that many of the sites with light occur along the southwestern limit

TABLE 8. Correlations of ecological cariables.

	Light		Humus depth		Litter depth		Water content		pH		*Fagus* nearest	
	n=670		n=670		n=670		n=20		n=40		n=670	
	(r)	(P)	(r)	(P)	(r)	(P)	(r)	(P)	(r)	(P)	(r)	(P)
Light			–0.008	0.844	–0.096	0.013	(–0.189)	0.424	(0.029)	0.859	–0.030	0.444
Humus depth	–0.008	0.844			0.150	<0.001	(0.811)	<0.001	(–0.674)	<0.001	–0.006	0.872
Litter depth	–0.096	0.013	0.150	<0.001			(–0.204)	0.388	(–0.072)	0.661	–0.084	0.029
Water content	(–0.189)	0.424	(0.811)	<0.001	(–0.204)	0.388			(–0.668)	0.001	(0.028)	0.908
pH	(0.029)	0.859	(–0.674)	<0.001	(–0.072)	0.611	(–0.668)	0.001			(–0.096)	0.554
Fagus nearest	–0.030	0.444	–0.006	0.872	–0.084	0.028	(0.028)	0.908	(–0.096)	0.554		

of the enclosure which borders on young *Picea* plantations, and where the wind has removed the leaf litter. Plots with light are evenly distributed in relation to humus depth (Fig. 23).

Litter depth is strongly correlated with humus depth and slightly negatively correlated with plots with *Fagus* nearest tree a fact which may be due to denser ground vegetation on plots without *Fagus* trees, where leaves may tend to accumulate.

Humus depth is strongly correlated with litter depth and water content and strongly negatively correlated with pH (Fig. 24). Sites on shallow humus thus have a thinner litter cover, dry out more quickly, and have higher pH than sites on deep humus. These sites are, accordingly, also likely to be particularly rich in extractable chemical elements such as Fe, P, Na, Mn and Al. Sites without a humus layer but with high pH are particularly rich in extractable Mn and P. These sites occur on brown earth.

Plots near *Fagus* trees are uncorrelated with the other variables. Plots near *Quercus* trees may tend to have a higher water content than plots near *Fagus* trees (Fig. 24).

TABEL 9. Significance of correlations of ecological variables (from Table 8).

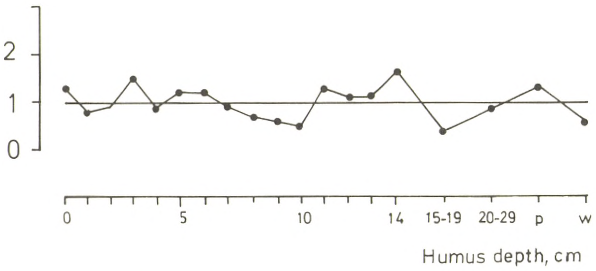
	Light	Humus depht	Litter depht	Water content	pH	*Fagus* nearest
Light			–			
Humus depht			+++	+++	–––	
Litter depht	–	+++				–
Water content		+++			–––	
pH		–––		–––		
Fagus nearest			–			

+,–: P<5%; ++,– –: P<1%; +++,– – –: P<0.1%

Comparisons of the vegetation with the ecological variables

The distribution and size of the canopy trees are compared with ecological variables such as soil texture, depth, humus depth and the surface relief.

Fig. 23. The distribution of plots with light (normalized frequencies) in relation to the depth of the humus layer. p, peat; w, wet sites.



The density data (frequencies and coverage points) for tree saplings and seedlings, and field plants were compared with light, litter depth, humus depth, and *Fagus* nearest tree - which were estimated at all the sample plots - and with water content and pH measured at 20 and 40 plots respectively.

Litter depth, humus depth, water content, and pH were measured as continous variables, whereas *Fagus* nearest tree and light were scored as either 1 or 0 for each plot. Averages of litter depth, humus depth, water content, and pH, and the percentages of plots with *Fagus* nearest tree and light, were calculated for each species. The data were weighted with density scores before the calculations. Hence, plots where a species is frequent have greater influence on the figures than do plots where the species is scarce. The averages for species were compared with the averages for all the plots, and the density percentages for *Fagus* nearest tree and light were compared with the total percentage frequencies of such plots (Tables 24 and 38). Probability was not calculated because of insufficiency of the data (uneven distributions, large variance ratios, and varying plot numbers).

As the distribution of the sample plots on litter depth, humus depth, water content, and pH was uneven (Fig. 22), the density distributions of the plant species were normalized with the plot distributions by dividing the percentage frequencies for species by the percentage frequencies for plots in each class of the variable,

$$d_{n(i)} = \frac{\check{d}_{(i)}}{\check{p}_{(i)}}$$

where $d_{n(i)}$ is the normalized density score for a species, $\check{d}_{(i)}$ is the density percentage of the species, and $\check{p}_{(i)}$ is the percentage of plots, in the i'th class of a variable. The normalized density score will be more than 1.0 in a class of the variable perferred by a species, 1.0 if the species is indifferent to the variable, and less than 1.0 if the species avoids that class. The normalized density distributions are shown for the most frequent plant species.

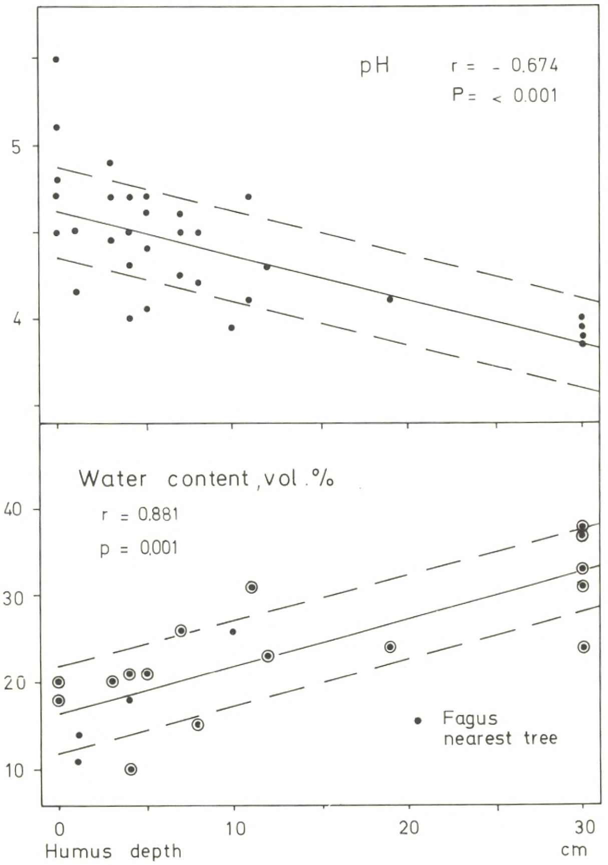


Fig. 24. pH and water content compared with the depth of the humus layer. The dashed lines indicate ± s.

Correlations of density to litter depth, humus depth, *Fagus* -nearest-tree, and light were calculated for species occurring in more than 10 plots (litter depth, humus depth) or more than 20 plots (*Fagus* -nearest-tree, light). Normalized density scores were used for litter depth and humus depth. Correlations were not calculated for water content and pH, because of the small numbers of plots.

Similar procedures were used for ground vegetation plot groups, but without weighting by densities.

THE CANOPY TREES

Three species are present in the tree canopy, *Fagus sylvatica Quercus petraea* and *Betula pendula.*

Quercus petraea in Eldrup Forest

As mentioned above, *Quercus petraea* is common in the natural woodlands in northern Djursland. In the Løvenholm forests we have seen only a few planted specimens of *Quercus robur.*

Hybrids have often been reported in cases where the two *Quercus* species occur together. Cousens (1965) and Wigston (1974) have shown that statistical analysis including several morphological characters is necessary for a distinction of intermediate forms from the parent species. Petiole length is the most easily observed continously variable character used by these authors. Pure populations of *Quercus robur* and *Q.petraea* thus showed only slightly overlapping ranges, whereas intermediate petiole lenght was frequent in mixed populations (Wigston 1974). A similar result was obtained by Fejlberg (1968).

In order to investigate the status of *Quercus petraea* in Eldrup Forest, two leaf samples from the research area were measured and compared with two samples from Draved Forest, southwest Denmark, believed to derive from *Quercus robur* alone. Each sample consisted of 100 leaves picked from the ground in *Quercus* stands within an area of 10x10m^2 November 1981. Total leaf length (lamina + petiole) and petiole length were measured on each leaf. Three distributions of total leaf length were normal (Table 10). Hence, it was assumed that the samples had been picked at random. The leaves from Eldrup Forest were slightly larger than those from Draved Forest.

Average petiole length from the two localities measured in milimeters or calculated as percentages of the total leaf length, differed widely (Table 10); however, there was considerable overlapping of the size ranges (Fig. 25). 28% of the specimens are intermediate, if petiole length measured in milimeters is considered. The large overlap is to some extent due to the fact that petiole length and total leaf length are correlated (Table 10). When drawn in a scatter diagram (Fig. 26), the frequency of intermediate specimens decreases to 13.5%. Hence, the *Quercus* in Eldrup Forest is well separated from the Draved populations and can be assumed to represent *Quercus petraea* in a high degree of purity.

The foliage of *Quercus petraea* in Eldrup Forest characteristically forms a regular leaf mosaic, in contrast to *Quercus robur*, the foliage of which tends to occur in clusters (cp. Jones 1959). As a result of

Fig. 25. The length of the petiole in 100 leaves from leaf litter in Draved Forest (*Quercus robur*, 2 samples) and in the enclosure in Eldrup Forest (*Quercus petraea*, 2 samples).

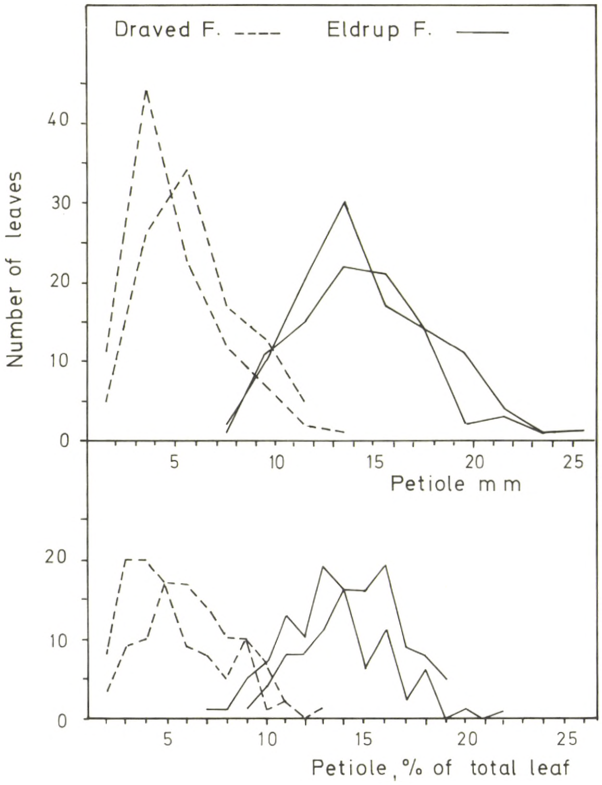


TABLE 10. Measurements on 100 leaves from leaf litter of *Quercus robur* (Draved Forest, 2 samples) and *Quercus petraea* (Eldrup Forest, 2 samples), normal distribution (n.d.) test for total leaf length, correlations of petiole length (p.l.) to total leaf length (t.l.), and petiole length in percentage of the total leaf length.

	Total length			Petiole length		Correlation		Petiole length	
	x̄ (mm)	s (mm)	n.d. (P)	x̄ (mm)	s (mm)	p.l. – (r)	t.l. (P)	x̄ (%)	s (%)
Draved Forest, 386	95.8	±22.5	0.263	4.90	±2.49	0.416	<0.001	5.13	±2.28
Draved Forest, 371	93.9	±21.5	0.003	5.94	±2.50	0.424	<0.001	6.33	±2.31
Eldrup Forest, centre	107.2	±21.9	0.065	14.06	±3.30	0.498	<0.001	13.38	±2.88
Eldrup Forest, SE	103.4	±19.8	0.067	14.76	±3.44	0.724	<0.001	14.41	±2.29

the difference in the leaf arrangement, *Quercus petraea* has a denser crown and casts a deeper shade than *Quercus robur* (cp. Fairbairn 1954).

Composition of the tree canopy

Trees not reaching the general canopy are scarce and nearly exclusively *Fagus sylvatica* (Table 11). In the canopy there are equal numbers of *Fagus* and

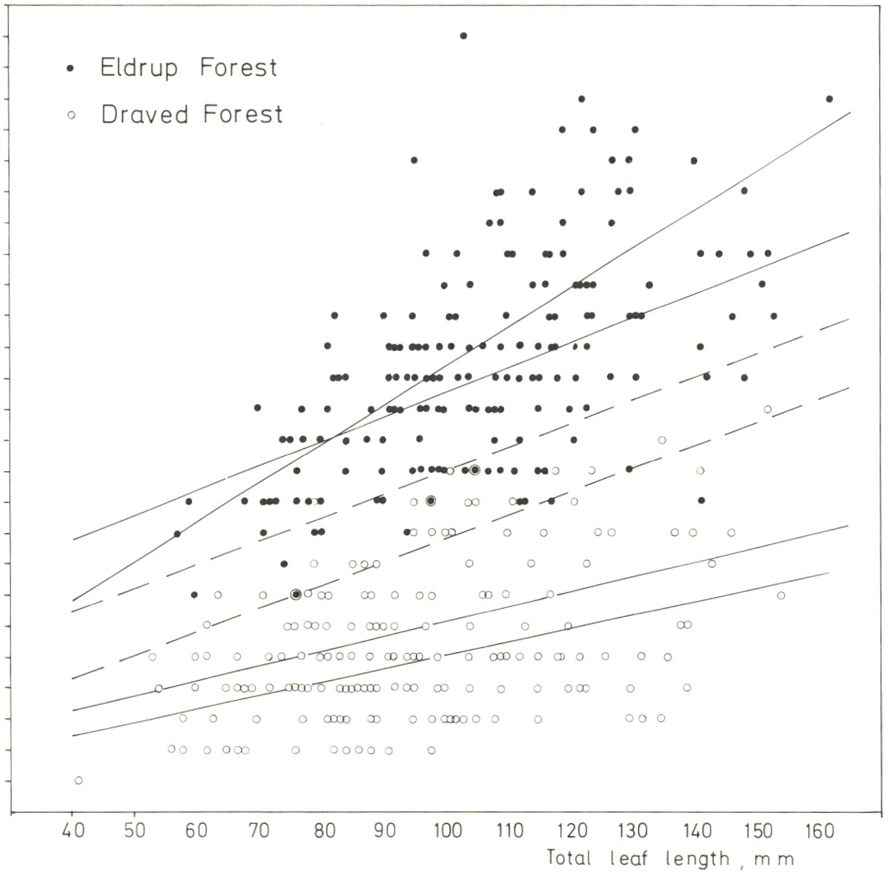


Fig. 26. The length of the petiole in relation to the total leaf length in the 4 samples from leaf litter. The full lines indicate regression lines for the 4 samples. The dashed lines indicate the upper limit for leaves from Draved Forest (*Quercus robur*, uppermost line), and the lower limit for leaves from Eldrup Forest (*Quercus petraea*, lowermost line).

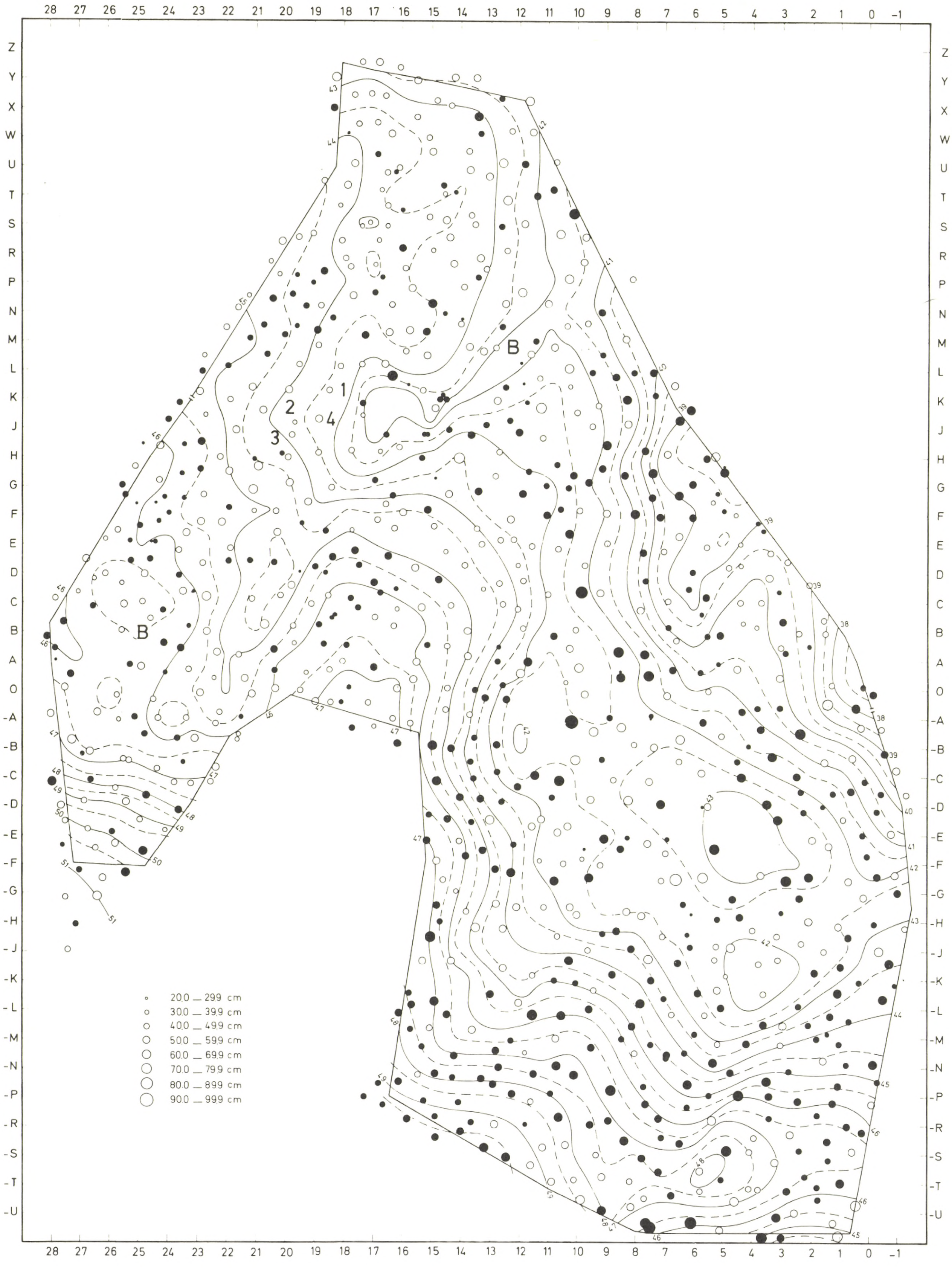


Fig. 27. The distribution of trees larger than 20 cm in diameter in the enclosure in Eldrup Forest. ●, *Fagus sylvatica,* ○, *Quercus petraea,* ○ B, *Betula pendula.* 1-4, trees felled in 1969.

TABLE 11. Numbers of trees thicker than 10 cm, and tree stumps thicker than 20 cm.

	Trees below canopy	Trees in canopy		Tree stumps		Trees and tree stumps	
	(n)	(n)	(%)	(n)	(%)	(n)	(%)
Fagus sylvatica	26	424	49.7	598	80.2	1022	63.9
Quercus petraea	2	427	50.1	148	19.8	575	36.0
Betula pendula		2	0.2			2	0.1
Total	28	853		746		1599	

TABLE 12. Total numbers of canopy trees and tree stumps, frequencies for tree stumps, and for *Fagus sylvatica* in the southeastern and the northwestern parts of the enclosure, and homogeneity tests (Hom.).

	Trees and tree-stumps	Tree stumps	*Fagus sylvatica* trees and tree-stumps	trees
	(n)	(%)	(%)	(%)
SE	869	50.2	73.4	60.6
SE, peat	59	52.5	59.3	53.8
NW	661	49.0	52.0	37.4
Hom. (P)		0.907	<.001	<.001

Quercus petraea, as well as two specimens of *Betula pendula*. *Fagus* dominance among the tree-stumps shows its selective removal and indicates that *Fagus* dominated the original tree vegetation (Table 11). No stumps of *Betula* were identified.

The distribution of canopy trees is shown in Fig. 27. *Fagus sylvatica* predominates on the slopes in the southeastern part of the enclosure mixed with a few *Quercus petraea* (Plate III), whereas *Quercus petraea* in that area occurs mainly in small stands on the slopes, on level ground, and on the largest peat area (Plate VI). *Fagus* occurs in clumps interspaced with nearly pure *Quercus* stands in the northwestern part of the research area (Plates IV-V).

The map showing trees and tree-stumps (Fig. 28) gives a better picture of the original tree population than does the tree map because of the selective felling of *Fagus* -trees. The distribution pattern is, however, very nearly the same, and the uneven distribution of *Fagus* and *Quercus* is emphasized.

The frequency of tree-stumps is the same in the southeastern area outside the peat, on peat, and in the northwest (Table 12). The thinning was thus equally intensive in the whole enclosure. *Fagus sylvatica* formerly dominated and still dominates the tree canopy in the southeast; *Fagus* and *Quercus* were and are nearly equally frequent on the peat, whereas *Quercus petraea* now dominates in northwest due to the selective thinning of *Fagus* trees (Table 12).

Tree size

The *Fagus* and *Quercus* trees are usually more or less straight, with few side branches below the crown (Plates III and V). Some crooked specimens occur, particularly in the northwestern part of the enclosure. A few *Fagus* trees with two or three trunks

TABLE 13. Diameters and heights of the canopy trees, and normal distribution tests (n.d.).

		n	Diameter x̄ (cm)	Diameter s (cm)	Diameter n.d. (P)	Height x̄ (m)	Height s (m)	Height n.d. (P)
SE,	*Fagus sylvatica*	277	53.3	±10.8	0.068	25.3	±2.3	0.159
	Quercus petraea	183	50.3	±8.3	0.030	23.4	±2.1	0.849
NW,	*Fagus sylvatica*	147	44.6	±10.1	0.298	22.1	±2.2	0.446
	Quercus petraea	244	48.6	± 7.8	0.556	22.0	±1.7	0.593

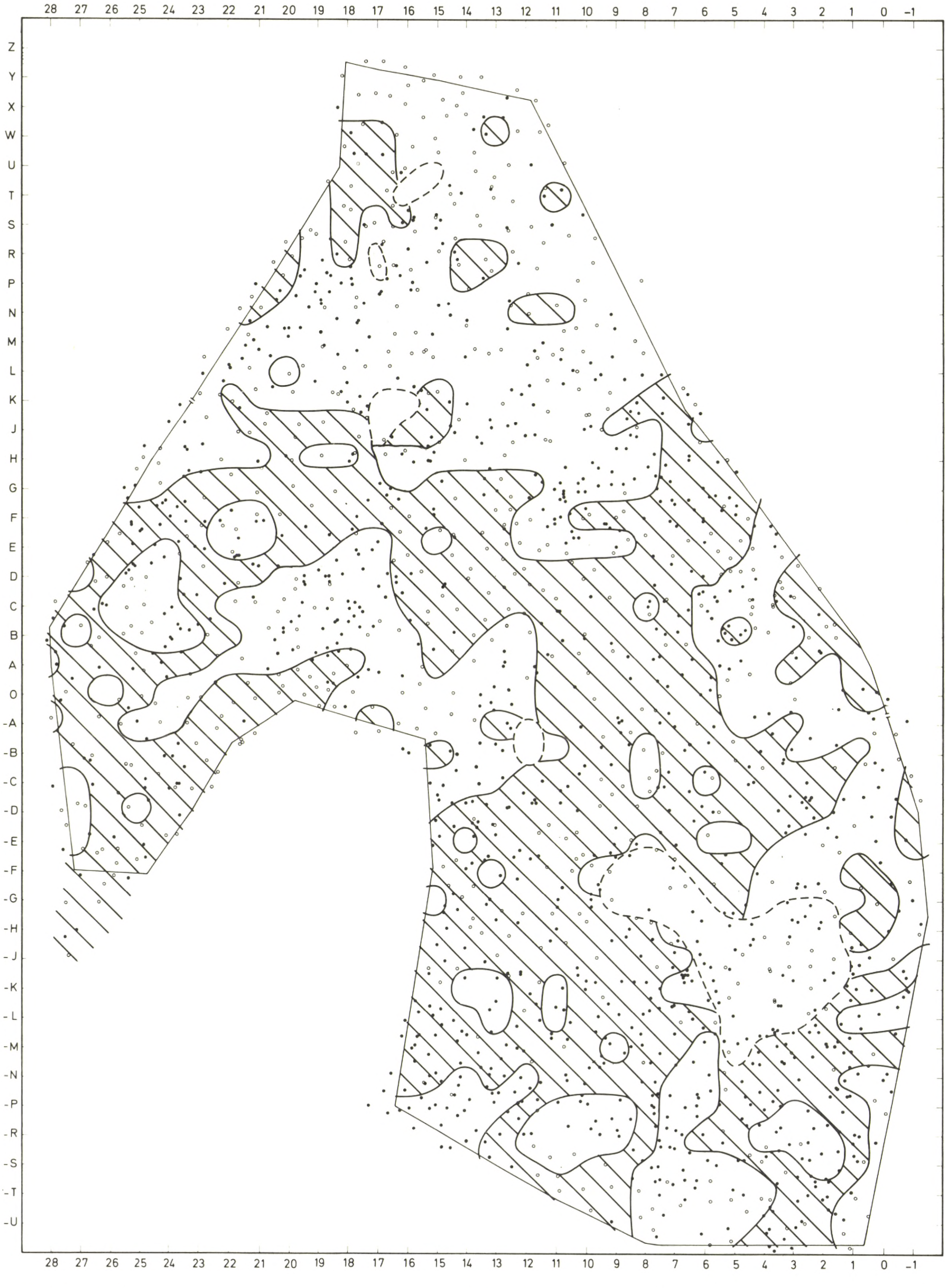


Fig. 28. The distribution of trees and tree stumps larger than 20 cm in diameter, and of soils with an A horizon deeper than 14 cm outside peat and wet areas (----). ●, *Fagus sylvatica*, ○, *Quercus petraea*.

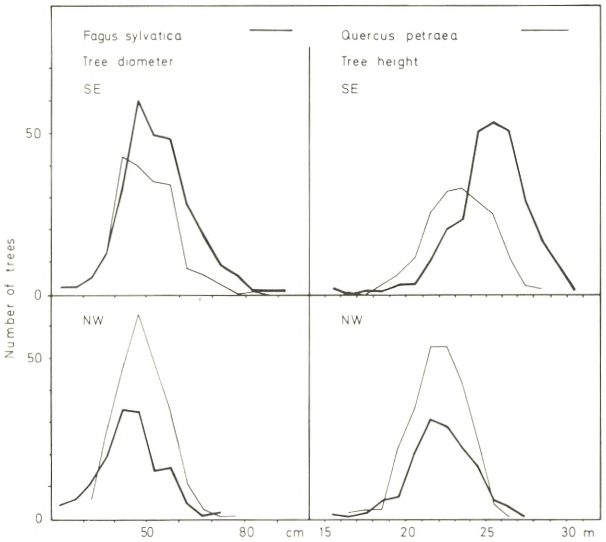
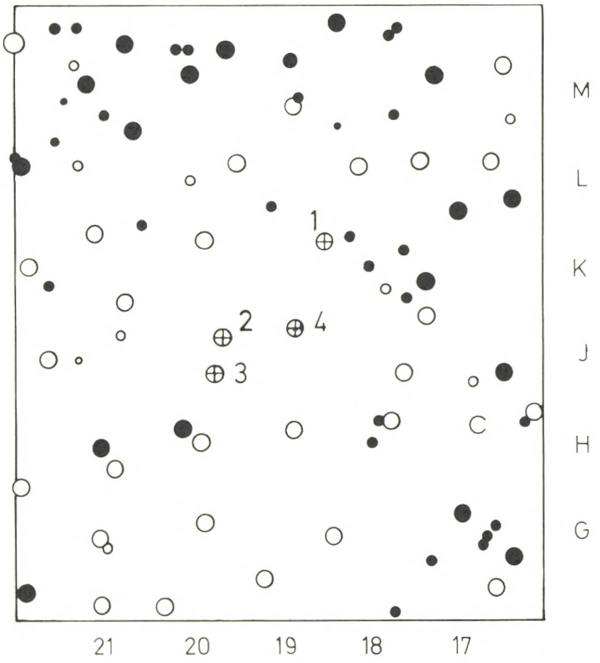


Fig. 29. Numbers of canopy trees in relation to tree diameter and tree height in the southeastern and the northwestern parts of the enclosure.

Fig. 31. Trees and tree stumps in the area around the four trees felled 1969. Large dots, trees; small dots, tree stumps. ●, *Fagus sylvtica;* ○ *Quercus petraea;* ⊕, *felled Quercus petraea.* The coordinate system with 10 m intervals is indicated (17-21, G-M).



occur; these trunks originated as sprouts from the stump of a felled tree. Many other trees reveal traces of having originated as sprouts from felled trees (Plates III-IV). It is, however, not possible to decide whether the tree originated as a sprout or as a seedling in all cases.

It was noticed that the trees found in the southeastern area were taller than those found in the northwest. Hence, the tree sizes were calculated separately for the two areas.

The diameters were normally distributed, except for *Quercus* in the southeast (Table 13, Fig. 29). Hence, it can be assumed that the trees are generally of about the same age. The *Fagus* trees in the southeastern area were definitely thicker than the *Fagus* trees in the northwest, whereas the *Quercus* trees differ only slightly (Fig. 30). The largest specimens of *Fagus* and *Quercus* were 94 and 84cm thick.

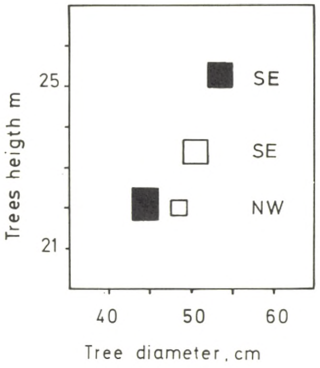


Fig. 30. Tree height and tree diameter. the squares indicate 95% confidence intervals. Black, *Fagus sylvatica;* white, *Quercus petraea.*

The tree heights were normally distributed (Table 13, Fig. 29). *Fagus* in the southeast is taller than *Quercus*, whereas *Fagus* and *Quercus* are the same height in the northwest, and lower than the trees in the southeast (Table 13, Fig. 30). The tallest *Fagus* was 30m, and the tallest *Quercus* 29m high.

The trees growing in the southeastern area are thus definitely larger than those found in the northwest.

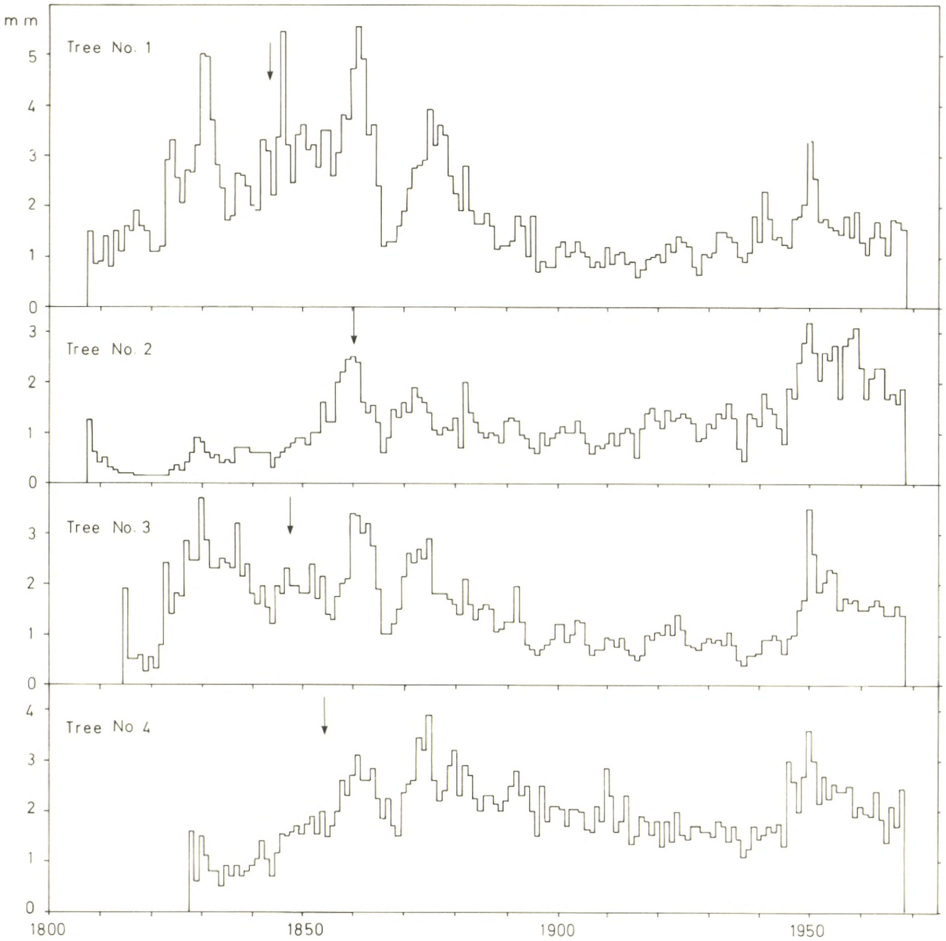


Fig. 32. Annual increment measured on basal discs from the four felled *Quercus petraea* trees (measured by T. S. Bartholin). The arrows indicate the year when the trees reached 6 m height.

Tree age

Annual increment was measured on the four *Quercus petraea* trees felled in 1969. The trees were located in the northwestern part of the enclosure (Fig. 27). The four trees occurred in a nearly pure stand of *Quercus* with a few scattered *Fagus* (Fig. 31).

The annual increment was meassured by T.S. Bartholin (Bartholin 1973) on discs secured near the ground and at 6m above ground. The oldest tree rings of the basal discs derive from 1808, 1808, 1815 and 1828 (Fig. 32, Table 14). The saplings were at that time 40, 24, 29 and 38cm tall. Their birth year cannot be determined exactly: the two youngest trees may derive from a famous mast year 1804 while the two oldest are difinitely older. The annual increment up to 1823 was l-2mm in tree no. l, and less than lmm in no's. 2 and 3; these saplings had reached a substantial size by 1822 (3.6, 1.0 and 1.lcm thick). The annual increment increased in 1823 or 1824, especially in trees 1 and 3. Tree no. 4 was 38cm tall in 1828; its annual increment remained rather low.

The four trees may thus have ocurred as suppressed saplings from some time before 1808. Three of them were 23-40cm tall 1808-1815 and had reached a substantial size by 1822. The trees were probably suppressed by cattle browsing before 1808, but browsing cannot have been intensive betwen 1808 and 1822. The three trees began to grow vigorously in the early 1820's and it is indi-

TABLE 14. Data for the four *Quercus petraea* trees felled in 1969.

Tree no	Level of the basal disc (cm)	1st tree ring (yr)	Diam. 1822 (cm)	Height 6 m (yr)	Diam. that year (cm)	Diam. 1969 (cm)
1	40	1808	3.6	1844	16.2	62.4
2	24	1808	1.0	1861	7.8	37.4
3	29	1815	1.1	1848	12.5	46.5
4	38	1828	–	1855	6.8	54.9

cated that the browsing ceased entirely at that time. As mentioned earlier, cattle grazing was generally intensive in Denmark in the 18th century, but was forbidden by the Forest Protection Law of 1805. The cattle browsing in Eldrup Forest apparently was slight in the years following 1805 and ceased entirely in the early 1820's. Trees 1 and 3 were 6m tall, and 16 and 13cm thick in the 1840's, whereas no's 2 and 4 were 6m tall in 1861 and 1855 and were at that time 7-8cm thick.

A vigorous regeneration of trees thus began in Eldrup Forest as a result of the forest protection. As mentioned above, the measurements of the tree diameters indicate that the trees presently growing in the enclosure are of about the same age. Hence, it appears that the present generation of trees there derives from the early 19th century, whereas the older tree generation was felled. Most of the present *Quercus* trees probably were derived from seedlings, but many of the *Fagus* derived as sprouts from the stumps of felled trees (p. 39). The trees growing on peat in the southeastern part of the enclosure are probably somewhat younger than the other trees, as they are likely to have originated after the artificial drainage of the peat by the middle of the 19th century (p. 24).

Of the four felled *Quercus* trees, the annual increment of no's 1 and 3 reached a maximum 1830-1880, and that of no's 2 and 4 1850-1890. The increment then decreased, but increased again suddenly 1946-47. This increase in growth was due to thinning in 1945. Some tree stumps still occur around tree no. 1, but none around 2, 3 and 4 (Fig. 31). Such stumps may have been removed for fuel, as mentioned earlier.

Tree no. 1 was still thickest in 1969, (62cm, Table 14); tree no. 4 had become the next thickest, whereas tree no. 2 remained thinnest (37cm), even though its growth rate had increased strongly after 1945. The four trees were of about the same height when they were felled.

Influence of the environment on the canopy trees

It has been shown that *Fagus* trees have been removed selectively, but the distribution pattern of the trees has not changed. The present distribution of the trees thus reflects conditions at the time when the tree generation originated. It was pointed out by means of pollen diagrams that the vegetation in the research area at that time was a mosaic of stands of *Fagus sylvatica* and grazed glades, and that the present *Quercus petraea* stands originated in the glades (Andersen 1979a, 1983). This question will be discussed further in connection with the vegetational history of Eldrup Forest.

Since the early 19th century, mature trees from still earlier times have been removed, and the density of the present tree stand has been reduced. No extensive tree-felling has occurred, however. The present woodland of intermingled stands of *Fagus sylvatica* and *Quercus petraea* trees offers therefore an opportunity to study the response in growth performance of these trees over 160 years to variations in the environment.

Tree distribution

Humus depth

As mentioned on p. 19, the humus layer which covers the mineral soil in the enclosure presumably dates from the 19th century, except for a few areas where the accumulation of humus began earlier. Humus layers older than the 19th century thus are more than 20 cm deep and occur in 2.5% of the 670 sample points. Hence, the trees in the enclosure established themselves at a time when there was practically no humus cover, and the present variations in humus depth are, accordingly, of no significance for the distribution of the tree species.

There are no trees on the wet areas except for the large peat area in the southeastern part of the enclosure. As mentioned on p. 41, the trees there probably established themselves after artificial drainage in the middle of the 19th century. 59% of the trees and tree stumps on the peat were *Fagus sylvatica* (Table 12). This species occurs mainly near the edges of the peat (Fig. 27-28), and *Quercus petraea* on the central part, a distribution pattern which indicates that the central part of the peat area was too wet for *Fagus* to establish itself. The *Quercus* growing on the peat have shallow root systems. One tree fell in 1972, and three trees were felled by a storm in November 1981.

Soil texture

The mineral soils in the enclosure have low water-retention capacity (p. 30). The soils are now podzolized; however, as mentioned above (p. 21), podzolization was initiated in the 19th century in most cases. The soils with a high silt and clay content may therefore have been more fertile at the time when the trees established themselves.

The content of fine particles in the mineral soil could not be evaluated during the mapping of the soils. It has been shown, however, that variations in the depth of the leached horizon (A) reflect variations in the content of fine particles.

Soils with a leached horizon 15cm deep or more are shown on the map Fig. 28. These soils are likely to contain less than 10% silt and clay (cp. Fig. 19). The *Fagus* trees and stumps may tend to be concentrated in the areas with a leached horizon less than 15cm deep in the northwestern part of the enclosure. The frequencies of *Fagus* on soils with an A-horizon either less or more than 15cm deep do not differ, however (Table 15). Hence variations in the content of fine particles in the mineral soil influenced the distribution of the species only slightly.

TABLE 15. The number of trees and tree stumps, the frequency of trees and tree stumps on soils with a leached horizon (A) more than 14 cm deep, the frequency of *Fagus sylvatica* trees and tree stumps on soils with a leached horizon (A) 0–14 and >14 cm deepn, and significance tests for differences, in the southeastern and the northwestern parts of the enclosure.

	Trees and tree-stumps		*Fagus sylvatica*		Difference
	Total (n)	A >14 cm (%)	A 0-14 cm (%)	A >14 cm (%)	(P)
SE	869	59.0	73.6	73.3	0.919
NW	661	40.8	54.0	49.5	0.243
Diff.(P)		<0.001			

TABLE 16. Numbers of canopy trees outside the peat area, frequencies of *Fagus sylvatica* trees, and correlation of the frequencies of *Fagus sylvatica* trees with the surface gradient angle in arrays of surface gradient.

	Trees	*Fagus sylvatica* Freq.	Correlation with surface gradient		
	(n)	(%)	(n)	(r)	(P)
SE	434	60.6	11	0.742	0.009
NW	393	37.4	10	0.175	0.628

Soils with an A-horizon deeper than 15cm dominate in the southeastern area (Table 15). The dominance of *Fagus* in southeast was therefore not due to higher fertility or better water supply at the time when the trees established themselves.

Køie (1951) found that *Fagus* woods were absent from soils with less than 8% particles smaller than 0.02mm. Such particles constitute less than 8% in the soils with less than 10% silt and clay in Eldrup Forest (Fig. 11). *Fagus* thus grows excellently there on soils with a lower fine particle content than the lower limit for *Fagus* woods found by Køie (1951).

pH

The pH of the topmost soils in the enclosure varies 3.8-5.5 (p. 31). It can be assumed, however, that the leached soils were less acid at the time of establishment of the tree generation.

TABLE 17. The number of plots outside the peat and wet areas, the frequencies of plots with 0–2 cm litter, and significance test for the difference, in the southeastern and the northwestern parts of the enclosure.

	Plots (n)	Litter depth 0–2 cm (%)
SE	351	26.2
NW	280	28.9
Diff. (P)		0.518

Surface relief

The *Fagus* and *Quercus* stands are scattered irregularly in the northwestern area, and the frequency of *Fagus* is independant of the surface gradient (Table 16). In southeast, the frequency of *Fagus* increases with the surface gradient, from less than 50% on level ground to 80% on the steepest slopes (table 16, Fig. 33). The reason may be that grazing by cattle was less intensive on the steep slopes, and that *Fagus* therefore regenerated more easily there than on the flat areas after the grazing was abandoned.

Conclusions

It seems impossible to relate the present distribution of the tree species in the enclosure to ecological factors, except for the presence of steep slopes, which have favoured *Fagus*.

Tree size

Holmsgaard (1955) found that the diameter-increment in *Fagus sylvatica* depends highly, and the growth of *Quercus robur* somewhat less, on the rainfall in the months from May to July; and Holstener-Jørgensen (1958) found that the height-growth in *Fagus* depends highly on the water supply during the growing season. There are no such investigations on the growth of *Quercus petraea*. Bartholin (1973) has shown, however, that the annual increment of *Quercus petraea* from Eldrup Forest is highly correlated to the increment of *Quercus robur*. It can be assumed, accordingly, that the supply of water during the summer is important for the growth of the trees in Eldrup Forest.

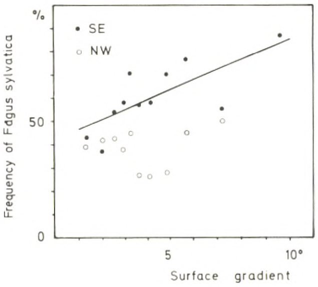


Fig. 33. Frequencies of *Fagus sylvatica* trees in surface gradient arrays, in the southeastern and the northwestern parts of the enclosure outside the peat area.

Soil texture

As soils with a deep A-horizon, and hence a low content of silt and clay particles, are more frequent in the southeastern area than in northwest (Table 15), the better growth performance of the trees in the former area (Fig. 30) is not due to a difference in the fine particle content of the soils in the two areas.

Litter depth

Sites with a thin litter cover are equally frequent in the southeastern and the northwestern part of the enclosure, outside the peat and the wet hollows (Table 17). The size of the trees growing on sites with a thin litter cover does not differ from the size of the trees growing at thick litter cover (Table 18). Hence, desiccation of the ground by wind does not affect the tree size in the research area.

Humus depth

The tree size on areas with a shallow humus layer does not differ from the size on sites with deep humus, whereas trees growing on the peat tend to be somewhat smaller than the other trees in the same area (Table 19). This difference may be due to the younger age of the trees growing on the peat.

pH

The trees occurring outside the peat area grow mostly on soils with pH 4.0-5.0, and sites with higher pH are scarce. Hence, the material is insuffi-

TABLE 18. Diameters and heights of trees outside the peat area at varying litter depth, in the southeastern and the northwestern parts of the enclosure. Significance tests for overall differences (paired observations test).

	SE						NW					
	Fagus sylvatica			*Quercus petraea*			*Fagus sylvatica*			*Quercus petraea*		
	n	x̄	s	n	x̄	s	n	x̄	s	n	x̄	s
Diameter (cm)												
Litter depth 0–2 cm	76	52.4	± 8.4	20	55.0	±8.8	29	45.6	±9.9	47	49.2	±8.9
Litter depth >2 cm	187	54.2	±11.4	151	49.9	±8.1	118	44.7	±9.8	197	48.4	±7.6
Differences (P) 0.444												
Height (m)												
Litter depth 0–2 cm	76	25.3	± 1.8	20	23.6	±1.4	29	21.9	±2.0	47	21.9	±1.6
Litter depth >2 cm	187	25.5	± 2.3	151	23.4	±2.2	118	22.2	±2.2	197	22.0	±1.8
Differences (P) 0.457												

TABLE 19. Diameters and heights of canopy trees outside the peat area at varying humus depth and on peat in the southeastern and the northwestern parts of the enclosure. Significance tests for overall differences (paired observations test).

	SE						NW					
	Fagus sylvatica			*Quercus petraea*			*Fagus sylvatica*			*Quercus petraea*		
	n	x̄	s	n	x̄	s	n	x̄	s	n	x̄	s
Diameter (cm)												
Humus depth 0– 9 cm	210	53.3	±10.0	127	50.7	±8.3	129	45.3	± 9.8	202	48.9	±7.8
Humus depth 10–29 cm	53	55.1	±12.9	44	50.1	±8.7	18	42.5	±10.2	42	47.0	±7.9
Differences (P) 0.441												
Peat	14	46.3	±11.0	12	46.6	±6.5						
Height (m)												
Humus depth 0– 9 cm	210	25.5	± 2.1	127	23.4	±2.3	129	22.2	± 2.2	202	21.9	±1.7
Humus depth 10–29 cm	53	25.0	± 2.4	44	23.3	±1.7	18	21.9	± 1.5	42	22.4	±1.6
Differences (P) 0.736												
Peat	14	21.9	± 3.4	12	22.9	±1.2						

cient for demonstrating a possible difference in growth performance on soils with differing pH.

Surface relief

Trees taller than 25m are nearly completely confined to the steep slopes facing east, northeast and north in the southeastern area (Fig. 34). The diameter and height of the *Fagus* and *Quercus* trees, grouped according to the surface gradient, is homogeneous and is not correlated with the surface gradient, except for the height of Fagus in the southeastern area (Table 20, Fig. 35). The height of the *Fagus* trees growing in the southeastern area thus depends on surface relief. These trees increase in height at surface gradients from 1.5° to 5.7° but do not increase further at still higher angles (Table 21, Fig. 36). The average height is 23.6m at 1.25°, and 26.0m at gradients at 5.7-14.6°.

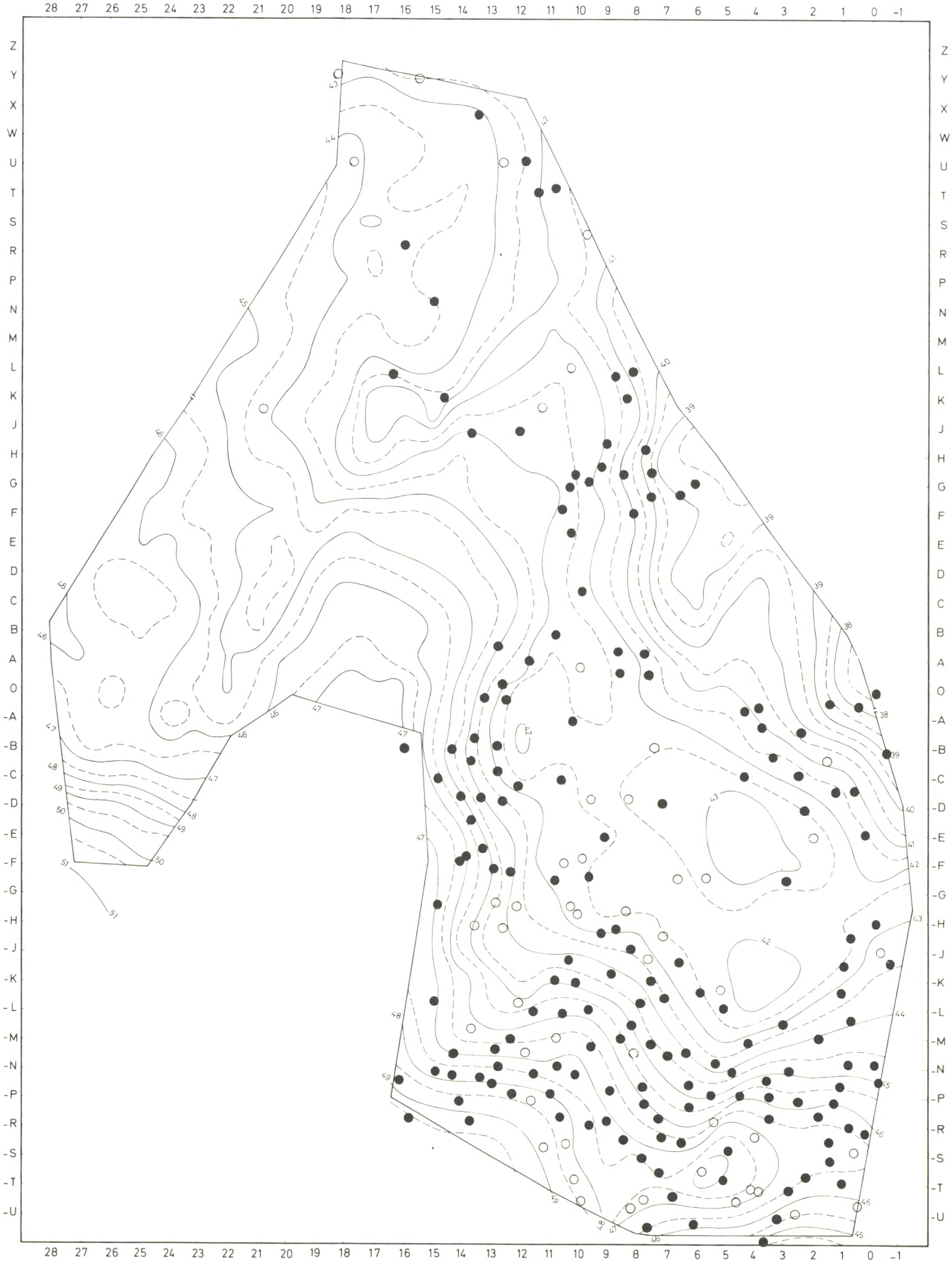


Fig. 34. Trees taller than 25 m in the enclosure. ●, *Fagus sylvatica;* ○, *Quercus petraea.*

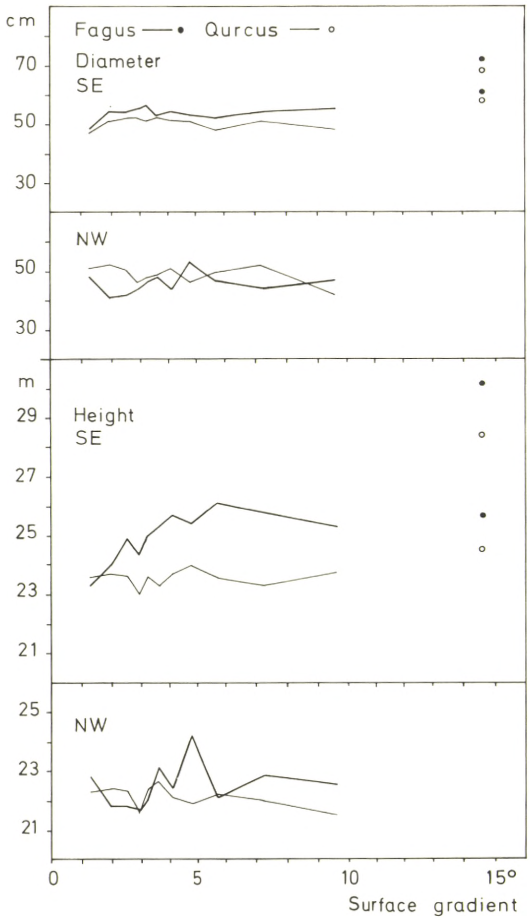


Fig. 35. Average diameter and height of *Fagus sylvatica* and *Quercus petraea* trees in surface gradient arrays, in the southeastern and the northwestern parts of the enclosure.

Fagus sylvatica thus utilizes better growth conditions on the larger slopes in the southeastern area, but the trees do not become taller than 26m in average; the increment in diameter is not improved on the slopes. Holstener-Jørgensen (1958) found an increase in the height of *Fagus* trees on a slope with impeded drainage. The soils on the slopes in Eldrup Forest are well-drained, and flushing does not occur there. Hence, there must be other reasons for the improved height-growth of *Fagus* on the slopes.

Two west-east and one south-north transects are shown in Figs. 37-39, which indicate the altitude of the surface, tree heights, and the altitude of the tree tops. Transect 0 (Fig. 37) crosses the plateau in the west and two slopes facing eastward. The average tree height is 21-22m at the westernmost 150m, and increases to 24-26m on the east-facing slopes. The tree-top altitude is about 68m at the westernmost 225m of the transect, and drops to about 64m at the easternmost part. The tops of the tallest trees growing on the east-facing slopes thus reach the same altitude as the trees to the west of them. The *Quercus* trees growing on the slopes are lower than the *Fagus*, and they are only slightly taller than the *Quercus* trees growing on the plateau west of the slope.

The second west-east transect (-F, Fig. 38) comprises only the high east-facing slope and the area east of it. The tree height decreases from 26m on the slope to 23m at 100m east of the top of the slope, and the tree top altitude decreases from 70 to 66m.

TABLE 20. Homogeneity of diameters and heights of the canopy trees in arrays of surface gradient angles, and the correlations for individual trees with the surface gradients, in the southeastern and the northwestern parts of the enclosure.

		Diameter Homogeneity		Correlation with surface gradient		Height Homogeneity		Correlation with surface gradient	
		(d.f.)	(P)	(r)	(P)	(d.f.)	(P)	(r)	(P)
SE, *Fagus sylvatica*	277	11,247	0.722	0.083	0.203	11,247	<0.001	0.215	<0.001
Quercus petraea	183	11,160	0.727	0.084	0.327	11,160	0.648	0.091	0.286
NW, *Fagus sylvatica*	147	10,113	0.386	0.092	0.340	10,113	0.436	0.092	0.341
Quercus petraea	244	10,193	0.051	–0.091	0.234	10,193	0.883	–0.071	0.353

TABLE 21. Correlations of the height of the canopy trees of *Fagus sylvatica* outside the peat area with the surface gradient angles in arrays of surface gradient, and the average height, in the southeastern part of the enclosure.

Surface gradient	Correlation with surface gradient (n)	(r)	(P)	n	x̄ (m)	s (m)
1.25°				6	23.5	±4.1
1.25°– 5.7°	9	0.861	0.003			
5.7° –14.6°	3	–0.968	0.161	107	25.9	±1.9

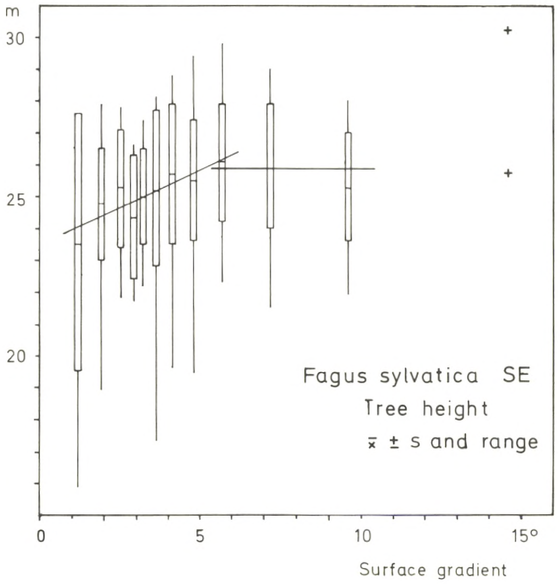


Fig. 36. Height of *Fagus sylvatica* trees in arrays of surface gradient, in the southeastern part of the enclosure.

The south-north transect follows the 40m line of the coordinate system (Fig. 39). The tallest trees occur on the slopes in the south and on a northeast-facing slope between 150 and 200m. The altitude of the tree tops follows the surface altitude more closely than in the other two transects.

Winds from west and southwest constitute about 50% of all wind directions in June-August (p. 29). The trees growing on the large east-facing slope are thus sheltered from the predominant winds during the growing season by the trees growing on the plateau to the west. Hence, the trees on the slopes have utilized the lee in such a way that the tree tops reach the same altitude as the tree tops on the plateau. The lee effect extends 50-100m eastward of

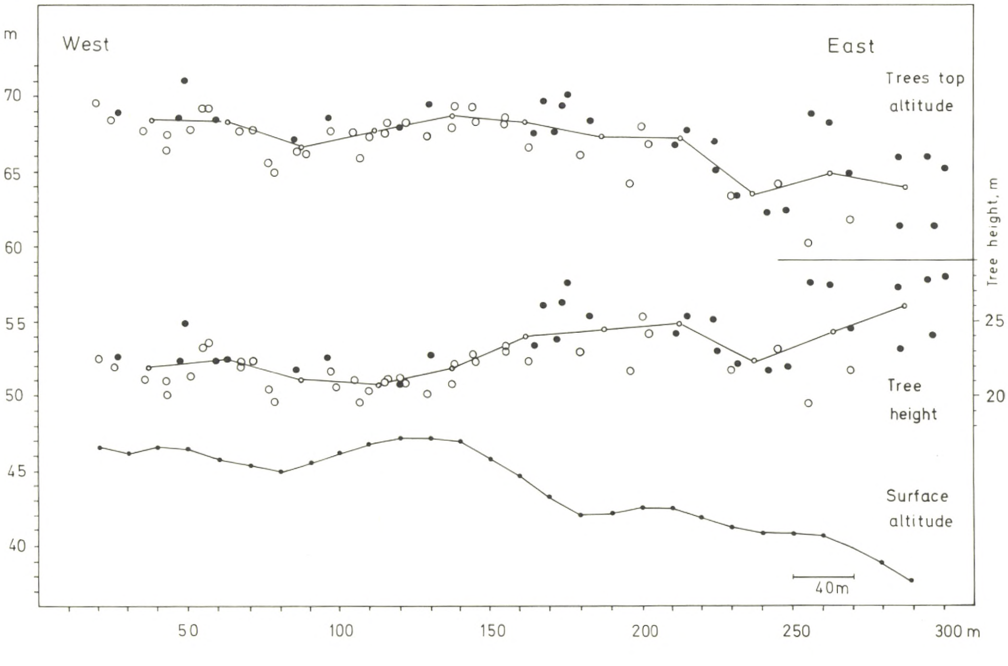


Fig. 37. Surface altitude, tree height and tree top altitude, in a west-east transect along the 0-line. Averages in 25 m arrays are shown (full lines).

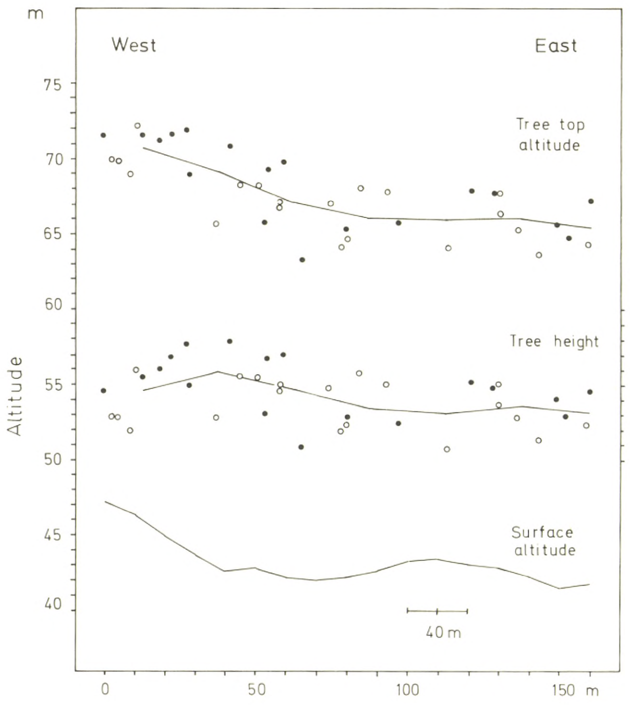


Fig. 38. Surface altitude, tree height and tree top altitude, in a west-east transect along the F-line.

the top of the slope; then the tree top altitude drops gradually towards the east, and the trees growing on level ground there are lower. The trees growing on the west-east orientated ridge in the southernmost part of the area are also particularly tall. The top of the ridge drops slightly towards east, and the trees growing on its top and its north and south-facing slopes utilize the shelter from trees growing further to the west. The tree height decreases on the lower part of the north-facing slope (Fig. 39). The predominant winds blow along the slope there, and not perpendicular to it as on the east-facing slopes.

The wind pattern over the tree tops thus seems to govern the height of the tree canopy in such a way that the tree tops reach the same altitude as trees growing to the windward side. The lee effect is more pronounced on the slopes facing away from the wind than on slopes that are parallel to the wind.

The height growth of *Fagus sylvatica* depends strongly on the supply of water during the growing season, as shown by Holstener-Jørgensen (1958). As the soils in Eldrup Forest have low water-retaining capability, it can be assumed that the height growth there is determined mainly by the rainfall and the evaporation during the summer.

TABLE 22. The average heights and diameters of the canopy trees in percentage of the average height and diameter of *Fagus sylvatica* in the northwestern part of the enclosure.

		NW (%)	SE Level ground (%)	Slopes (%)
Height,	*Fagus sylvatica*	100	106	117
	Quercus petraea	100	106	106
Diameter,	*Fagus sylvatica*	100	120	120
	Quercus petraea	109	113	113

The wind speed increases drastically at the tree top level, when the trees are fully leaved (Geiger 1956), and it appears that the trees growing on the slopes and somewhat to the east of them have utilized decreased evaporation in the tree tops due to the lee effect from the trees growing at a higher level to the west. *Fagus sylvatica* and *Quercus petraea* obtain about the same height in the northwestern area (22.1 and 22.0m, Table 13), and *Fagus* is not taller on the steep slopes there (Fig. 35), probably because there are no large slopes which face away from the wind.

Due to the lee effect, the *Fagus* and *Quercus* trees growing on level ground in the southeastern area are 6% taller than the trees in the northwest (Table 22); and the *Fagus* trees growing on the slopes falling away from the wind are 17% taller than the trees in northwest, whereas the *Quercus* trees growing on the slopes do not increase further in height (Table 22). Hence, *Quercus petraea* cannot reach an average height more than 23m even on the most sheltered sites (Table 13), whereas *Fagus sylvatica* obtains an average height of 26m on these sites (Table 21).

Quercus petraea growing in the northwestern area is 9% thicker than *Fagus sylvatica* (Table 22). The

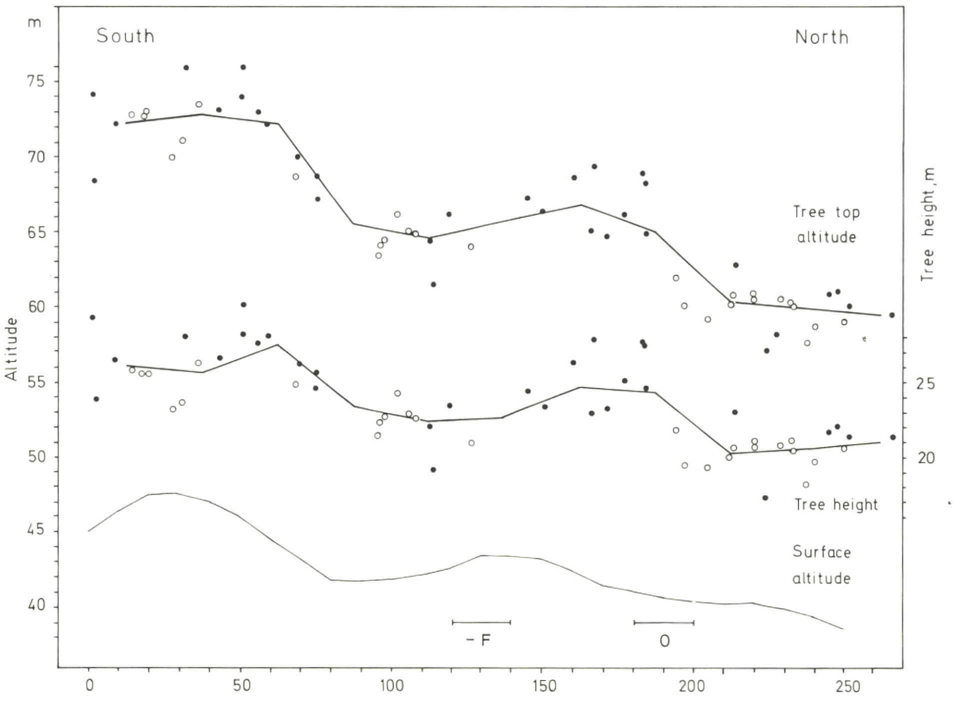


Fig. 39. Surface altitude, tree height and tree top altitude, in a south-north transect along the 40 m line.

thickness of *Fagus* increases more in the southeastern area (20%) than that of *Quercus* (13%). It was mentioned on p. 43 that the diameter increment of *Fagus sylvatica* is likely to be more sensitive to variations in rainfall than that of *Quercus petraea*. Hence, a better water balance in the southeastern area has caused a higher thickness growth in *Fagus* than in *Quercus*. Neither species has higher thickness growth on the slopes than on the level ground in southeast.

Conclusions

The growth of the trees in the enclosure is thus limited by water deficit. The growth in height as well as thickness is improved on the sheltered locations, but the growth of *Fagus sylvatica* is more positively affected that that of *Quercus petraea*. *Fagus* thus has a higher growth potential than *Quercus*, but is apparently more sensitive to water deficit probably because of its shallower root system.

THE REPRODUCTIVE TREE LAYER

Since the reproductive trees were removed in 1968, *Fagus sylvatica* saplings have sprouted from the stumps left at ground level, and the new saplings were up to lm tall by 1976. Many saplings of *Quercus petraea* and *Sorbus aucuparia* had appeared, and the *Ilex aquifolium* shrubs had started growing in height. A few saplings of *Sorbus intermedia* and *Betula pendula* were also recorded (Table 23). In addition, a few other woody species had appeared in the artificial clearing (p. 57).

The saplings of *Fagus sylvatica*, which occurred mostly in clumps (Fig. 40), were abundant (Table

23); *Quercus petraea* saplings were scarcer and were scattered irregularly in the enclosure (Table 23, Fig. 40, Plates V-VI). Since 1975 was a poor flowering year due to low summer temperatures in 1974 (Andersen 1980a), seedlings of *Fagus* and *Quercus* were scarce 1976. Seedlings of these trees were, however, very abundant 1977 (Table 23, Fig. 40).

The saplings of *Sorbus aucuparia* were scattered in the northern part of the enclosure (Fig. 40), and are likely to have derived from seeds dispersed by birds. (Mature *Sorbus* trees are frequent in a bog just northeast of the enclosure). Seedlings were noticed on two plots in 1976.

Ilex aquifolium shrubs were scattered within the enclosure (Fig. 40). They are likely to be root suckers. The age of the shrubs is unknown; however, as there are very few seed sources within the Løvenholm area, it is not unlikely that the shrubs have survived since the 18th century, at least. *Ilex* shrubs thus are known to be able to survive browsing almost indefinitely (Peterken & Lloyd 1967). A few flowers and fruits have been noticed on the new vertical shoots, and seedlings occurred on two plots 1976.

The saplings of *Betula pendula* may have derived from the few mature trees in the enclosure, whereas the *Sorbus intermedia* saplings derive from seeds transported to the area from elsewhere. (Planted *Sorbus intermedia* are found near Løvenholm Castle).

Environment

The density of saplings and seedlings was compared with six environmental variables. Tables 24 and 25 show averages and correlations with litter depth, humus depth, *Fagus* -nearest-tree and light, and averages for water content and pH. Fig. 41 shows normalized density distributions in relation to litter depth, humus depth, water content and pH.

Light

The *Fagus* saplings and seedlings, and the *Quercus* seedlings, were uncorrelated - but the *Quercus* saplings strongly correlated to plots with light. Hence, the germination of *Fagus* and *Quercus* was independant of illumination, but the development of *Quercus* saplings showed a preference for sites with fair light conditions. *Quercus* seedlings thus do not tolerate permanent shade and need more light than the *Fagus* seedlings in order to develop into saplings. Future countings will reveal how well the many seedlings from 1977 have survived.

The density percentages for *Sorbus* and *Ilex* on light plots are low, indicating that these species have been independant of the light conditions.

TABLE 23. The numbers of plots ($1 m^2$) with tree saplings and seedlings, and the highest frequencies per plot, observed in 1976 and 1977.

	1976			1977	
	Saplings		Seedlings	Seedlings	
	Plots	Highest frequency	Plots	Plots	Highest frequency
Fagus sylvatica	317	28	78	252	134
Quercus petraea	63	16	26	327	373
Sorbus aucuparia	19	5	2		
Ilex aquifolium	13	14	2		
Sorbus intermedia	2	3			
Betula pendula	1	1			

Litter depth

The saplings and seedlings of *Fagus* and *Quercus* were uncorrelated to the depth of the litter layer. The distribution curves show that the seedlings of *Fagus* and *Quercus* occur mostly on sites with moderate and thick litter cover, and are scarce on sites with thin litter. Fruits uncovered by leaf litter are exposed to predators of which mice are abundant in the enclosure, and such fruits germinate less well than fruits covered by litter due to drought (Watt 1919, Jarvis 1964).

The saplings of *Sorbus aucuparia* are independant of the litter depth, whereas *Ilex* occurs mainly on sites with more than 4cm litter. Leaves apparently tend to accumulate within the *Ilex* shrubs.

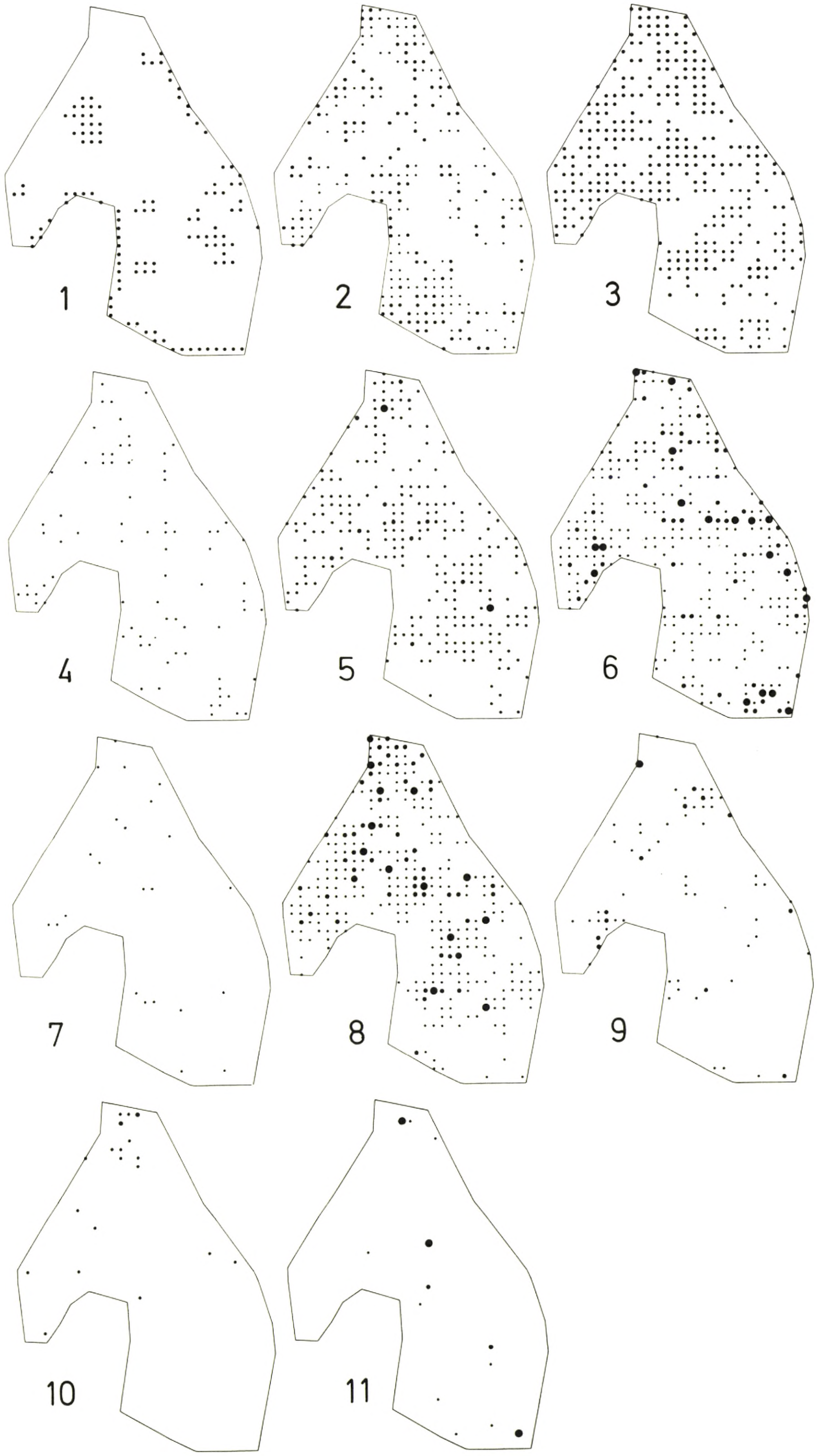


Fig. 40. The distribution of plots with light, humus depth 0-4 cm, and without *Fagus* trees, and the distribution of saplings and seedlings of tree species, in the enclosure.

1. Plots with light.
2. Humus depth 0-2 and 3-4 cm.
3. Plots without *Fagus* trees.
4. *Fagus sylvatica,* seedlings 1976 (coverage + and 1).
5. *Fagus sylvatica,* seedlings 1977 (frequencies 1-39, 40-79, >79).
6. *Fagus sylvatica,* trees <4 m 1976 (fr. 1-4, 5-9, >9).
7. *Quercus petraea,* seedlings 1976 (cov. + and 1).
8. *Quercus petraea,* seedlings 1977 (fr. 1-39, 40-79, >79).
9. *Quercus petraea,* trees <4 m 1976 (fr. 1-4, 5-9, >9).
10. *Sorbus aucuparia,* trees <4 m 1976 (fr. 1-2, 3-5).
11. *Ilex aquifolium,* trees <4 m 1976 (fr. 1-4, 5-9, >9).

Humus depth

The seedlings of *Fagus sylvatica* from 1976 were slightly negatively correlated with the depth of the humus layer, and the seedlings show a slight preference for sites with less than 6cm humus. They were scarce on peat and wet sites 1976, and frequent there 1977. The difference is probably due to the dry conditions in 1977, and it is indicated that the *Fagus* fruits do not germinate on the wettest sites in normal years. The saplings were negatively correlated with the humus depth; they occurred mainly on sites with less than 10cm humus, and they avoid peat and wet sites. Hence, the many seedlings found on peat and wet sites in 1977 are unlikely to survive.

The *Quercus petraea* seedlings were evenly distributed on humus depth and were frequent on peat and wet sites both years. The *Quercus* fruits, accordingly, germinate well on the wettest sites. The *Quercus* saplings were particularly frequent on sites without humus and were absent on peat and wet sites. Hence, the seedlings survive particularly well on sites without humus and perish on peat and wet sites. The lack of *Quercus* saplings on peat cannot be due to shade, because some peat sites are well illuminated (Fig. 23).

The saplings of *Sorbus aucuparia* and the *Ilex* shrubs occur at varying humus depth, predominantly at 10-29cm. The predominance of deep humus under *Ilex* is probably due to the accumulation of leaf litter there.

Water content

The saplings and the seedlings of *Fagus* and *Quercus* ocurred at varying levels of water content. They tend to avoid the driest sites. Watt (1919) and Jones (1959) found that *Quercus* fruits are sensitive to drought, those of *Quercus petraea* in particular, according to Jones (1959).

The plots with *Ilex aquifolium* had intermediate water content, and there were no plots with high and with low water content. This result is in accordance with the fact that *Ilex* is most frequent on sites with deep litter and humus layers and is absent on peat.

pH

The seedlings and the saplings of *Fagus* and *Quercus* seem to prefer sites with high pH (between 5.0 and 5.5). Bornebusch (1923-25) and Lindquist (1931) found that the numbers of *Fagus* saplings increased with increased pH.

Ilex aquifolium occurred at varying pH.

Fagus nearest tree

Saplings and seedlings of *Fagus sylvatica* and *Quercus petraea* were strongly negatively correlated to *Fagus* -nearest-tree plots (Tables 24 and 25). On shaded sites, a sharp borderline could be seen 1977 on the ground between *Fagus* and *Quercus* trees. Seedlings of both trees were abundant near the *Quercus* trees and nearly absent below *Fagus*. The difference cannot have been due to a difference in illumination, as the crowns of the *Quercus* trees are nearly as dense as those of the *Fagus* trees, and because it is unlikely that a slight difference in illumination could affect the germination of the fruits, which usually were covered by leaf litter. The *Fagus* and *Quercus* fruits thus germinate badly under *Fagus* trees rather because the *Fagus* root mat is more superficial than that of *Quercus*, a fact, which was noticed when digging holes in the top soil. The distribution patterns of the seedlings and saplings are strikingly similar to those of the plots without *Fagus* trees (Fig. 40).

It can be suggested that the dense root mats of *Fagus* consume the water reserves of the topmost soil quickly and hence prevent the germination of *Fagus* and *Quercus* fruits. Plots near *Fagus* thus tend to have lower water content than plots near *Quercus* (Fig. 24). Jarvis (1964) found that water-extracts from *Deschampsia flexuosa* humus inhibited the growth of primary roots in *Quercus* seedlings; similar experiments on *Fagus* humus are, however, lacking. Excretion of toxic substances from *Fagus* roots thus has not been proved (Borner 1960, Woods 1960).

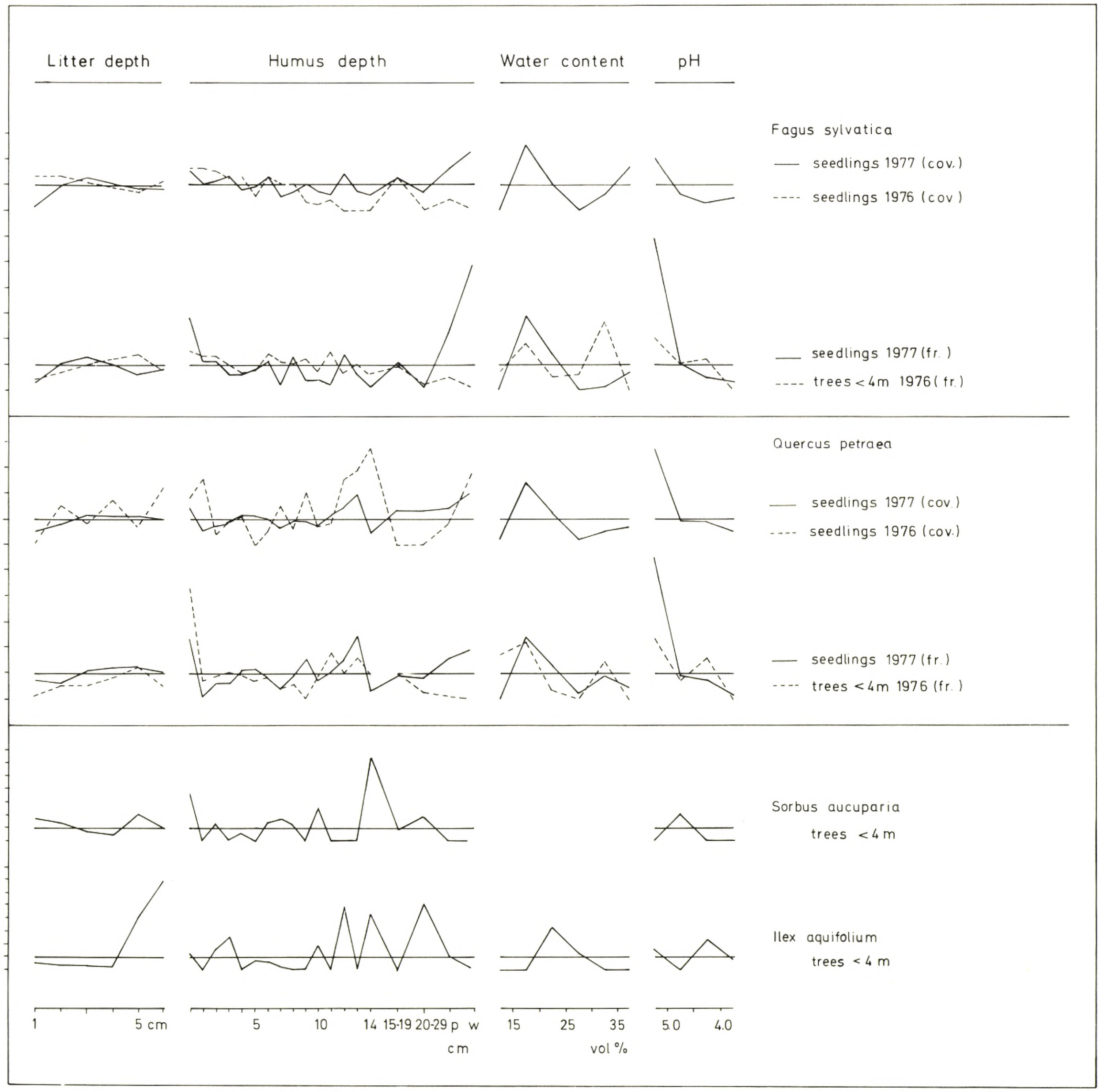


Fig. 41. Normalized density scores in relation to litter deptht, humus depth, water content and pH, for seedlings and saplings of tree species. p, peat; w, wet sites.

Saplings of *Sorbus aucuparia* also avoid sites near *Fagus*, as only 30% of them occurred on such sites, whereas *Ilex* is independant of the *Fagus* trees; 51% of the sprouts occurred near *Fagus*.

The germination of the fruits of *Fagus* and *Quercus* is independant of light, but the seedlings of *Quercus* do not tolerate permanent shade. *Sorbus aucuparia* and *Ilex* occur independently of the light conditions.

TABLE 24. Numbers of plots with tree saplings and seedlings, averages and density percentages (D), and correlations with ecological variables, observed in 1976 and 1977.

	Year	Plots	Litter depth			Humus depth			*Fagus* nearest		
			$\bar{x}$	Correlation n=6		$\bar{x}$	Correlation n=18		D	Correlation n=670	
		(n)	(cm)	(r)	(P)	(cm)	(r)	(P)	(%)	(r)	(P)
All plots		670	3.3			7.5			49		
Fagus sylvatica, trees <4 m	1976	317	3.6	0.581	0.227	6.4	–0.670	0.002	25	–0.256	<0.001
Fagus sylvatica, seedlings	1976	78	3.1	–0.630	0.179	5.7	–0.568	0.014	36	–0.107	0.005
Fagus sylvatica, seedlings	1977	252	3.2	0.398	0.435	7.7	0.039	0.877	30	–0.090	0.021
Quercus petraea, trees <4 m	1976	63	3.7	0.628	0.182	5.2	–0.374	0.126	22	–0.175	<0.001
Quercus petraea, seedlings	1976	26	3.4	0.634	0.176	7.1	–0.113	0.656	8	–0.152	<0.001
Quercus petraea, seedlings	1977	327	3.5	0.772	0.072	8.3	0.411	0.090	16	–0.351	<0.001
Sorbus aucuparia, trees <4 m	1976	19	3.5	–0.157	0.767	6.2	–0.001	0.995	30		
Ilex aquifolium, trees <4 m	1976	13	4.8	0.822	0.044	8.3	–0.423	0.080	51		
Betula pendula, trees <4 m	1976	1	2.0			8.0			0		
Sorbus intermedia, trees <4 m	1976	2	3.8			6.5			0		

TABLE 25. Significance of correlations with ecological variables, and numerical differences for averages and density percentages (in brackets, from Table 24).

	Year	Light	Litter depth	Humus depth	Water content	pH	*Fagus* nearest
Fagus sylvatica, trees <4 m	1976	0	0	––	(0)	(0)	–––
Fagus sylvatica, seedlings	1976	0	0	–		(0)	––
Fagus sylvatica, seedlings	1977	0	0	0	(0)	(+)	–
Quercus petraea, trees <4 m	1976	+++	0	0	(–)	(0)	–––
Quercus petraea, seedlings	1976	0	0	0		(+)	–––
Quercus petraea, seedlings	1977	0	0	0	(0)	(+)	–––
Sorbus aucuparia, trees <4 m	1976	(–)	0	0	(–)	(+)	(–)
Ilex aquifolium, trees <4 m	1976	(–)	+	0	(0)	(–)	(0)
Betula pendula, trees <4 m	1976	(+)	(–)	(0)			(–)
Sorbus aucuparia, trees <4 m	1976	(+)	(+)	(–)			(–)

O: P>5%; +,–: P<5%; ++,––: P<1%; +++,–––: P<0.1%
(0): $\bar{x} = \bar{x}$ (all plots) or D% = D% (all plots)
(+): $\bar{x} > \bar{x}$ (all plots) or D% > D% (all plots)
(–): $\bar{x} < \bar{x}$ (all plots) or D% < D% (all plots)

D (%)	Light Correlation n=670 (r)	(P)	Plots (n)	Water content x̄ (%)	Plots (n)	pH x̄
18			20	23	40	4.4
19	0.065	0.091	11	23	24	4.5
17	0.002	0.963			4	4.4
16	0.007	0.862	9	24	19	4.6
46	0.171	<0.001	7	20	10	4.4
23	0.028	0.471			5	4.6
17	0.020	0.606	14	22	24	4.6
10			1	18	1	4.8
12			4	22	5	4.3
100						
75						

Conclusions

The fruits of *Fagus sylvatica* and *Quercus petraea* germinate particularly well on shallow humus with high pH, but the fruits are exposed to predators and germination is impeded by drought on sites with a thin litter cover and, furthermore, on sites with superficial mats of *Fagus* roots. Saplings are scarce on such sites as well. The fruits germinate well on sites with a thick litter cover and without *Fagus* root mats. Seedlings of *Quercus* may occur on peat and wet sites, and those of *Fagus* on peat in dry years, but saplings are scarce there. Germination of the fruits is thus favoured by high pH and is sensitive to drought, and the seedlings do not survive on the wettest sites.

Saplings of *Sorbus aucuparia* occur mainly on humus deeper than 10cm. The *Ilex aquifolium* shrubs tend to collect litter and form a deep humus layer.

TREE SUCCESSION

Fagus to-day rejuvenates vigorously within the *Quercus* stands and is independent of light conditions, whereas the saplings of *Quercus* prefer such sites with good illumination. It can be assumed, accordingly, that *Fagus* will become dominant in the present *Quercus* stands in the future. The illuminated sites with *Quercus* saplings are artificial, as they derived from the felling of single trees, or occur along the borders to young *Picea* plantations. Outside the large peat area, no trees had been felled by storms up to 1980, as the trees are still vigorous, being only 150-170 years old, but six trees on dry ground were felled by storms in 1981. One can assume that *Quercus petraea* saplings can survive at such places in the future and thus remain permanently in the tree community.

The present investigation gives no information about how the *Fagus* stands regenerate. Regeneration is scarce under *Fagus* trees due to the dense root mats. *Fagus* growing on soils where it forms such root mats may possibly rejuvenate better when the trees become senescent and the root systems weakened. Rejuvenation of *Fagus* may also become promoted in openings created by the felling of trees by storms, and under *Quercus* trees, which have survived in former clearings caused by storm fall. Some of the *Fagus* stands in the research area have existed for more than 1500 years (Andersen 1978a, 1979a). Here they were mixed with *Quercus*, which have probably regenerated in clearings created by storm fall or by human influence, and have concomitantly helped *Fagus* to regenerate.

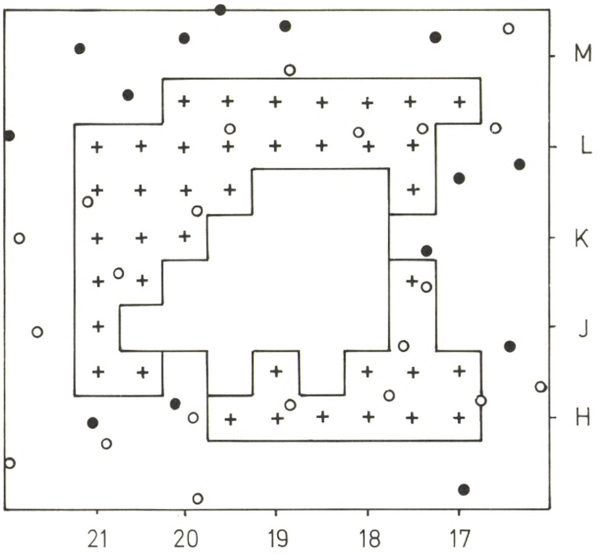
THE CLEARING. ILLUMINATION

The plots classified as "light" plots are shaded for part of the day. Hence, the clearing was established 1968 by the felling of four *Quercus* trees in order to study the effect of full illumination on the ground vegetation (Plate VII).

The lm^2 plots analyzed for ground vegetation 1976 and 1981 were distributed at 5m intervals within the clearing and in a strip around it (Fig. 42). In addition, all saplings taller than lm were counted within and around the clearing 1981. Some of the plots bordering the clearing receive light from the side, and are therefore not fully shaded. Plots near *Fagus* trees were omitted in order to exclude the influence of competition from the superficial *Fagus* roots. The humus depth was nearly the same inside and outside the clearing (Table 26).

The ground vegetation in the clearing was compared with the vegetation in the strip around the clearing. The density percentage for each species in the open area was divided by the percentage of plots in the open area (33%); these normalized densities for the 1976 and 1981 analyses are shown in Table 27. The scores are 1.0 if the species is equally frequent in the shaded and the open area; less than 1.0 if the species prefers the shaded plots, and more than 1.0 if the species prefers the plots without crown cover. The frequency percentages for saplings taller than lm in the open area were normalized by division with the areal percentage of the open area (30%).

Fig. 42. Map of the clearing (white), and the sample plots covered by tree crowns used for vegetation analysis (crosses). ●, *Fagus sylvatica* tree; ○, *Quercus petraea* tree. The coordinate system with 10 m intervals is indicated (17-21 and H-M).



Fagus sylvatica saplings were less frequent in the open than in the shaded area. This pattern may be influenced by the fact that many of the saplings have sprouted from those cut down 1968; hence the figures in Table 27 may reflect conditions from before the trees were felled. The scarcity of *Fagus* saplings in the open area may thus have been due to greater distance to seed sources in the present open area than in the shaded area (Fig. 42). *Fagus* seedlings were very scarce 1976 and 1981. Following the mast year 1976 there were 7 *Fagus* seedlings 1977; none of them occurred in the open area, and the frequencies of saplings had increased only slightly 1976-1981. Hence *Fagus* has not spread to the open area. The tall *Fagus* saplings (›lm) had nearly the same score 1981 as the saplings 1976 in the shaded and the open area. Hence, the height growth of the *Fagus* saplings is nearly the same in the shaded and the open area.

Quercus petraea saplings were slightly less frequent in the open area than in the shaded area. The plants recorded 1976 probably derive from seedlings es-

TABLE 26. The numbers of plots at varying humus depth, and normalized frequency of plots in the open area of the clearing. The normalized plot frequencies did not differ from 1.0 ($P>5\%$).

Humus depth	n	Frequency in open (%)	normalized
0– 4 cm	39	36	1.08
5– 9 cm	12	33	1.00
10–15 cm	9	22	0.67

TABLE 27. Total density (n), normalized density in the open area, and density in 1981, divided by the density in 1976, for tree saplings and seedlings, and fields plants in and around the clearing. Significance tests by the χ^2 method.

	1976		1981		1981/1976	
	n	Density in open	n	Density in open	Shaded	Open
Fagus sylvatica, saplings	109	0.22*	128	0.21*	1.18	1.13
Fagus sylvatica, saplings >1 m 1)			972	0.32*		
Fagus sylvatica, seedlings	4	0.75	1			
Quercus petraea, saplings	71	0.76	668	0.75*	9.43*	9.33*
Quercus petraea, saplings >1 m 1)			16	3.98*		
Quercus petraea, seedlings	4	0.75	48	0.69	12.33*	11.00*
Sorbus aucuparia, saplings	7	1.71	10	1.50	1.67	1.25
S. aucuparia+*S. intermedia*, >1 m 1)			218	1.32*		
Salix caprea, saplings, >1 m 1)			6	2.12		
Betula pendula saplings >1 m 1)			24	3.01*		
Molinia caerulea	6	1.00	6	1.00	1.00	1.00
Vaccinium myrtillus	48	1.06	33	1.27	0.61*	0.82
Deschampsia flexuosa	204	1.34*	140	2.04*	0.40*	1.04
Melampyrum pratense	54	1.44	17	1.94*	0.21*	0.42*
Pteridium aquilinum	213	1.54*	288	1.53*	1.16	1.35*
Maianthemum bifolium	11	1.64*	7	2.57*	0.20	1.00
Carex pilulifera	26	2.08*	23	1.83*	1.13	0.78
Holcus mollis	27	2.00*	22	2.32*	0.56	0.94
Luzula pilosa	59	2.08*	37	1.82*	0.78	0.56*
Trientalis europaea	16	2.44*	8	3.00*	0.00	0.62
Galium saxatile 2)	5	3.00*	4	3.00*		0.80

1) all saplings, 2) restricted to the open area, * P<5%.

tablished since the fencing 1968. Their numbers had increased greatly 1981, probably mainly due to the mast year 1976. Seedlings were scarce 1976 and more frequent 1981; 1980 was thus a good mast year for *Quercus*. The scores for seedlings were nearly the same in the open area and in the shaded area; *Quercus* thus has invaded the open area. The scores for saplings were the same as the scores for seedlings. Hence, the seedlings survive equally well in the shaded and in the open area. The tall saplings occurred predominantly in the open area 1981. The height growth of *Quercus petraea* saplings is thus strongly dependant on light, in contrast to that of *Fagus* saplings.

Saplings of *Sorbus aucuparia* and *S.intermedia* were somewhat more frequent in the open than in the shaded area 1976 and 1981. Their numbers had not increased significantly 1981.

Saplings of *Salix caprea* and *Betula verrucosa* were more frequent in the open than in the shaded area in 1981. A few saplings of *Betula pubescens*, *Populus tremula*, *Malus sylvestris* and *Frangula alnus* occurred in the open area in 1981 (Table 28).

Of the more common herbaceous plants (Table 27), *Molinia caerulea* and *Vaccinium myrtillus* were nearly equally frequent in the open and the shaded areas. All the other species listed in Table 27 were more frequent in the open than in the shaded area.

Most species, accordingly, are favoured by full illumination.

Illumination of the ground flora has changed somewhat 1976 to 1981 due to the height increase of *Fagus* saplings in the shaded area and expansion of *Pteridium* in the open area. All speies except for *Molinia caerulea*, *Pteridium* and *Carex pilulifera* had decreased in the shaded area, and *Melampyrum pratense*, *Luzula pilosa* and *Trientalis europaea* had decreased in the open area. The first mentioned species may thus be more shade tolerant, and the latter more light dependent, than the other species listed in Table 27. These tendencies are to be studied over a longer period.

Of the scarcely represented species listed in Table 28, *Oxalis acetosella* was restricted to the shaded area, *Calamagrostis arundinacea*, *Rubus idaeus* and *Epilobium augustifolium* to the open area, and *Calluna vulgaris* occurred in both.

The majority of the species found in the open area have been recorded elsewhere in the enclosure. Hence, mostly local species have spread to the clearing. Of new species only a few, *Betula pubescens*, *Populus tremula*, *Salix caprea*, *Frangula alnus*, *Malus sylvestris* and *Epilobium angustifolium*, have appeared.

Mosses recorded in 1981 are shown in Table 29. Seven species were distinctly more common in the open than in the shaded area. Four scarcely-represented species occurred only in the shaded area, and three only in the open area.

In conclusion, few species have preferred or have been favoured by shade. *Fagus sylvatica* has not spread to the clearing, but this may be due to lack of seeds. The *Fagus* saplings grow vigorously in height in both area. The seedlings of *Quercus petraea* survive well in the shaded area. It should be remembered that the shaded area around the clearing recieves side light, and that the seedlings of *Quercus* do not survive in permanent shade (p. 50). The *Quercus* saplings show a vigorous height growth only at full illumination. *Oxalis acetosella* and four moss speies are absent from the clearing and may prefer shade. Most other species recorded are favoured by full illumination. The flora found in the clearing is essentially local, and only a few new immigrants were recorded.

TABLE 28. Total density of tree saplings and field plants with density less than 4 in and around the clearing.

	1976	1981
Only in shaded area		
Oxalis acetosella	3	3
Only in open area		
Betula pubescens, saplings >1 m[1])		2
Populus tremula, saplings >1 m[1])		2
Frangula alnus, saplings >1 m[1])		2
Malus sylvestris, saplings >1 m[1])		1
Calamagrostis arundinacea		1
Rubus idaeus	2	2
Chamaenerium angustifolium	2	2
In shaded and open areas		
Calluna vulgaris	3	

[1]) all saplings.

TABLE 29. Total density and normalized density of bryophytes in and around the clearing in 1981.

	n	Density in open
Polytrichum formosum	19	2.05*
Dicranella heteromalla	11	2.18*
Pleurozium schreberi	4	2.25
Hypnum cupressiforme	6	2.50*
Dicranum scoparium	7	2.63*
Pohlia nutans	7	2.63*
Oxyrrhynchium praelongum	4	3.00*
Only in shaded area		
Atrichum undulatum	1	
Dicranum majus	3	
Mnium hornum	1	
Plagiothecium curvifolium	1	
Only in open area		
Rhytidiadelphus loreus	2	
Scleropodium purum	1	
Thuidium tamariscinum	1	
In shaded and open areas		
Lophocolea bidentata	2	

* $P<5\%$.

TABLE 30. Percent contribution to the total variance by the first 10 principal components.

Principal Component	Contributation per eigenvalue	cumulative
1	6.61	6.61
2	5.56	12.17
3	4.93	17.10
4	4.66	21.76
5	4.59	26.35
6	4.13	30.48
7	3.96	34.44
8	3.81	38.26
9	3.62	41.88
10	3.40	45.28

TABLE 31. Differences from the averages loadings on the first three principal components.

	Component		
	1	2	3
1. *Holcus mollis*	+		+
Viola riviniana	+		+
Lapsana communis	+		+
2. *Melampyrum pratense*	+		–
Luzula pilosa	+	+	–
Oxalis acetosella	+		–
Deschampsia flexuosa	+	+	–
3. *Quercus petraea,* seedlings	+	–	
Quercus petraea, trees <4 m	+		
4. *Ilex aquifolium,* seedlings	–		+
Ilex aquifolium, trees <4 m	–	+	+
5. *Pteridium aquilinum*	–		
Milium effusum	–		
Glyceria fluitans	–		
6. *Dryopteris carthusiana*	–	–	–
Molinia caerulea	–	–	–
Rubus idaeus	–	–	–
Carex curta	–	–	

+: loading $>\bar{x}+0.17$; –: loading $<\bar{x}-0.17$.

Tree saplings and field vegetation were included in the analyses of the ground vegetation. No attempt was made to distinguish *a priori* plant communities; instead, an attempt was made to structure the ground vegetation by statistical analysis and to compare the units distinguished with ecological variables.

Principal components analysis (PCA)

The percent contribution of the first principal components to the total variance is low (Table 30). Hence, principal components analysis cannot contribute very sucessfully to the separation of units. Certain features can, however, be suggested.

Species loadings

The species loadings on the first three components are shown in Fig. 43, with the species arranged according to decreasing loadings on the 1st component. The species with the largest differences from the mean values are shown in Table 31. They can, to some degree, be arranged according to their loadings. *Holcus mollis*, *Viola riviniana* and *Lapsana communis* (1) thus have high loadings on the 1st and the 3rd components, *Melampyrum pratense*, *Luzula pilosa*, *Oxalis acetosella* and *Deschampsia flexousa* (2) have high loadings on the 1st and 2nd, and low loadings on the 3rd component, and *Quercus petraea* seedlings and saplings high loadings on the 1st component. In contrast, *Ilex aquifolium* (4) has low loadings on the 1st and high loadings on the 3rd component, *Pteridium aquilinum*, *Milium effusum* and *Glyceria fluitans* (5) low loadings on the 1st component, and *Dryopteris carthusiana*, *Molinia caerulea*, *Rubus idaeus* and *Carex curta* have low loadings on all of the first three components.

Plot scores

No attempt was made to group the 670 plots by their scores on the principal components, because

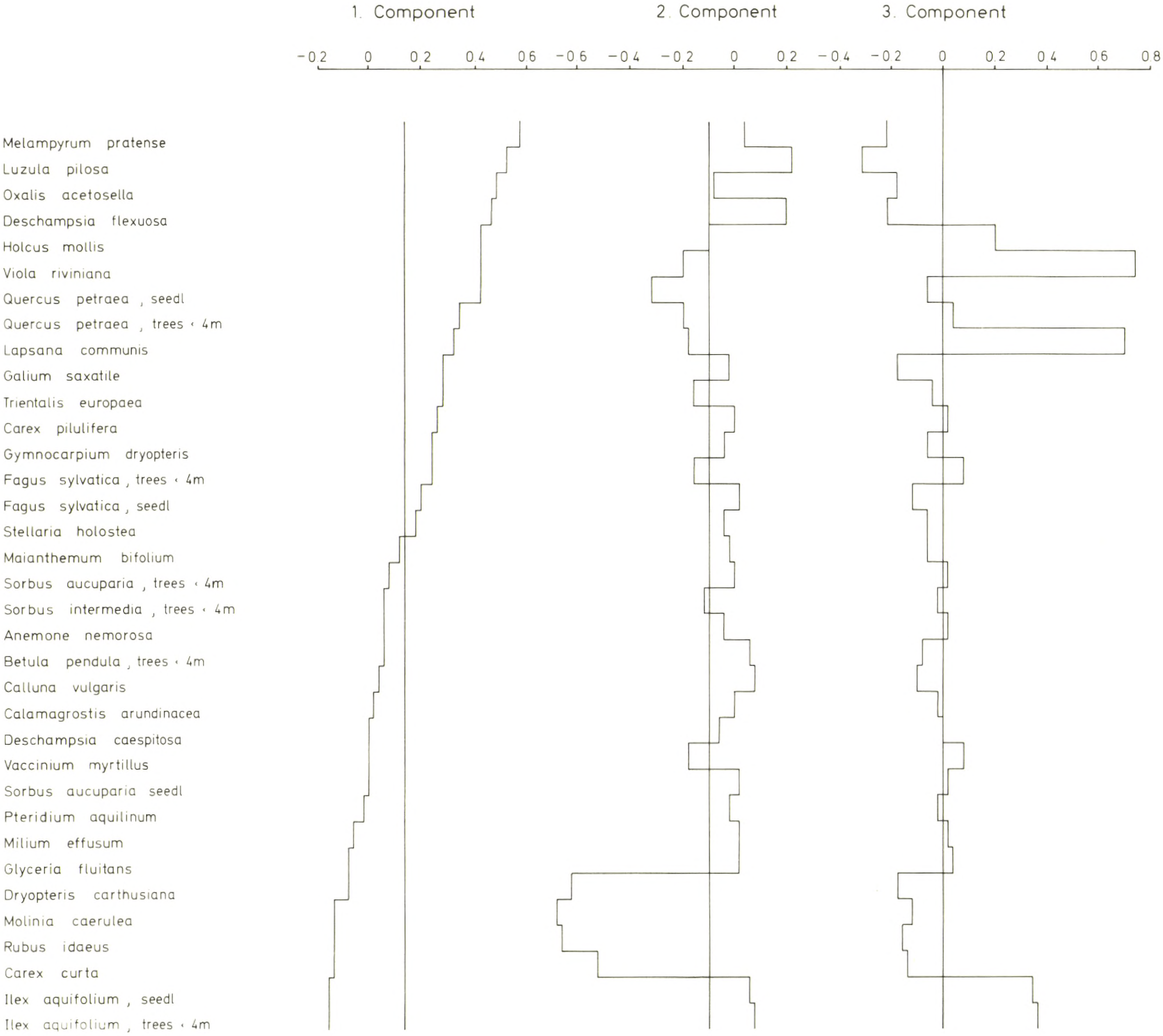


Fig. 43. Loadings for species on the first three principal components. The vertical lines indicate the average loadings for all species.

no discrete differences could be observed. The correlations of plot scores with ecological variables were used to highlight significant variables. As it was noticed that species with high loadings on the lst principal component seemed to occur on plots with many species, and species with low loadings on plots with few species, the number of species and the total density of plants on the plots were also considered (cp. Huntley & Birks 1979). 40 plots with contrasting high and low scores on the first three principal components were selected for soil analysis. Their scores were compared with species numbers, plant density and five ecological variables. Correlations are shown in Tables 32 and 33. The scores on the lst principal component were strongly correlated with species number, plant den-

TABEL 32. Correlations of the plot scores on the first three principal components to ecological variables. n=40 and 20 (water content).

	Species number		Plant density		Light		*Fagus* nearest		Humus depth		pH		Water content	
	(r)	(P)	(r)	(P)	(r)	(P)	(r)	(P)	(r)	(P)	(r)	(P)	(r)	(P)
1. component	0.785	<0.001	0.695	<0.001	0.207	0.199	–0.294	0.065	–0.574	<0.001	0.541	<0.001	–0.519	0.019
2. component	0.076	0.642	0.027	0.864	0.023	0.889	0.000	0.998	–0.757	<0.001	0.392	0.012	–0.728	<0.001
3. component	0.152	0.384	–0.073	0.652	0.107	0.512	–0.156	0.336	–0.266	0.098	0.379	0.016	–0.127	0.593

TABLE 33. Significance of correlations with ecological variables (from Table 32).

	Species number	Plant density	Light	*Fagus* nearest	Humus depth	pH	Water content
1. component	+ + +	+ + +	0	0	–––	+ + +	–
2. component	0	0	0	0	–––	+	–––
3. component	0	0	0	0	0	+	0

0: p>5%; +,–: P<5%; + +,—: P<1%; + + +,–––: P<0.1%.

sity and pH, and strongly negatively correlated with humus depth; the scores on the 2nd component were strongly negatively correlated with humus depth and water content, and the 3rd component scores were slightly correlated with pH. The coefficients of correlation on the lst principal component were largest for species number (0.785) and plant density (0.695), and on the 2nd component for humus depth (-0.757) and water content (-0.728).

The principal components analysis thus initially unites plots which are rich or poor in plant species and individuals, secondly plots on shallow or deep humus and with low or high water content, and thirdly plots with high or low pH.

Conclusions

The lack of contrast in the variance contributed by the first principal components is probably due to the facts that the vegetation analyses were not selected within discrete species combinations but were scattered uniformly within the enclosure, and that transitions between typical plant combinations were gradual. Nevertheless, some typical species combinations and ecological gradients can be suggested. As species loadings and plot scores on the principal components are related, it can be assumed that the species combinations reflect the same ecological gradients as do the plot scores.

The principal components analysis thus emphasizes that *Holcus mollis*, *Viola riviniana* and *Lapsana communis* occur on plots that are rich in species and individuals, and where pH is high; *Melampyrum pratense*, *Luzula pilosa*, *Oxalis acetosella* and *Deschampsia flexuosa* on similar plots, with shallow humus and with lower pH; and *Quercus petraea* saplings and seedlings on plots rich in species. In contrast, *Ilex aquifolium*, *Pteridium aquilinum*, *Milium effusum* and *Glyceria fluitans* occur on plots poor in species and individuals, and *Dryopteris carthusiana*, *Molinia caeruela*, *Rubus idaeus*, and *Carex curta* on sites poor in species and with deep humus and low pH.

Some of these results were confirmed by the TWINSPAN analysis.

Vegetation structure (TWINSPAN analysis)

The vegetation analyses from the 670 plots were examined by the TWINSPAN procedure. This analysis arranges the vegetation analyses in a two-dimensional system with sample plots united to plot groups and species to species groups. Tree saplings were included, whereas the seedlings were excluded, because they are not permanent members of the plant communities.

TABLE 34. Constancy percentage (C) and density percentage (D) for species in the plot groups 1–8.

Plot group	1		2		3		4		5		6		7		8	
Total plots and density	2	6	362	2137	229	1468	6	38	17	80	1	2	2	2	51	
	C	D	C	D	C	D	C	D	C	D	C	D	C	D	C	D
1. *Glyceria fluitans*													100	100		
2. *Lapsana communis*			+	+												
Viola riviniana			+	+												
Calluna vulgaris			1	+												
Galium saxatile			1	+												
Betula pendula			+	+												
Sorbus intermedia			1	+												
3. *Calamagrostis arundinacea*			1	+	+	+										
Luzula pilosa			46	8	9	1	17	3								
Holcus mollis			8	2	5	1										
Deschampsia flexuosa			91	48	59	16	50	8	12	3						
Carex pilulifera			9	2	4	1										
4. *Gymnocarpium dryopteris*			+	+	+	+										
Melampyrum pratense			49	10	36	7			6	1						
5. *Anemone nemorosa*			+	+	+	+										
Stellaria holostea			1	+	2	+										
Sorbus aucuparia			2	+	4	1										
6. *Maianthemum bifolium*			10	2	6	1			6	1						
Quercus petraea			4	1	21	6			6	1						
Fagus sylvatica			41	10	73	30			18	5						
7. *Trientalis europaea*			10	2	5	1			6	3						
8. *Dryopteris carthusiana*			1	+	2	+			35	8						
Rubus idaeus					+	+			18	4						
Deschampsia caespitosa									6	4						
Molinia caerulea			2	+	5	2			88	53						
Cares curta									12	4	100	100				
Ilex aquifolium			1	+	1	+	100	79								
9. *Vaccinium myrtillus*			7	2	38	16	33	8	24	5						
10. *Milium effusum*	100	33														
Pteridium aquilinum	50	50	16	4	50	15										
Oxalis acetosella	50	17	38	7	7	1	17	3	47	10						

Plot groups

The TWINSPAN program arranged the 670 vegetation plots into eight plot groups and the 31 species into ten species groups. Table 34 shows the constancy and relative density of the species within the 7 plot groups with ground vegetation. The 8th plot group comprises plots, that have no ground vegetation.

Plot group 1 comprises two plots with *Milium effusum*. Other species occurring here are *Pteridium aquilinum* and *Oxalis acetosella*.

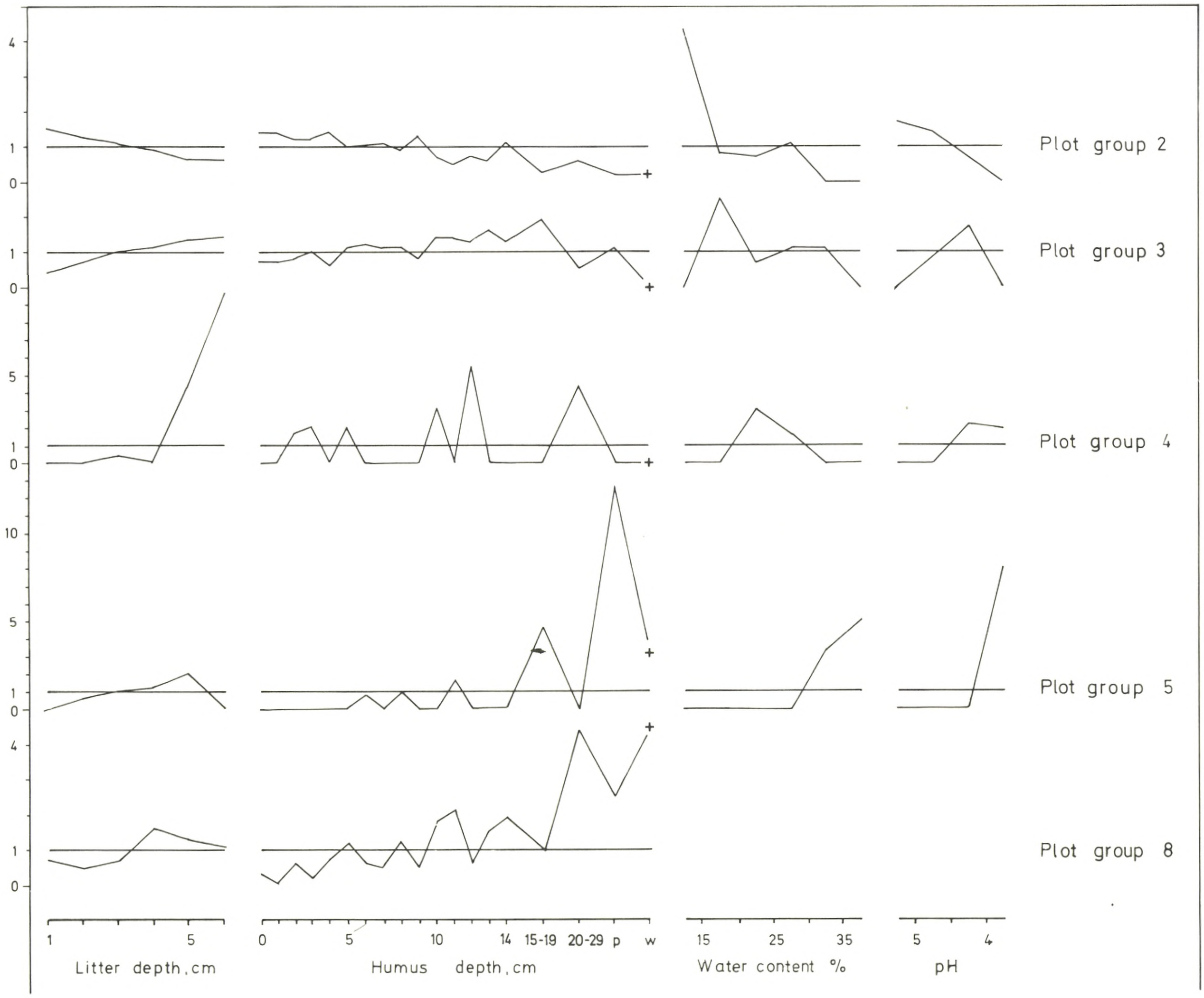


Fig. 44. Normalized frequency scores for the plot groups 2-4 and 8 in relation to litter depth, humus depth, water content and pH. p, peat; w, wet site.

Plot group 2 comprises 362 plots, or 54% of all plots, with 26 species. *Deschampsia flexuosa*, *Melampyrum pratense*, *Luzula pilosa*, *Fagus sylvatica* saplings and *Oxalis acetosella* are the most important species.

Plot group 3 comprises 229 plots or 34% of all plots, with 21 species. *Fagus sylvatica* saplings, *Deschampsia flexuosa*, *Pteridium aquilinum*, *Vaccinium myrtillus*, *Melampyrum pratense* and *Quercus petraea* saplings are most important.

Plot group 4 comprises 6 plots with a high density of *Ilex aquifolium*. *Deschampsia flexuosa* and *Vaccinium myrtillus* ocur with high constancy but low density.

Plot group 5 comprises 17 plots with 13 species. *Molinia caerulea*, *Oxalis acetosella*, *Dryopteris carthusiana* and *Vaccinium myrtillus* are most important.

Plot groups 6 and 7 include a few plots with *Carex curta* or *Glyceria fluitans* alone.

Plot group 8, finally, with no ground vegetation,

TABLE 35. Numbers of plots in the plot group 1–8, averages ($\bar{x}$) and density percentages (D), and correlation of plot numbers with, ecological variables.

Plots		Litter depth			Humus depth			*Fagus* nearest			Light		
		$\bar{x}$	correlation n=6		$\bar{x}$	correlation n=18		D	correlation n=670		D	correlation n=670	
		(cm)	(r)	(P)	(cm)	(r)	(P)	(%)	(r)	(P)	(%)	(r)	(P)
All plots	670	3.3			7.5			49			18		
1	2	2.0			8.0			100			50		
2	362	3.0	–0.978	0.008	5.4	–0.835	<0.001	57	0.172	<0.001	14	–0.096	0.013
3	229	3.6	0.970	0.001	8.7	0.287	0.248	28	–0.303	<0.001	25	0.143	<0.001
4	6	5.0			9.0			67			17		
5	17	3.6	0.289	0.579	23.5	0.681	0.002	35			18		
6	1				wet						0		
7	2				wet						50		
8	51	3.9	0.705	0.117	11.8	0.799	<0.001	84	0.203	<0.001	6	–0.089	0.021

comprises 51 plots, or 8% of all the plots.

Plot groups 2, 3 and 5 are thus the most important, whereas groups 1, 4, 6 and 7 comprise plots characterized by only one species, and group 8 plots with no species.

Plot groups and environment

The eight plot groups were compared with six environmental variables. Tables 35 and 36 show averages and correlations for litter depth, humus depth, *Fagus* -nearest-tree and light, and averages for water content and pH. Normalized plot frequencies (p. 33) were used for correlations with litter depth and humus depth. For correlations with *Fagus* -nearest-tree and light, the plots within a plot group were scored as 1 and other plots as 0. Fig. 44 shows normalized plot frequency distributions on litter depth, humus depth, water content and pH.

The two plots assigned to plot group 1 occurred on sites with shallow litter, moderately deep humus and near *Fagus* trees.

The plots assigned to plot group 2 are strongly negatively correlated with litter depth and humus depth. They are strongly correlated with *Fagus* -nearest-tree, and negatively correlated with light. The normalized frequency-distribution curves show that the plots occur mainly at a litter cover less than 4cm, on humus less than 10cm deep, at water content less than 15%, and at pH higher than 4.5. The plant combinations in this group thus avoid thick litter cover and are restricted to shallow-humus and dry sites with high pH, do not avoid *Fagus* trees, and tolerate shade.

The plots assigned to plot group 3 are strongly correlated with litter depth and light, and they are strongly negatively correlated with *Fagus* -nearest-tree. The plots occur mainly on sites with more than 3cm litter and with 10-20cm humus. They are absent from the driest and wettest sites, and occur at pH 4.0-5.0. The plant combinations assigned to plot group 3 thus tolerate deep litter, prefer a moderately deep humus layer with moderate moisture and pH, avoid root competition from *Fagus* and require some illumination.

The plots in plot group 4 occur mostly on sites with more than 4cm litter, more than 10cm humus, intermediate water content, pH less than 4.5, and near *Fagus* trees. These plots are rather similar to those of plot group 3, but differ by occurring mostly near *Fagus* trees.

Water content Plots (n)	x̄ (%)	pH Plots (n)	x̄
20	23	40	4.4
6	17	23	4.6
6	22	9	4.3
4	23	4	4.2
4	35	4	3.9

TABLE 36. Significance of correlations with ecological variables, and numerical differences for averages and density percentages (from Table 35).

Plot group	Litter depth	Humus depth	Water content	pH	*Fagus* nearest	Light
1	(–)	(0)			(+)	(+)
2	––	–––	(–)	(+)	+++	–
3	+++	0	(0)	(0)	–––	+++
4	(+)	(+)	(0)	(–)	(+)	(0)
5	0	++	(+)	(–)	(–)	(0)
6		wet				(–)
7		wet				(+)
8	0	+++			+++	–

0: P>5%; +,–: P<5%; ++,––: P<1%; +++,–––: P<0.1%.
(0) x̄ = x̄ (all plots) or D% = D% (all plots).
(+) x̄ > x̄ (all plots) or D% > D% (all plots).
(–) x̄ < x̄ (all plots) or D% < D% (all plots).

The plots assigned to plot group 5 are correlated with humus depth. They occur mostly on sites with more than 3cm litter, on humus deeper than 15cm, on peat and on wet sites. The water content is higher than 30%, pH is lower than 4.0, and the plots occur rarely near *Fagus* trees. Hence, these plant combinations prefer sites on deep humus and peat with high water content and low pH, where litter tends to accumulate.

The plots in the plot groups 6 and 7 occur on wet sites.

The plots without ground vegetation in plot group 8 are strongly correlated with humus depth and *Fagus* trees, and are slightly negatively correlated with light. The plots occur at moderate litter cover, mainly on humus more than 10cm deep, on peat and on wet sites, and often near *Fagus* trees.

The grouping of the sample plots thus reflects ecological contrasts. Sites with shallow litter and humus layers near *Fagus* trees tend to dry out more quickly than sites with deep litter and humus and without *Fagus*. The plot groups 1-7 accordingly contain various plant combinations with increasing requirements to soil moisture. They also reflect a gradient from comparatively high to low pH.

The TWINSPAN method has accordingly arranged the sample plots with ground vegetation according to a distinct ecological gradient. It should be remembered in this connection that no ecological information was included in the data, and that the arrangement of the plots was based *solely* on the vegetational data.

In addition, plot group 2 mainly occurs on shaded sites, whereas plot group 3 is restricted to sites with some light.

The plots without ground vegetation (plot group 8) were shown to occur mainly on sites with moderate or deep humus, on peat and on wet sites, near *Fagus* trees, and preferentially in shade. Such sites were apparently least suited for ground vegetation, probably because of shade and competition from the superficial *Fagus* roots on humus sites and because of shade on peat and wet sites.

Species groups

The species groups unite species with the same preferences for the various plot groups. To illustrate this, the total density of each species in each plot

TABLE 37. Normalized densities for species in the plot groups 1–8.

Plot group Plots, n Plots, %	1 2 0.3	2 362 58.4	3 229 37.0	4 6 1.0	5 17 2.8	6 1 0.2	7 2 0.3	Total plots 619	Total density 3733
1. *Glyceria fluitans*							310	2	2
2. *Lapsana communis*		1.71						1	1
Viola riviniana		1.71						2	2
Calluna vulgaris		1.71						2	3
Galium saxatile		1.71						5	5
Betula pendula		1.71						1	1
Sorbus intermedia		1.71						2	3
3. *Calamagrostis arundinacea*		1.28	0.68					3	4
Luzula pilosa		1.52	0.29	0.53				188	194
Holcus mollis		1.28	0.68					41	56
Deschampsia flexuosa		1.39	0.50	0.25	0.06			471	1251
Cares pilulifera		1.37	0.54					43	45
4. *Gymnocarpium dryopteris*		1.14	0.90					2	3
Melampyrum pratense		1.18	0.82		0.11			262	118
5. *Anemone nemorosa*		0.57	1.80					2	3
Stellaria holostea		0.64	1.69					8	8
Sorbus aucuparia		0.78	1.47					19	22
6. *Maianthemum bifolium*		1.23	0.72		0.61			49	60
Quercus petraea		0.39	2.06		0.32			63	113
Fagus sylvatica		0.57	1.79		0.22			317	669
7. *Trientalis europaea*		1.20	0.70		1.35			49	54
8. *Dryopteris carthusiana*		0.39	0.83		17			13	13
Rubus idaeus			0.68		27			4	4
Deschampsia caespitosa					36			1	3
Molinia caerulea		0.22	0.85		20			35	73
Carex curta					27	155		4	7
Ilex aquifolium		0.21	0.40	75				13	41
9. *Vaccinium myrtillus*		0.21	2.31	1.10	0.52			118	281
10. *Milium effusum*	310								
Pteridium aquilinum	2.88	0.49	1.90					173	222
Oxalis acetosella	1.82	1.44	0.27	0.61	1.71			167	170

group was calculated in percentage of all the densities of that species. As the species will appear to be concentrated in the plot groups with many plots, the density perentages were normalized by dividing the density percentages of the species in each plot group by the plot frequency in the same plot group in percentage of the total number of plots. The normalized density score for a species in a plot group will be more than 1.0 if the species prefers that plot group, and less than 1.0 if the species avoids the plot group. These ”fidelity” scores are shown in Table 37.

Species assigned to the same species group generally have similar scores in Table 37. The species

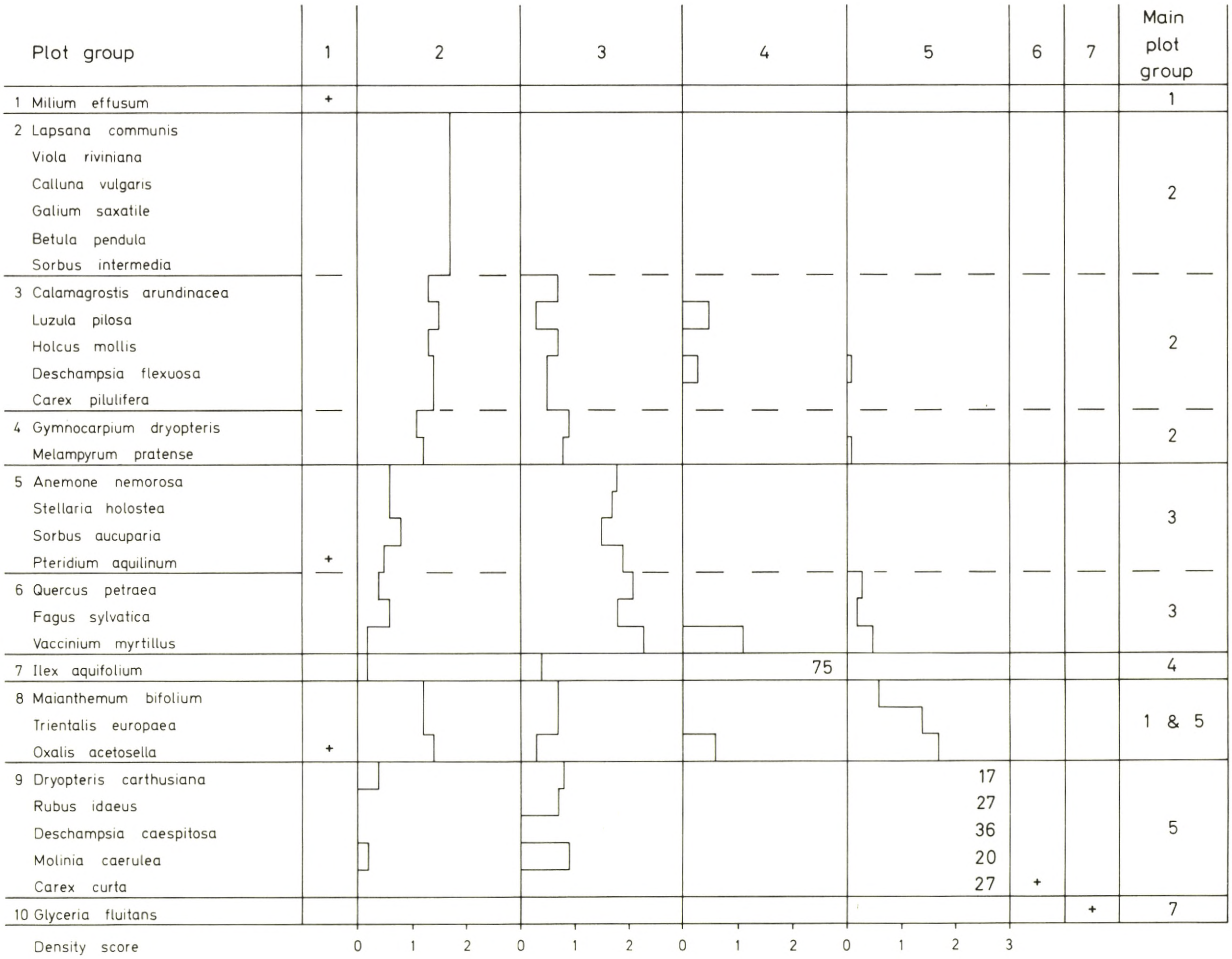


Fig. 45. Normalized density scores for species in the plot groups 1-7.

groups are thus in accordance with the fidelity scores. Still there are some discrepancies. The assignment of *Ilex aquifolium* to species group 8 is mysterious, and the species should rather be assigned to its own species group. Some species, furthermore, have been assigned to a species group in accordance with a high score in a plot group with a low plot number, without regard for their scores in plot groups with high plot numbers. If one, rather, disregards the scores in plot groups with few plots, then *Vaccinium myrtillus*, *Pteridium aquilinum*, *Oxalis acetosella* and *Maianthemum bifolium* can, with advantage, be moved from species groups 9, 10 and 6 to groups 6, 5 and 7 respectively.

Revised species groups are shown in Fig. 45; here they have been rearranged to bring the array of the species groups into accordance with the array of the plot groups.

It can be seen from Fig. 45 that the 10 revised species groups unite species with similar distributions over the plot groups. Species group 1 is confined to plot group 1. Groups 2-4 have highest scores in plot group 2, groups 5-6 in plot group 3, group 7 in plot group 4, and group 9 in plot group 5.

Most of these species groups have low scores in the neighbouring plot groups. Species group 8 is ambiguous, as its species have high scores both in plot group 2 as well as in plot group 5. Species group 10 is confined to plot group 7.

Phytosociological units are distinguished by the occurrence of species, which show preferences for a particular unit. Such characteristic or differential species need not to be quantitatively important in that particular community. The plot groups in the Eldrup Forest ground vegetation distinguished by means of the TWINSPAN program thus resemble phytosociological units.

The plot groups and species groups were not based on samples of pre-selected vegetation units, but the plots were, rather, distributed uniformly within a certain area. Although vegetational transitions were gradual, the program has been successful in detecting vegetational differentiations which are useful for structuring plant communities and species groupings. The TWINSPAN program is thus well suited for studies of vegetation structure on an objective basis.

It may be noticed that several species groups distinguished by the TWINSPAN analysis are common with species groups distinguished by the principal components analysis. Species group 3 thus coincides with group 2 in Table 31, species group 7 with group 4, and species group 9 with group 6.

Plant species and environment

As the plot groups are distinctive ecologically, the ecological characteristics of the species in a species group should resemble each other and ought to be similar to the ecological conditions peculiar to the plot group in which they mainly occur. Species distributed over several plot groups are likely to have broader ecological amplitudes than those of the plot group where they mainly occur.

Average values and correlations of species to environmental variables are shown in Tables 38 and 39. Normalized distribution curves and maps are shown in Figs. 46-51. Due to the low plot numbers (20 and 40), the distribution curves for water content and pH are somewhat uncertain.

Species group 1

Milium effusum is confined to plot group 1 and the figures in Table 39 are the same as for that plot group. The species occurs on a few sites with shallow litter and moderately deep humus, and near *Fagus* trees.

Species groups 2-4

The species referred to species groups 2-4 generally occur on sites with shallow litter and humus and low water content. In these respects, their ecological characteristics are similar to those of plot group 2.

The species in group 2 are scarce and are confined to plot group 2 (Fig. 45). They occur rarely near *Fagus* trees and frequently on sites with light. These species of accidental occurrence have, accordingly, selected sites from plot group 2, which are near *Quercus* trees and with light.

The species belonging to species group 3 occur mainly in plot group 2, and transgress to plot group 3. *Luzula pilosa*, *Deschampsia flexuosa* and *Carex pilulifera* prefer sites with less than 3 cm litter cover. These plants are of low growth form with densely-leaved shoots, and they do not appear to be able to penetrate a thick litter layer. *Deschampsia flexuosa* thus is killed, if covered by leaf litter (Watt 1931, Ovington 1953). *Holcus mollis*, which has elongated shoots, is independent of litter depth, except for the deepest litter layers (›5cm). Watt (1931), Ovington (1953) and Sydes & Grime (1981) reached similar conclusions. *Calamagrostis arundinacea*, which has coarse leaf rosettes, is probably also suited for penetrating a litter cover, as the few occurrences of the species are found on sites with moderate litter.

Holcus mollis and *Carex pilulifera* are nearly confined to sites with shallow or no humus, whereas *Luzula pilosa* and *Deschampsia flexuosa* transgress to sites with 10-15cm deep humus. *Luzula*, *Holcus* and *Deschampsia* do not occur on the wettest sites, and *Holcus* also avoids the driest sites. *Holcus* avoids sites

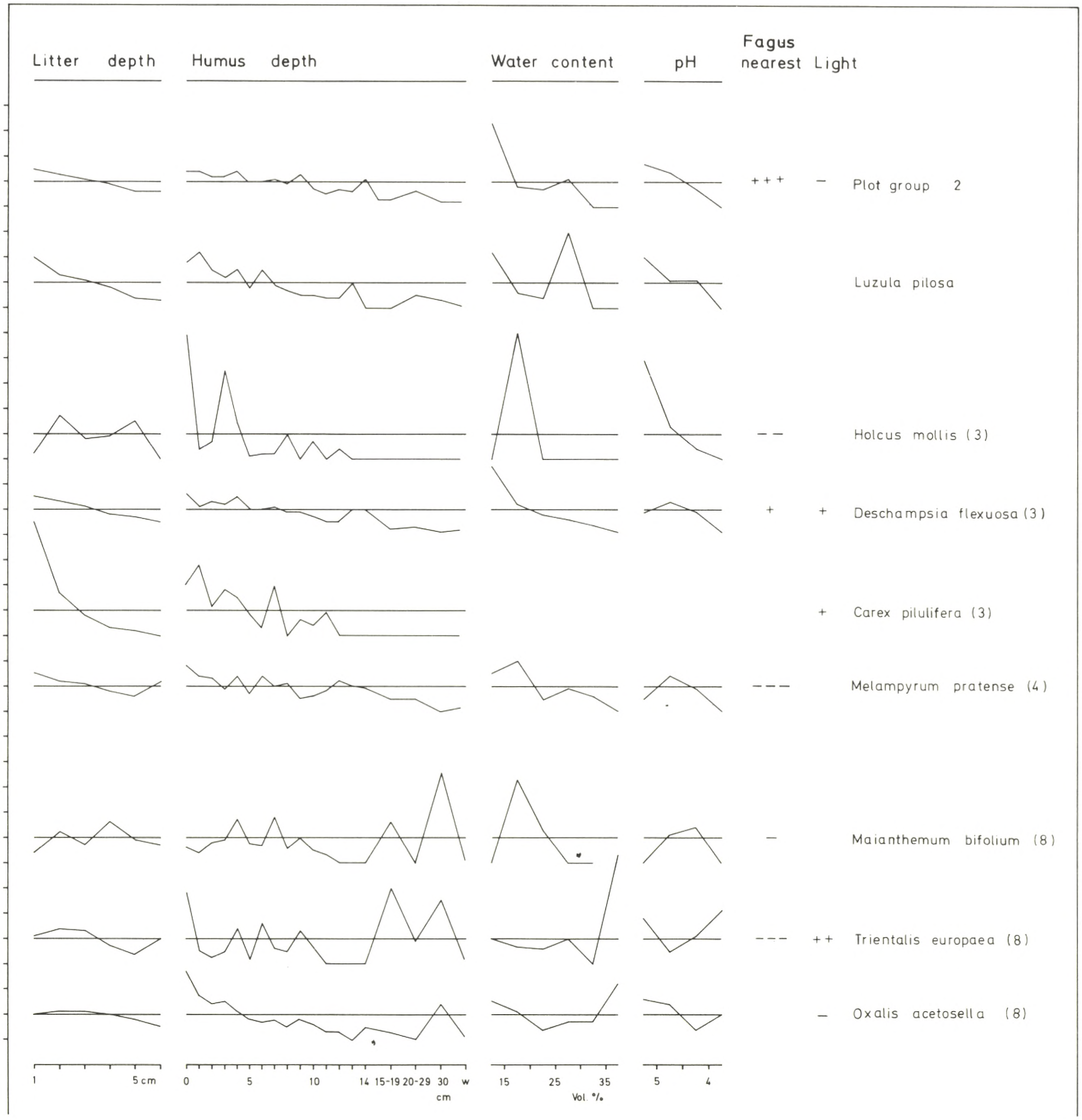


Fig. 46. Normalized density scores in relation to litter depth, humus depth, water content and pH, for plot group 2 and species from the species groups 3, 4 and 8. p, peat; w, wet site.

near *Fagus* trees as well, whereas *Luzula*, *Deschampsia* and *Carex* are independent of the tree species.

Luzula pilosa, *Deschampsia flexuosa* and *Carex pilulifera* thus prefer thin litter and shallow humus and tolerate dryness. Their occurrence on sites with pH

TABLE 38. Numbers of plots, averages and density percentages (D), and correlations with ecological variables for species.

	Plots	Litter depth			Humus depth			*Fagus* nearest			Light			Plots	Water content	Plots	pH
		x̄	correlation n=6		x̄	correlation n=18		D	correlation n=670		D	correlation n=670			x̄		x̄
	(n)	(cm)	(r)	(P)	(cm)	(r)	(P)	(%)	(r)	(P)	(%)	(r)	(P)	(n)	(%)	(n)	
All plots	670	3.3			7.5			100			18			20	23	40	4.4
1. *Milium effusum*	2	2.0			8.0			100			50						
2. *Lapsana communis*	1	2.0			3.0			0			0					1	5.5
Viola riviniana	2	3.5			1.5			0			50			1	10	1	4.3
Calluna vulgaris	2	2.8			5.0			75			100			3	16	3	4.4
Galium saxatile	5	3.8			2.7			17			50						
Betula pendula	1	2.0			8.0			0			100						
Sorbus intermedia	2	3.8			6.5			0			75						
3. *Calamagrostis arundinacea*	3	4.0			5.0			0			20						
Luzula pilosa	188	2.8	−0.974	0.001	4.7	−0.721	0.001	46	−0.038	0.321	22	0.056	0.147	6	20	16	4.5
Holcus mollis	41	3.2	−0.122	0.817	2.9	−0.503	0.034	22	−0.103	0.008	26	0.041	0.295	3	17	13	4.7
Deschampsia flexuosa	471	3.0	−0.996	<0.001	5.0	−0.868	<0.001	54	0.083	0.032	21	0.095	0.015	16	18	36	4.5
Carex pilulifera	43	2.1	−0.864	0.026	4.0	−0.698	0.001	33	−0.061	0.114	36	0.081	0.036	1	20	2	4.6
4. *Gymnocarpium dryopteris*	2	3.8			0.0			0			0			2	19	2	4.6
Melampyrum pratense	262	3.1	−0.574	0.233	5.3	−0.793	<0.001	26	−0.271	<0.001	19	0.019	0.615	8	20	21	4.5
5. *Anemone nemorosa*	2	3.3			1.0			25			75						
Stellaria holostea	8	3.4			4.0			33			33			1	18	2	4.4
Sorbus aucuparia	19	3.5	−0.157	0.767	6.2	−0.001	0.995	30			10			1	18	1	4.8
Pteridium aquilinum	173	3.2	−0.406	0.424	6.9	−0.423	0.080	24	−0.265	<0.001	46	0.265	<0.001	3	14	9	4.5
6. *Quercus petraea*	63	3.7	0.628	0.182	5.2	−0.374	0.126	12	−0.175	<0.001	46	0.171	<0.001	7	20	10	4.5
Fagus sylvatica	317	3.6	0.581	0.227	6.4	−0.670	0.002	25	−0.256	<0.001	19	0.065	0.091	11	23	24	4.5
Vaccinium myrtillus	118	4.4	0.958	0.003	9.9	0.448	0.062	12	−0.262	<0.001	27	0.084	0.029	7	21	11	4.3
7. *Ilex aquifolium*	13	4.8	0.822	0.044	8.3	0.320	0.194	51			12			4	22	5	4.3
8. *Maianthemum bifolium*	49	3.4	0.188	0.721	9.8	0.324	0.190	30	−0.980	0.022	18	0.001	0.980	2	19	5	4.4
Trientalis europaea	49	3.0	−0.611	0.198	9.1	0.206	0.411	23	−0.126	0.001	34	0.104	0.007	5	27	9	4.3
Oxalis acetosella	167	3.2	−0.766	0.076	5.6	−0.507	0.032	50	0.018	0.651	13	−0.076	0.049	8	24	21	4.5
9. *Dryopteris carthusiana*	13	3.7	0.336	0.514	23.0	0.637	0.004	33			20			4	33	4	3.9
Rubus idaeus	4	2.8			23.5			25			0			2	36	2	3.9
Deschampsia caespitosa	1	wet			wet						100						
Molinia caerulea	35	3.6	0.198	0.707	19.4	0.753	<0.001	25	−0.090	0.019	34	0.073	0.059	7	33	7	4.0
Carex curta	4	4.1			30.0			100			60			2	34	2	3.9
10. *Glyceria fluitans*	2	wet			wet						50						

higher than 4.0 may be due to the fact that pH is highest on the shallow-humus sites, where the mineral soil is near the surface, and on sites without humus. Their soil requirements thus coincide with the soil characteristics of plot group 2.

Holcus mollis differs somewhat from the other species in group 3. This species prefers shallow-humus sites with high pH, but avoids such sites when they tend to dry out due to shallow litter and/or root competition. *Holcus* obviously requires higher moisture than the other group 3 species.

Deschampsia flexuosa and *Carex pilulifera* are slightly dependent on light.

Melampyrum pratense in species group 4 has higher scores in plot group 3 than the group 3 species. The species is independent of the litter depth, is frequent on sites with up to 15cm humus, and is negatively correlated to *Fagus* -nearest-tree sites. *Melampyrum pratense* thus favours sites near *Quercus* trees in plot group 2 and transgresses to plot group 3-sites with moderate litter and humus. *Gymnocarpium dryopteris* occurs on a few plots with moderate litter, no humus, and without *Fagus* trees. This species also has a rather high score in plot group 3.

Melampyrum pratense avoids sites with the highest pH (›5.0) and occurs on shaded sites as well as on sites with light.

The maps in Fig. 49 show that the distribution patterns of *Luzula pilosa* and *Deschampsia flexuosa* are very similar to the distribution of sites with shallow humus and litter. *Holcus mollis* and *Carex pilulifera* avoid the sites with dense *Deschampsia flexuosa* mats in the southeastern part of the enclosure. *Melampyrum pratense* is particularly frequent on sites in the central part of the enclosure, which belong to plot group 3 (Fig. 50).

Species group 8

The species included in species group 8 are somewhat similar to the species in groups 2-4, as they also have high scores in plot group 2, but they transgress to plot group 5 sites.

Maianthemum bifolium, *Trientalis europaea* and *Oxalis acetosella* occur mostly on sites with shallow litter cover and are frequent on sites with less than 10cm humus, but they differ from the group 3 species by high scores on sites with more than 15cm humus and on peat (Fig. 46). The three species are also ambiguous with respect to water content and pH; however, it appears that sites with *Maianthemum* on peat with high water content and low pH were missed in the selection of sites for soil analysis. *Maianthemum*, *Trientalis* and *Oxalis* avoid sites with intermediate humus depth. These sites belong to plot group 3 communities, where *Pteridium aquilinum* and *Vaccinium myrtillus* are frequent, and it may be indicated that the three species do not tolerate competition from these taller, densely growing species.

Maianthemum bifolium and *Trientalis europaea* avoid sites near *Fagus* trees, and *Trientalis* is correlated with light sites. *Oxalis acetosella* has no preference for tree species and occurs mostly on shaded sites.

The maps for *Maianthemum bifolium* and *Trientalis europaea* (Fig. 48) show the occurrences of these species on shallow humus and on the peat area in the southeastern part of the enclosure. *Oxalis acetosella* can be seen to avoid shallow-humus sites with light (Figs. 49 and 50).

Species groups 5 and 6

The species referred to species groups 5 and 6 have high scores in plot group 3. They prefer sites without *Fagus* trees.

The group 5 species have low scores in plot group 2. *Sorbus aucuparia* saplings and *Pteridium aquilinum* are independent of litter depth and humus depth, but are nearly absent from the peat, and *Pteridium* avoids sites with the lowest pH (‹4.0, Fig. 47). The few plots with *Anemone nemorosa* and *Stellaria holostea* occur at moderate litter cover and shallow humus. These four species avoid sites near *Fagus* trees, and *Pteridium* and *Anemone* occur mainly on plots with light.

The group 6 species have low scores in plot groups 2 and 5. The *Fagus sylvatica* and *Quercus petraea* saplings occur mainly, and *Vaccinium myrtillus* exclusively, at sites with deep litter cover. The three species occur on varying humus depth. *Quercus* saplings are common on sites without humus, and *Quercus* and *Fagus* are scarce on peat and wet sites with high water content and low pH, whereas *Vaccinium myrtillus* transgresses to peat sites.

The three species in plot group 6 avoid sites near *Fagus* trees. The *Quercus* saplings are strongly, and *Vaccinium* slightly, dependent on light, whereas the *Fagus* saplings are independent of light. On the survival of *Fagus* and *Quercus* seedlings see p. 55.

TABLE 39. Significance of correlations with ecological variables, and numerical differences for averages and density percentages (from Table 38).

	Litter depth	Humus depth	Water content	pH	*Fagus* nearest	Light	Main plot group
1. *Milium effusum*	(–)	(0)			(+)	(+)	1
2. *Lapsana communis*	(–)	(–)			(–)	(–)	
Viola riviniana	(+)	(–)		(+)	(–)	(+)	
Calluna vulgaris	(–)	(–)	(–)	(–)	(+)	(+)	
Galium saxatile	(+)	(–)	(–)	(0)	(–)	(+)	
Betula pendula	(–)				(–)	(+)	
Sorbus intermedia	(+)	(–)			(–)	(+)	
3. *Calamagrostis arundinacea*	(+)	(–)			(–)		2
Luzula pilosa	–––	–––	(–)	(+)	0	0	
Holcus mollis	0	–	(–)	(+)	––	0	
Deschampsia flexuosa	–––	–––	(–)	(+)	+	+	
Carex pilulifera	–	–––	(–)	(+)	0	+	
4. *Gymnocarpium dryopteris*	(+)	(–)	(–)	(+)	(–)	(–)	
Melampyrum pratense	0	–––	(–)	(+)	–––	0	
5. *Anemone nemorosa*	(0)	(–)			(–)	(+)	
Stellaria holostea	(+)	(–)	(–)	(0)	(–)	(+)	
Sorbus aucuparia	0	0	(–)	(+)	(–)	(–)	
Pteridium aquilinum	0	0	(–)	(+)	–––	+ + +	3
6. *Quercus petraea*	0	0	(–)	(+)	–––	+ + +	
Fagus sylvatica	0	––	(0)	(+)	–––	0	
Vaccinium myrtillus	+ +	0	(–)	(–)	–––	+	
7. *Ilex aquifolium*	+	0	(0)	(–)	(0)	(–)	4
8. *Maianthemum bifolium*	0	0	(–)	(0)	–	0	
Trientalis europaea	0	0	(+)	(–)	–––	+ +	2/5
Oxalis acetosella	0	–	(0)	(+)	0	–	
9. *Dryopteris carthusiana*	0	+ +	(+)	(–)	(–)		
Rubus idaeus	(–)	(+)	(+)	(–)	(–)	(–)	
Deschampsia caespitosa	wet	wet				(+)	5
Molinia caerulea	0	+ + +	(+)	(–)	–	0	
Carex curta	(+)	(+)	(+)	(–)	(+)	(+)	
10. *Glyceria fluitans*	wet	wet				(+)	7

0: P>5%; +.–: P<5%; + +,––: P<1%; + + +,–––: P<0.1% (+): $\bar{x} > \bar{x}$ (all plots) or D% < D% (all plots)
(0): $\bar{x} = \bar{x}$ (all plots) or D% > D% (all plots)
(–): $\bar{x} > \bar{x}$ (all plots) or D% < D% (all plots).

The species in groups 5 and 6 thus differ from the group 3-4 species. They tolerate at least moderate litter cover, are common on moist sites and are sensitive to root competition from *Fagus*. *Pteridium*, *Quercus* and *Vaccinium* avoid shaded sites.

The maps in Fig. 50 show that the distribution

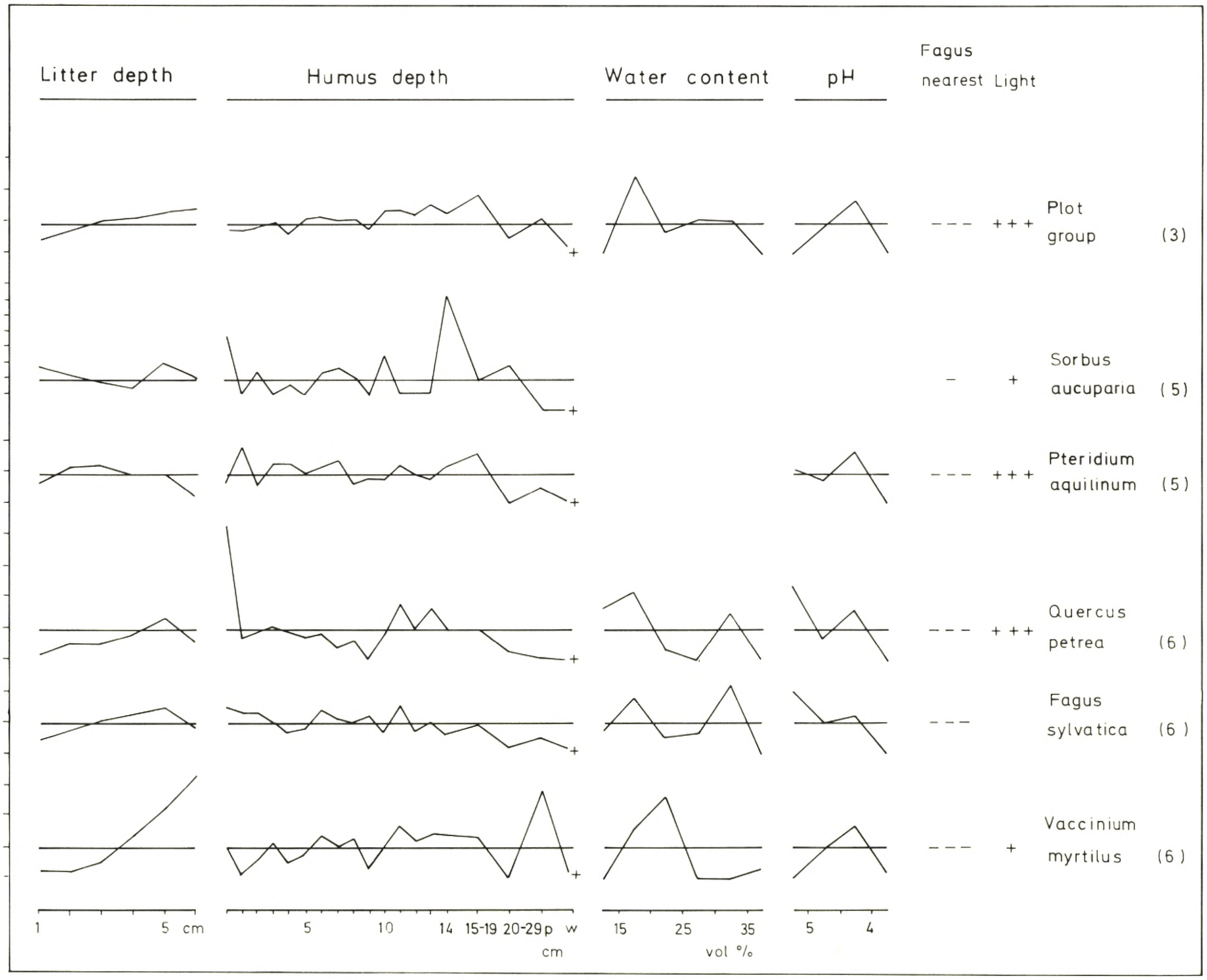


Fig. 47. Normalized density scores in relation to litter depth, humus depth, water content and pH, for plot group 3 and species from the species groups 5 and 6.

patterns of *Pteridium aquilinum*, *Quercus* and *Fagus* saplings, and *Vaccinium myrtillus*, resemble the distribution of sites without *Fagus* trees. *Pteridium* and *Quercus* also reflect the occurrence of sites with light, but *Pteridium* is surprisingly scarce in the northern part of the enclosure.

Species group 7

Only *Ilex aquifolium* is referred to species group 7. All plots with *Ilex* frequencies at 4 or higher were referred to plot group 4 and the plots with less *Ilex* to the plot groups 2 and 3.

The *Ilex* plots usually have a deep litter cover (Fig. 48), presumably because leaves tend to accumulate within the dense *Ilex* shrubs (cp. p. 50). *Ilex* shrubs occur at varying humus depth, predominantly on humus deeper than 10cm, probably because the thick litter promotes accumulation of humus (cp. p. 19). The plots with *Ilex* on shallow humus were referred to plot group 2, and those on deep humus and peat to plot group 3. The water content on *Ilex* plots is moderate and the pH-range is wide. *Ilex* is independent of the presence of tree species and light.

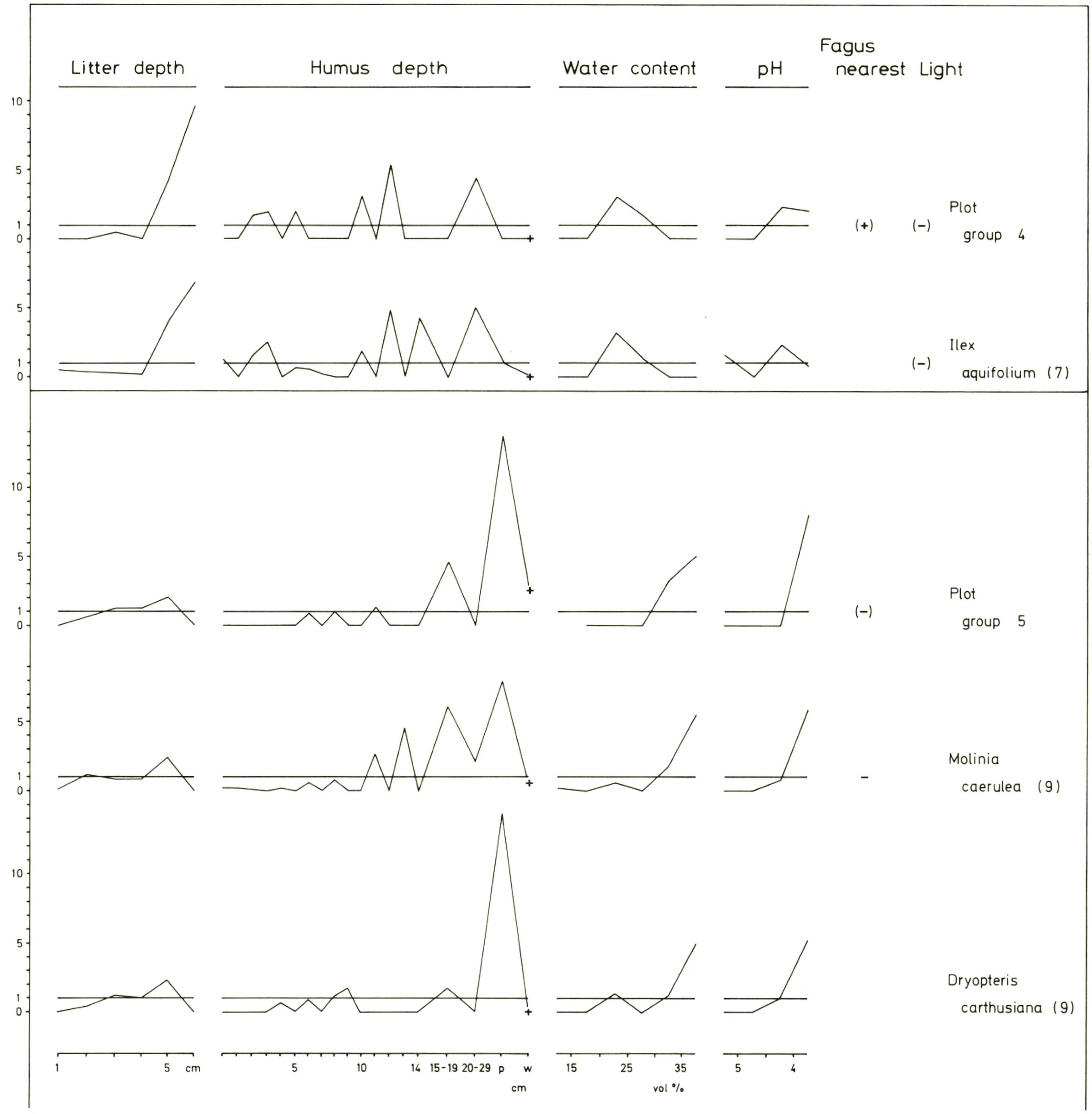


Fig. 48. Normalized density scores in relation to litter depth, humus depth, water content and pH, for plot group 4, species from species group 7, plot group 5, and species from species group 9.

The *Ilex* shrubs were scattered within the enclosure (Fig. 51).

Species group 9

The five species referred to species group 9 are almost restricted to plot group 5. *Dryopteris carthusiana* and *Molinia caerulea* have low scores in plot groups 2 and 3, and *Rubus idaeus* in plot group 3.

The five species occur at moderate litter depth (Fig. 48). *Molinia* and *Dryopteris carthusiana* occur mainly on humus deeper than 15cm, and on peat, and rarely on humus less than 10cm deep (*D. assimilis* occurred on one plot with 12cm humus). *Rubus idaeus* occurs on deep humus and peat, *Deschampsia caespitosa* on wet sites, and *Carex curta* on peat. *Molinia* and *Dryopteris carthusiana* prefer sites with high water content, and both species occur on sites with pH less than 4.5.

The species in group 9 rarely occur near *Fagus* trees, and they are independent of light.

The group 9 species thus occur mainly on deep humus, peat and wet sites with high water content and low pH, and *Fagus* is absent from most of the sites. The occurrence of *Rubus idaeus* may show that the peat is becoming decomposed, probably an effect of artificial drainage. The *Molinia caerulea* and *Dryopteris carthusiana* sites on shallow humus are found on the slopes in the southeastern part of the enclosure (Fig. 51). Their presence there may indicate locally impeded drainage.

Species group 10

Glyceria fluitans is restricted to a wet hollow in the northern part of the enclosure. This hollow may dry out in the summer. No other aquatics occur there.

PLANT COMMUNITIES IN ELDRUP FOREST

Two tree species predominate in the tree canopy in the enclosure in Eldrup Forest, *Fagus sylvatica* and *Quercus petraea*, whereas *Betula pendula* is represented by only a few specimens. *Fagus sylvatica* and *Quercus petraea* occur mostly in small stands of either species.

Three characteristic plant combinations predominate in the ground vegetation. One of them (plot group 2) is associated with *Fagus sylvatica* trees, one of them (plot group 3) with *Quercus petraea*, and one occurs on plots with or without *Quercus* trees (plot group 5). Plots without ground vegetation (plot group 8) occur beneath *Fagus sylvatica*.

Information about plant communities in Denmark and elsewhere used below was derived mainly from Bornebusch (1923-25), Ellenberg (1963, 1979), Gram Jørgensen & Køie (1944), Hansen (1976), Køie (1951, 1968), Lindquist (1931), Oberdorfer (1957, 1962), Olsen (1921, 1938), Runge (1980), and Tüxen (1956, 1960, 1962).

Fagus sylvatica - Deschampsia flexuosa community

(plot group 2, Table 40, Plate III).

Sites mainly under *Fagus sylvatica* trees - with a thin litter cover and shallow or no humus layer, that tend to dry out, and have pH 4.0-5.5 - are occupied by ground vegetation characterized by *Deschampsia flexuosa*, *Luzula pilosa* and *Carex pilulifera* (from species group 3). *Holcus mollis* and *Melampyrum pratense* prefer sites under *Quercus* trees; they are not restricted to sites with thin litter cover and transgress to sites which belong to the *Quercus petraea - Fagus sylvatica* community (see below). *Maianthemum bifolium*, *Trientalis europaea* and *Oxalis acetosella* (species group 8) are highly concentrated in the *Fagus sylvatica - Deschampsia flexuosa* community, but these species also occur on deep humus and on peat.

Species from the *Quercus petraea - Fagus sylvatica* community transgress to the *Fagus sylvatica - De-*

Fig. 49. The distribution of plots in plot group 2, plots with humus depth 0-4 cm, plots with litter depth 0-2 cm, and species from the species groups 3, 4 and 8, in the enclosure.

1. Plot group 2.
2. Humus depth (0-2 and 3-4 cm).
3. Litter depth 0-2 cm.

Species group 3:

4. *Luzula pilosa.*
5. *Holcus mollis.*
6. *Deschampsia flexuosa.*
7. *Carex pilulifera.*

Species group 4:

8. *Melampyrum pratense.*

Species group 8:

9. *Maianthemum bifolium.*
10. *Trientalis europaea.*
11. *Oxalis acetosella.*

Coverage (herbs): 1-2, 3-4, 5-10.

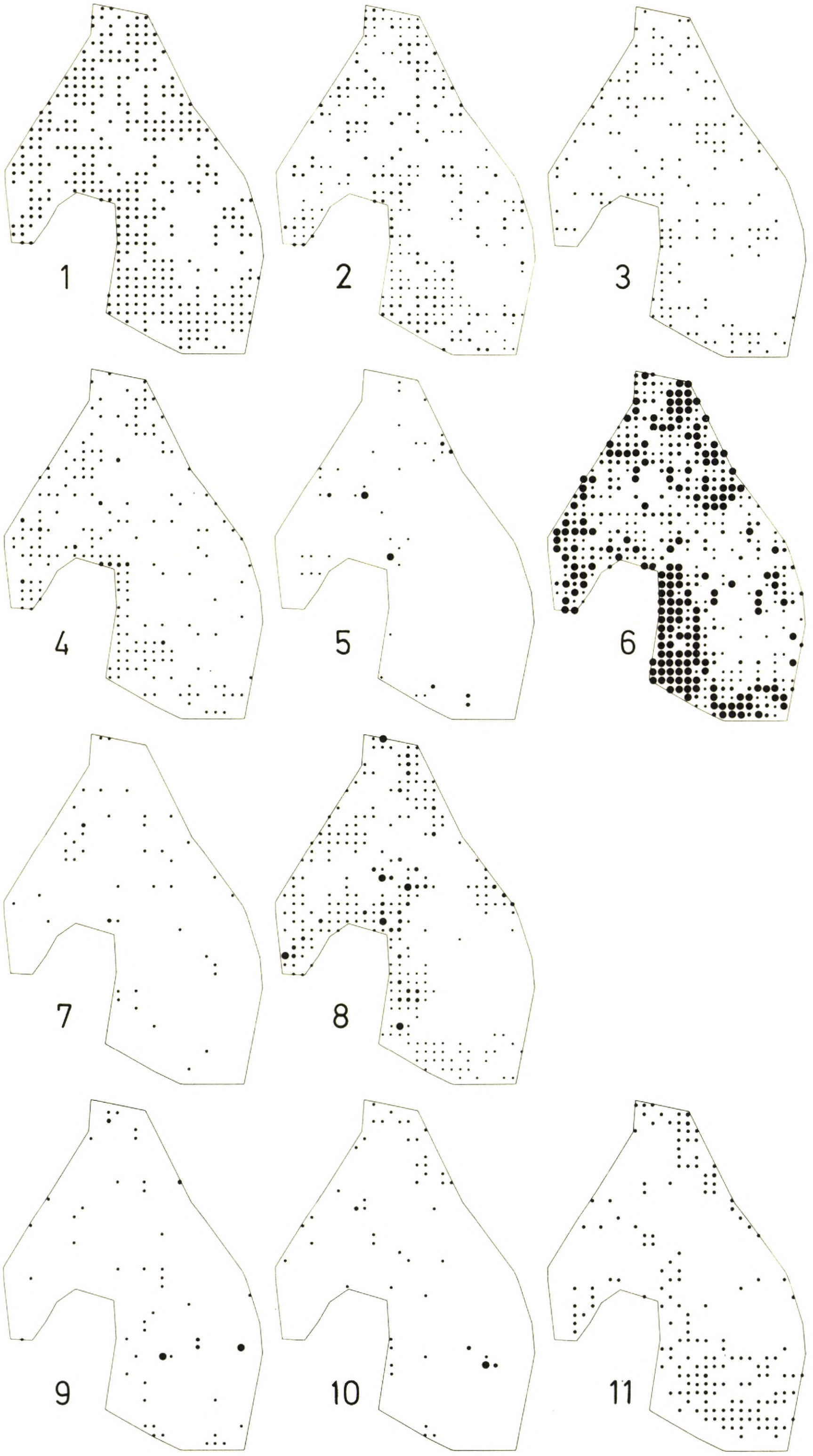


Fig. 50. The distribution of plots in plot group 3, plots without *Fagus* trees, plots with light, and species from the species groups 5 and 6, in the enclosure.

1. Plot group 3.
2. Plots without *Fagus* trees.
3. Plots with light.

Species group 5:

4. *Sorbus aucuparia,* trees <4 m (frequencies 1-2, 3-5).
5. *Pteridium aquilinum.*

Species group 6:

6. *Quercus petraea,* trees <4 m (fr. 1-4, 5-9, >9).
7. *Fagus sylvatica,* trees <4 m (fr. 1-4, 5-9, >9).
8. *Vaccinium myrtillus.* Coverage (herbs): 1-2, 3-4, 5-10.

schampsia flexuosa community. *Fagus sylvatica* saplings, *Pteridium aquilinum* and *Vaccinium myrtillus* are most important here.

The ground vegetation of the *Fagus sylvatica* - *Deschampsia flexuosa* community is somewhat bound to shaded sites with one species, *Oxalis acetosella,* prefering shaded sites.

Most of the species of the *Fagus sylvatica* - *Deschampsia flexuosa* community are widespread in *Fagus* forests on moderately acid podzolized soils (*Luzulo* - *Fagion*). Few of them are, however, restricted to such associations, and the majority of the species transgress to other forest communities on acid soils (*Quercion roboris* - *petraeae*) and heaths (*Nardo* - *Callunetea*). The community seems closely related to the *Melampyro* - *Fagetum* in Oberdorfer (1957) and the *Trientalis* - *Fagetum* in Tüxen (1960).

A few species are characteristic of brown earths

Fig. 51. The distribution of plots in the plot groups 1 and 4-7, plots with humus depth 10-29 cm, peat and wet sites, plots from plot group 8, and species from the species groups 7 and 9, in the enclosure.

1. Plot groups 1, 4, 5, 6 and 7.
2. Humus depth 10-29 cm (1), peat (2), and wet sites (3).
3. Plot group 8.

Species group 7:

4. *Ilex aquifolium,* trees <4 m (frequencies 1-4, 5-9, >9).

Species group 9:

5. *Molinia caerulea.*
6. *Dryopteris carthusiana.* Coverage (herbs): 1-2, 3-4, 5-10.

in *Fagus* forest (*Lapsana communis*, *Gymnocarpium dryopteris*) or *Quercus* forest (*Holcus mollis*, *Viola riviniana*). *Holcus mollis* occurs in Eldrup Forest mainly on sites with shallow or no humus layer; the species prefers moist sites with moderate litter cover and high pH, under *Quercus* trees. *Gymnocarpium*, *Lapsana* and *Viola* occur on sites with moderate litter cover and shallow humus, near *Quercus* trees (on brown earth). The four species are probably concentrated in the *Fagus sylvatica - Deschampsia flexuosa* community because of their preference for shallow-humus sites with high pH.

Quercus petraea - Fagus sylvatica community

(plot group 3, Table 41, Plate V)

Moist sites under *Quercus* trees with deep litter cover, moderately deep humus, pH 4.0-5.0, and some light, are occupied by a ground community which is characterized by saplings of *Fagus sylvatica* and *Quercus petraea*, and by *Pteridium aquilinum* and *Vaccinium myrtillus*. The *Fagus* saplings are very frequent, whereas the *Quercus* saplings are restricted to sites with light. The community thus will tend to develop into *Fagus* forest in the future and few *Quercus* saplings are likely to survive, as they require full illumination for a vigorous height growth. Species from the *Fagus sylvatica - Deschampsia flexuosa* community such as *Deschampsia flexuosa*, *Luzula pilosa Holcus mollis*, and *Melampyrum pratense* transgress to this community, and species from species groups 7, 8 and 9 occur rarely.

Species characteristic of the *Quercus petraea - Fagus sylvatica* community are widespread in *Quercus* forests on acid soils (*Quercion roboris - petraea*), and some are common in *Fagus* forests (*Luzulo - Fagion*) or other plant communities. *Vaccinium myrtillus* is characteristic of copses of *Quercus petraea* and *Quercus robur* on acid humus in central and western Jutland

TABLE 40. *Fagus sylvatica–Deschampsia flexuosa* community.

	Characteristic species
	Lapsana communis (2)
	Viola riviniana (2)
	Calluna vulgaris (2)
	Galium saxatile (2)
	Betula pendula (2)
	Sorbus intermedia (2)
	Calamagrostis arundinacea (3)
+ +	*Luzula pilosa* (3)
+	*Holcus mollis* (3)
+ + +	*Deschampsia flexuosa* (3)
+	*Carex pilulifera* (3)
	Gymnocarpium dryopteris (4)
+ +	*Melampyrum pratense* (4)
	Species from *Quercus petraea–Fagus sylvatica* comunity
	Anemone nemorosa (5)
	Sorbus aucuparia (5)
+	*Pteridium aquilinum* (5)
	Quercus petraea (6)
+ +	*Fagus sylvatica* (6)
+	*Vaccinium myrtillus* (6)
	Transgress to *Quercus petraea–Molinia caerulea* community
+	*Maianthemum bifolium*
+	*Trientalis europaea*
+ +	*Oxalis acetosella*
	Species from other communities
	Ilex aquifolium (7)
	Molinia caerulea (9)
	Dryopteris carthusiana (9)

+: C6–19%; + +: C20–49%; + + +: C>49% (Table 34).

TABLE 41. *Quercus petraea–Fagus sylvatica* community.

	Characteristic species
	Anemone nemorosa (5)
	Stellaria holostea (5)
	Sorbus aucuparia (5)
+ + +	*Pteridium aquilinum* (5)
+ +	*Quercus petraea* (6)
+ + +	*Fagus sylvatica* (6)
+ +	*Vaccinium myrtillus* (6)
	Species from *Fagus sylvatica–Deschampsia flexuosa* community
	Calamagrostis arundinacea (3)
+	*Luzula pilosa* (3)
	Holcus mollis (3)
+ + +	*Deschampsia flexuosa* (3)
	Carex pilulifera (3)
	Gymnocarpium dryopteris (4)
+ +	*Melampyrum pratense* (4)
	Species from other communities
	Ilex aquifolium (7)
+	*Maianthemum bifolium* (8)
	Trientalis europaea (8)
+	*Oxalis acetosella* (8)
	Dryopteris carthusiana (9)
	Rubus idaeus (9)
	Molinia caerulea (9)

+: C6-19%; + +: C20-49%; + + +: C>49% (Table 34).

(Bornebusch 1923-25, Olsen 1938). These copses are strongly influenced by culture (Vaupell 1863, Olsen 1938, Worsøe 1980), and *Fagus sylvatica* is scarce (Oppermann 1932, Ødum 1968). Otherwize, the *Quercus petraea - Fagus sylvatica* community in Eldrup Forest resembles the *Quercus* copses on acid humus (*Fageto - Quercetum petraeae*, in Tüxen 1956), whereas species characteristic of the somewhat richer *Quercus* copses on brown earth (*Viola - Quercetum* Tüxen 1956) are scarce in Eldrup Forest (*Holcus mollis*, *Viola riviniana*, *Galium saxatile*, *Anemone nemorosa*, *Stellaria holostea*).

Quercus petraea - Molinia caerulea - Dryopteris carthusiana community

(plot group 5, Table 42, Plates VI and VIII)

Sites near *Quercus* trees on deep humus, peat and wet ground with moderate litter cover, high water content, and pH below 4.0 are characterized by *Molinia caerulea* and *Dryopteris carthusiana* (from species group 9). *Rubus idaeus*, *Deschampsia caespitosa* and *Carex curta* also have high scores in this community. *Maianthemum bifolium*, *Trientalis europaea* and *Oxalis acetosella* (species group 8) from the *Fagus sylvatica - Deschampsia flexuosa* community, and *Vaccinium myrtillus* from the *Quercus petraea - Fagus sylvatica* community are frequent. The peat sites have been drained artificially by ditches.

Species characteristic of the *Quercus petraea - Molinia caerulea - Dryopteris carthusiana* community are widespread in various plant communities on wet ground (*Alnion*, *Molinion*, *Caricion canescentis*). *Molinia caerulea* and *Dryopteris carthusiana* transgress to acid wet sites of the *Quercion roboris - petraeae* (*Querco - Betuletum molinietosum*) and are frequent on such sites in the *Quercus* copses of western Jutland (Gram, Jørgensen & Køie 1944). *Carex curta* is characteristic of acid wetlands (*Caricion canescentis*), whereas *Deschampsia caespitosa* often occurs on somewhat better sites (*Alno - Padion*, *Carpinion*). *Rubus idaeus* is particularly frequent in plant communities in forest clearings (*Epilobietalia angustifolii*), and its presence on peat in Eldrup Forest is presumably due to artificial drainage (p. 24).

Vaccinium myrtillus, *Maianthemum bifolium*, *Trientalis europaea* and *Oxalis acetosella* are particularly widespread in *Picea abies* forests on deep acid humus (*Vaccinio - Piceetalia*), but they also occur on acid humus in other forest communities (*Luzulo - Fagion* and *Quercion roboris - petraeae*). Their frequent occurrence in the *Quercus petraea - Molinia caerulea - Dryopteris carthusiana* community on peat in Eldrup Forest has probably been favoured by artificial drainage.

TABLE 42. *Quercus petraea–Molinia caerulea–Dryopteris carthusiana* community.

	Characteristic species
+ +	*Dryopteris carthusiana* (9)
+	*Rubus idaeus* (9)
+	*Deschampsia caespitosa* (9)
+ + +	*Molinia caerulea* (9)
	Species fom *Fagus sylvatica–Deschampsia flexuosa* commity
+	*Deschampsia flexuosa* (3)
+	*Melampyrum pratense* (4)
+	*Maianthemum bifolium* (8)
+	*Trientalis europaea* (8)
+ +	*Oxalis acetosella* (8)
	Species from *Quercus petraea–Fagus sylvatica* community
+	*Quercus petraea* (6)
+	*Fagus sylvatica* (6)
+ +	*Vaccinium myrtillus* (6)

+: C6-19%; + +: C20-49%; + + +: C>49% (Table 34).

Fagus sylvatica community

Fagus forest without ground vegetation (plot group 8) occurs particularly on sites with a deep litter cover and a moderate or a deep humus layer, and in shade. Bornebush (1923-25) and Lindquist (1931) found mature *Fagus* forest without ground vegetation on similar sites, and rarely on brown earths.

Other plant communities

Plots dominated by *Ilex aquifolium* (plot group 4) occur mainly under *Fagus sylvatica* in Eldrup Forest. The species is particularly characteristic of *Fagus* forest on acid soil (*Luzulo - Fagion*), but it spreads to other plant communities on a great variety of soils on the European continent and the British Isles (Peterken & Lloyd 1967). The species is associated with *Deschampsia flexuosa* and *Vaccinium myrtillus* in particular in Eldrup Forest; it occurs occasionally in the *Fagus sylvatica - Deschampsia flexuosa* and *Quercus petraea - Fagus sylvatica* communities

Milium effusum (plot group 1) is associated with *Fagus* forest on neutral or slightly acid brown earths (*Eu - Fagion*). The species is scarce in Eldrup Forest.

Glyceria fluitans (plot group 7) is characteristic of eurotrophic reed communities (*Sparganio - Glycerion*). The species occurs in a wet hollow in Eldrup Forest, which may dry out in the summer.

Conclusion

The principal plant communities in Eldrup Forest are thus related mainly to *Fagus sylvatica* or *Quercus* forest communities on acid soils (*Luzulo - Fagion* and *Quercion roboris - petraeae*) and to communities on acid wetlands. The *Fagus sylvatica - Deschampsia flexuosa* community is stable, but the *Quercus petraea - Fagus sylvatica* community is emphemeral and will develop into *Fagus* forest, problaby mixed with some *Quercus petraea*. The *Quercus petraea - Molinia caerulea - Dryopteris carthusiana* community is stable, but trees may become scarcer in the future because of missing rejuvenation. The composition of this community is somewhat influenced by artificial drainage. Species from acid brown earths (*Eu - Fagion*, *Viola - Quercetum*) and richer wetlands (*Alno - Padion*, *Sparganio - Glycerion*) are scarce. They are probably relics from a time before podzolization and acidification of the soils became pronounced.

The vegetation and the soils of Eldrup Forest in the past

The purpose with this study of vegetational history and soil development in the research area in Eldrup Forest is to elucidate the history of the landscape during the Holocene, and to discover how the present vegetation and soils originated. In this way, insight may be gained into the development of a forest ecosystem throughout 10,000 years.

SELECTION OF SITES

It has been recognized since the earliest days of pollen analysis (von Post 1916) that the pollen spectra from deposits covered by vegetation may be of mainly local origin and, hence, may record the temporal variation of plant communities in the immediate vicinity of the sampling site. Pollen analysis has thus been applied widely in studies of the local vegetational succession in peats and terrestrial soils. It was realized later that the pollen found in deposits from wet hollows situated in upland areas may in fact record former dry-land vegetation (cp. Iversen 1960). A pollen diagram from a small hollow, showing upland forest development during a major part of the Holocene, derived from the current research area in Eldrup Forest (Andersen 1973). Based on this experience, it was deduced that the vegetational history of the research area could be elucidated by further studies of other wet hollows, combined with studies of terrestrial soil sections. Preliminary results of such studies were published by Andersen (1978a, 1979a, 1983). Experience in Eldrup Forest has led to the discovery that small wet hollows are numerous in Danish woodlands. Roberts et al. (1973) and Andersen (1973) have shown that similar sites can be useful for studying the changes in vegetation caused by Man. Pollen diagrams from small hollows can thus help to localize and describe in detail human activities of the past.

If a wet hollow in a woodland is sufficiently small, the crowns of the trees growing along its margins will extend across the hollow. In that case, pollen transported in the trunk space of the trees predominates in the deposit. Such pollen is likely to derive from trees growing up to 20-30m away (Andersen 1970, Raynor et al. 1975). If the site, furthermore, is situated in an upland area, and if its banks are sufficiently steep, there will be no space for wetland trees, and the upland tree community will be recorded directly. The small peatbogs and oxbows examined by Janssen (1960) and van Leeuwarden (1982) had local wetland tree vegetation or were situated in lowland areas; lowland tree communities, therefore, dominated the pollen assemblages in these cases. In the case, that a hollow is so large that the canopy is disrupted, air masses moving above the tree canopy will have access to the site and can deposit pollen there. The pollen content of such air masses differs from that of the trunk space and derives from a wide area (Tauber 1977).

In view of these considerations, three wet hollows, which were less than 20m in smallest diameter, were selected within the research area in Eldrup Forest for studies of its vegetational history, whereas the somewhat larger hollow in the southeastern part (80x40m) was not studied in detail. In addition, seven soil sections occurring in varying situations were studied (Fig. 8).

In order to obtain a pollen diagram which shows regional vegetational development, sections from the ajacent Elsborg Bog were investigated.

FIELD METHODS

Samples for analysis of micro- and macrofossils and radiocarbon dating were secured from excavated sections, when possible, and otherwize with a piston sampler, 5cm in diameter. The samples for macrofossil analysis and radiocarbon dating were stored in a freezer. Sediment diagnoses are in accordance with Troels-Smith (1955). Sections within the enclosure are indicated by the nearest main point of the coordinate system, and the distances in meters from that point.

LABORATORY METHODS

Microfossil analysis

All samples used for microfossil analysis were boiled 6 minutes in KOH, boiled (10 minutes) or soaked (24 hours) in HF, boiled (1 minute) in acetolysis mixture, dehydrated with ethanol, and transferred to silicone oil via benzene. Residual benzene was evaporated at 50°C for 1-2 days (Andersen 1978b). Pollen and spore analysis was performed with a Leitz Ortholux microscope with phase contrast equipment. Fragments of fungal hyphae were drawn by means of a Leitz drawing apparatus and measured with a ruler (Andersen 1984).

Macrofossil analysis

Moist samples were soaked in diluted HNO_3, washed on sieves 2.0 and 0.5mm in mesh size, and sorted. The number of macrofossils was calculated per unit sample volume.

Geochemical analysis

The samples from peat and gyttja were ignited at 1000°C, and the loss on ignition calculated as percent of the original dry weight. Geochemical analysis of the soil samples was described on p. 12.

Radiocarbon dating

Moist samples of peat or wood were soaked in water, and rootlets and live fungal mycelium were removed. The amount removed was weighed and calculated in percentage of the weight of the dried sample. The samples were dated at the C-14 Dating Laboratory of The Geological Survey of Denmark and The National Museum. There, before dating, all samples were boiled in ln HCL, and then in distilled water. Wood samples were boiled repeatedly in ln HCL, and in ln NaOH until soluble substances had been removed, and then in distilled water. The dating technique is described by Tauber (1960); some of the specifications, however, were changed slightly before dating of these samples, (H. Tauber, personal communication). The content of ^{13}C was determined with a mass-spectrometer at the Geophycical Isotope Laboratory of the University of Copenhagen on samples with K-numbers higher than 2419. ^{13}C is given as deviations from the international PDB-standard. These dates were normalized to a ^{13}C-deviation at -25°/oo. All other dates are uncorrected. Ages are given as conventional radiocarbon years before 1950 (half life 5720 years) or as calendar years, calibrated according to Clark (1975). The standard deviations include statistical uncertainties of sample counting, background counting, and modern sample counting.

Elsborg Bog

Elsborg Bog (Elsborg Mose) is situated in a low-lying area just south of Eldrup Forest (Figs. 7 and 9). The bog is divided into a northern and a southern part. The northern part is 900x500m and had, up to 1940, a nearly even surface with only minor peat diggings. In 1940-45 most of the peat was exploited and the original peat surface is preserved only in a small area in the north-easternmost part of the bog. The peat there is drained and is now overgrown by *Betula pubescens* and *Molinia caerulea*.

The glacigeneous substrate of the bog is very uneven with several deep kettles which were filled by clay and gyttja before the entire present bog area was overgrown by swamp vegetation.

Samples were collected at two sections in the eastern part of the preserved peat area (Fig. 7). The distance to the northern edge of the bog is 160m, and the site lies about 600m southwest of the research area.

Samples were secured 1972 and 1974 from open sections of the old peat wall, after removal of 30cm peat, and in borings with the piston sampler.

The sediments in the section from 1972 are described in Table 43. The clay-gyttja layers below 212cm were deposited in a kettle in Late Weicselian time; the clay-gyttja at 286-298.5cm is from the Allerød Chronozone. The kettle was filled by gyttja in the early Holocene and then overgrown by oligotrophic swamp vegetation which formed the peat layers.

The section from 1974 was 7.5m north of the section from 1972, and the surface of the peat there was 40cm higher than at the section from 1972. The topmost part of the section is described in Table 44. Here, the light-brown *Sphagnum* -peat found above 74cm in section 1972 was absent. The surface of the reddish-brown peat was thus about lm higher at section 1974 than at section 1972. A gradual rise in the surface was observed at the peat wall between the two sections. The sediments at section 1974

TABLE 43. Elsborg Bog, section 1972.

A.	0– 7 cm	Brown, humified *Spagnum* peat, brittle (strf 0, lim inf 2, Tb (Sphag)^3 4). Many modern rootlets and fungal hyphae.
B.	7– 74 cm	Light-brown, weakly humified *Sphagnum* peat; a few tufts of *Eriophorum vaginatum* (strf 0–1, lim inf 2, Tb (Sphag)^2 4). A few modern rootles.
C.	74–146 cm	Reddish-brown, humified peat (strf 2, lim inf 2, Th^3 4). Horizontal wood with bark of *Alnus* sp. at 103–105 cm; horizontal wood of *Populus* sp. at 109–114 cm; a horizontal trunk of *Quercus* sp. at 88–120 cm. A sand layer at 90 cm.
D.	146–164 cm	Reddish-brown humified telmatic peat (root mat); tufts of *Eriophorum vaginatum* (strf 3, lim inf 3, Th^3 4).
E.	164–176 cm	Yellow-brown telmatic peat (root mat); leaves of *Vaccinium oxycoccus*, tufts of *Eriophorum vaginatum* (strf 2–3, lim inf 2, Th^2 4). The lower limit was found at 181 cm in the cored section.
F.	176–212 cm	Greyish-brown gyttja, with a slight content of rootlets (strf 2, lim inf 2, Th^2 1, Ld^2 3).
G.	212–217 cm	Brownish-grey gyttja, with a slight content of rootlets (strf 2, lim inf 2, Th^2 0–1, Dg 1, Ld^2 2, Ag+As 1).
H.	217–233 cm	Brownish-grey clay-gyttja (strf 2, lim inf 1, Ld^1 2, Ag+As 2).
J.	233–286 cm	Yellow-grey clay with gyttja (strf 1, lim inf 2, Ld^1 0–1, Ag+As 4).
K.	286–298.5 cm	Greyish-brown-olive coloured clay-gyttja (strf 2, lim inf 2, Ld^1 3, Ag+As 1).
L.	298.5–337 cm	Bluish-grey clay (strf 0, lim inf 3, Ag+As 4).
M.	337–(340) cm	Grey sand (strf 0, Ga+Gs 4).

TABLE 44. Elsborg Bog, section 1974.

A.	0– 3 cm	Brown humified *Sphagnum* peat, brittle (strf 0, lim inf 2, Tb (Sphag)^2 4). Many modern rootlets.
B.	3–66 cm	Reddish-brown humified peat (strf 2, lim inf 2, Th^3 4). Many modern rootlets above, and a few below 38 cm.

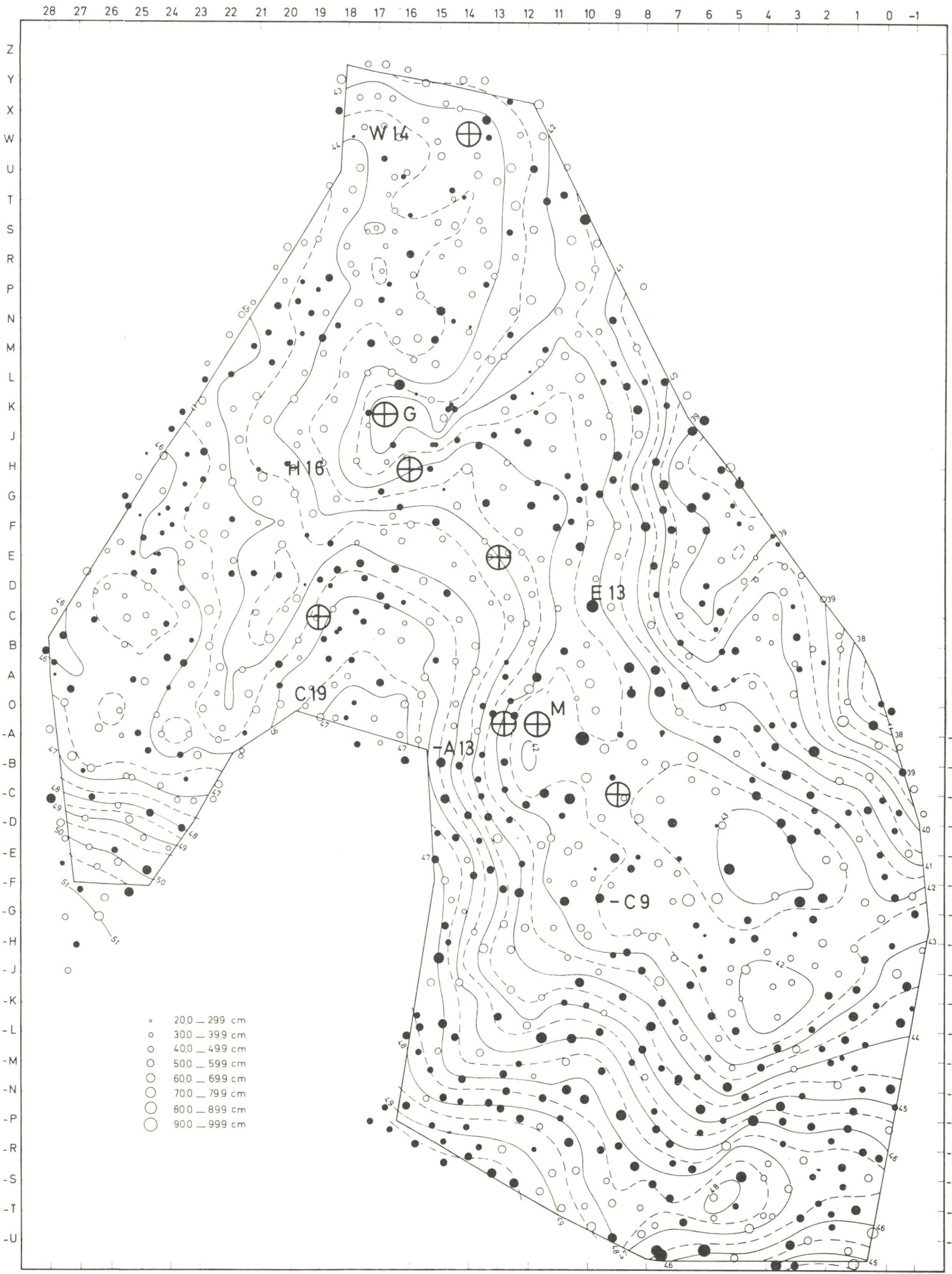


Fig. 52. The enclosure with the peat and soil sections studied by pollen analysis. G, *Glyceria* hollow; M, *Molinia* hollow.

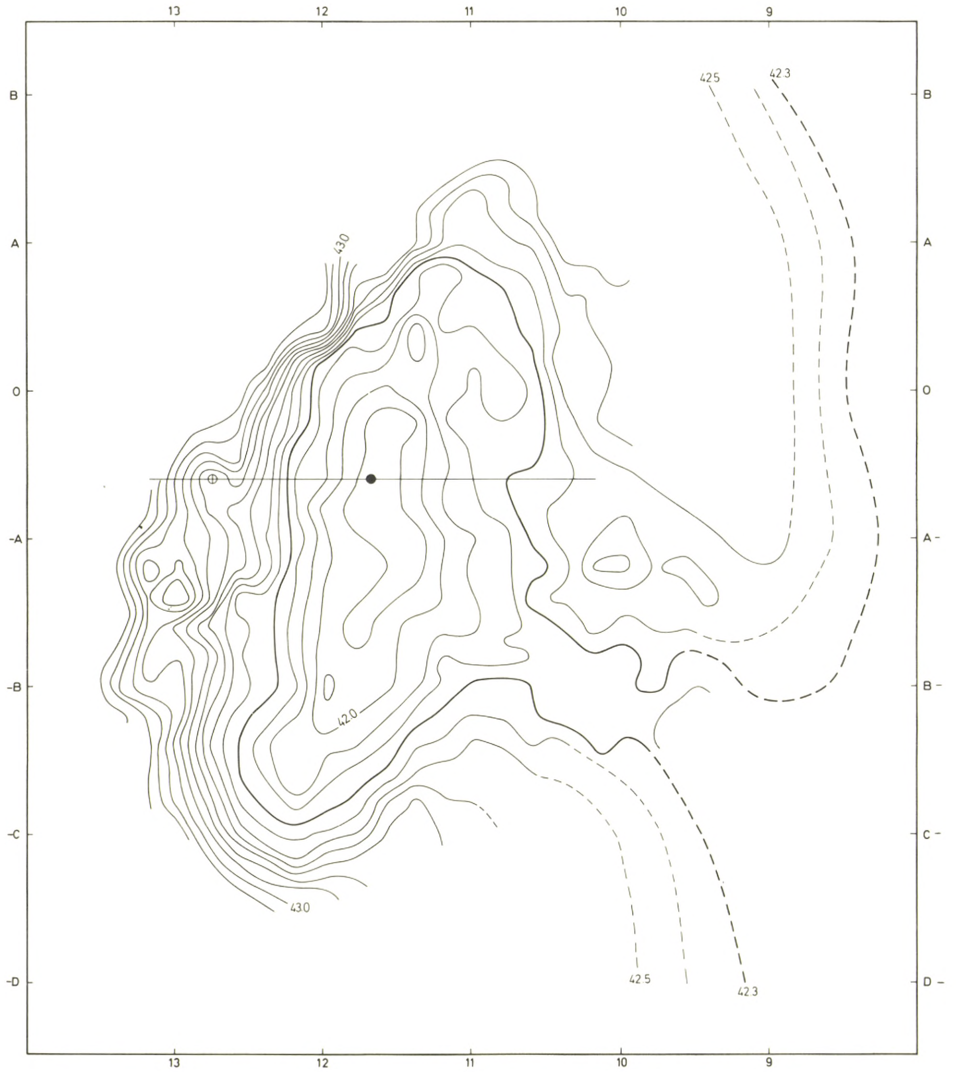


Fig. 53. *Molinia* hollow. Surface contours at 10 cm intervals. Altitudes in meters. The horizontal line indicates the transect in Fig. 54. ●, section -A 12, N4, W3; ⊗, soil section -A 13, N4, E2.

were otherwize similar to section 1972. The surface of the Holocene gyttja was 84cm deeper, and the surface of the Late-Weichselian clay 95cm deeper than at section 1972. The peat layers at section 1974 are thus considerably deeper than at section 1972.

Wet hollows in the research area in Eldrup Forest

Three wet hollows in the research area were examined; one in the southeastern part of the enclosure (*Molinia* hollow, Fig. 52), one in the central part (*Glyceria* hollow, Fig. 52), and one at the northwest corner of the research area (Matrikel hollow, Mah, Fig. 8). The two former were named for their predominant vegetation; the latter, because of its nearness to the earth bank which marks the limit between the Eldrup Farm and the Løvenholm properties.

Molinia hollow

The *Molinia* hollow is an oblong depression situated

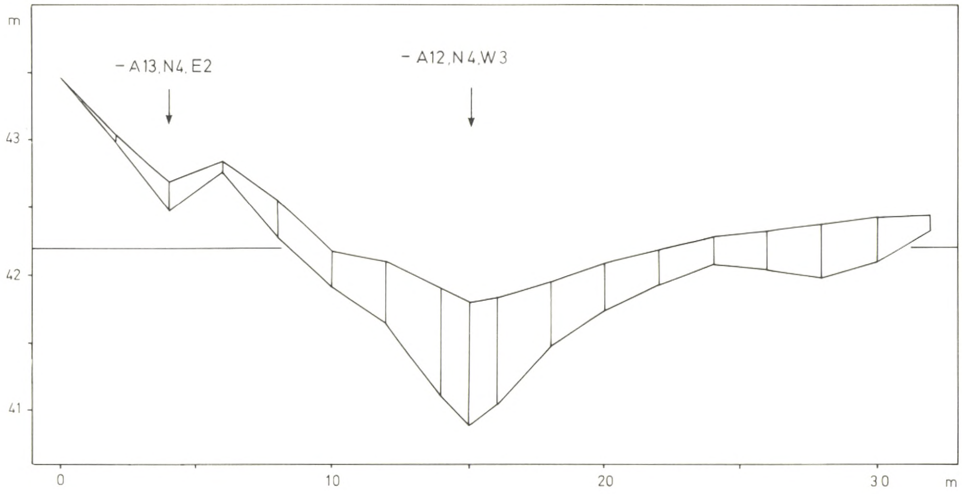


Fig. 54. *Molinia* hollow. Transect at -A, N4, indicating the surface of the mineral soil and the present surface. The horizontal line indicates the highest level of the mineral surface at the outlet (at 42.2 m altitude).

TABLE 45. Eldrup Forest, *Molinia* hollow, section –A 12, N4, E3.

A.	0– 3 cm	Light-brown, brittle humus with leaf fragments (strf 0, lim inf 2, Sh 4).
B.	3– 32 cm	Reddish-brown humified peat (strf 0, lim inf 1, Th^3 4, Ga 0–1). Seeds of *Rubus idaeus* (1), *Rumex acetosella* (1), *Ranunculus flammula* (25), *Carex rostrata* (7), *C. caespitosa* (9) at 26–28 cm. At 6–7 cm a dark-coloured horizon with sand lenses.
C.	32– 53 cm	Yellow-brown, slightly sandy gyttja (strf 0, lim inf 1, Ld^3 4, Ga 0–1).
D.	53– 63 cm	Brown, slightly sandy gyttja (strf 0, lim inf 2, Ld^3 3, Ga 1). Seeds of *Alnus* sp. (1) and *Rubus idaeus* (1) at 53–63 cm. Wood of *Quercus* sp. 57–60 cm.
E.	63– 72 cm	Greyish-brown, sandy gyttja (strf 0, lim inf 0, Ld^2 2, Ga 2).
F.	72– 92 cm	Greyish-brown sand with slight gyttja content (strf 0, lim inf 1, Ld^2 1), Ga 3).
G.	92–150 cm	Brownish-grey sandy till.
H.	150–(500) cm	Grey sandy till.

Numbers of seeds pr. 300 ml, det. G. Jørgensen.

just east of the major eastward slope in the enclosure (Fig. 52, Plate VIII). The detailed surface topography of the hollow and its surroundings is shown in Fig. 53.

The hollow has a shallow outlet towards southeast, at between 42.2 and 42.3m altitude (Fig. 53). Before the deposition of humus there, the outlet was at between 42.1 and 42.2m altitude. The outlet was traversed by a ditch in the middle of the 19th century (p. 24). The hollow is bordered to the west by the steep eastward slope. To the southeast, deep humus layers occur between the hollow and the large peat area (Fig. 16). The diameters of the hollow are 40m in north-south and 16m at the broadest point. The trees growing around the hollow nearly cover it with their crowns, leaving only a small disruption of the canopy. *Fagus sylvatica* predominates and only a few *Quercus petraea* occur (Figs. 52 and 55). *Molinia caerulea*, *Carex curta* and *Pteridium aquilifolium* occur on the peat.

The bottom of the hollow is rather irregular. The deepest point is at 40.9m altitude. The maximum water depth thus was originally 1.2m.

A cross section of the hollow at its deepest point is shown in Fig. 54. Samples were collected in a vertical column at the deepest point (-A 12, N4, E3). A soil section in a shallow depression on the slope west of the hollow was also sampled (-A 13, N4, E2, Fig. 54).

The section -A 12, N4, E3 was studied in an excavation. The sediments are described in Table 45. The substrate is brown and grey sandy till. The lowermost sandy gyttja is 60cm, and the peat 32cm deep. Due to the artificial ditch, the peat was drained. Rootlets of *Molinia caerulea* now penetrate the deposits.

Glyceria hollow

The *Glyceria* hollow occupies a depression in the erosional gully, which crosses the northwestern part of the enclosure (p. 13, Fig. 52, Plate VIII). In the winter, the hollow contains a pond which dried out during the dry summers of the mid-1970's but was permanent throughout the year in the wet early 1980's. There is no artificial outlet. The natural outlet is near 42m altitude, and the maximum dimensions of the water-covered area are 20x20m. The surface of the deposits is at 41.4m altitude. The present maximum water depth is thus 0.5m. The hollow is covered by tree crowns except for a small opening in the canopy. *Fagus sylvatica* and *Quercus petraea* trees occur around the hollow (Fig. 52) and *Glyceria fluitans* grows in the pool but flowers rarely, due to shade.

The hollow was used intensively by red deer for wallowing up to 1969. During this process, the males trample round in the pool, urinate, lie down on their backs and wallow vigorously (E. Due, personal communication).

A core was extracted from the central part of the hollow, (K 17, S2, E2, Table 46). Sandy till occurred below 460cm and silts and clays below 103.5cm. Disturbed gyttja occurred in the clays and silts at 175cm. In a core 3m to the east (K 16, N0, W5), similar gyttja occurred at 115-132.5cm beneath the surface. A gyttja layer was apparently ground into the deposit, which contains pebbles and thus bears evidence of solifluction. Holocene gyttja occupies the topmost 103cm of the deposit. Fresh leaves of *Fagus sylvatica* in the uppermost part indicate the activity of the red deer.

Matrikel hollow

This hollow is situated at the northwest corner of the research area (Mah, Fig. 8). Shallow peat and gyttja (Table 47) occupy a small depression 18x8m

TABLE 46. Eldrup Forest, *Glyceria* hollow, section K 17, S2, E2.

A.	0– 45 cm	Brown gyttja (strf 0, lim inf 0, Ld^3 4). Fresh withered leaves of *Fagus sylvatica* present.
B.	45– 71 cm	Brown silty gyttja (strf 0, lim inf 0, Ld^3 3, Ag 1).
C.	71– 83 cm	Yellowish-brown, silty gyttja (strf 0, lim inf 0, Ld^2 3, Ag 1).
D.	83– 95 cm	Blackish-brown, silty gyttja (strf 0, lim inf 1, Ld^2 3), Ag 1).
E.	95–103.5 cm	Brownish-grey, sandy gyttja (strf 0, lim inf 2, Ld^2 2, Ag 1, Ga 1).
F.	103.5–200 cm	Grey, sandy silt, with a few pebbles (strf 0, lim inf 0, Ag 2, Ga 2, Gg (maj 0–1). A disturbed gyttja layer at 175 cm.
G.	200–300 cm	Grey, silty sand (strf 0, lim inf 0, Ag 1, Ga 3).
H.	300–460 cm	Grey, silty sand (strf 0, lim inf 0, Ag 0–1, Ga 4).
G.	460– cm	Grey, sandy till.

TABLE 47. Eldrup Forest, Matrikel hollow, Mah.

A.	0–23 cm	Brown peat (strf 0, lim inf 1, Th^4 4, Ga 0–1).
B.	23–34 cm	Greyish-brown, sandy gyttja (strf 0, lim inf 1, Ld^2 2, Ga 2).
C.	34– cm	Yellow-grey, silty sand with a few pebbles (strf 0, Ag 1, Ga 3, Gg (maj) 0–1).

TABLE 48. Eldrup Forest, soil sections. Matrikel bank (Ma) and –A 13, N4, E2.

		Ma
	60– 0 cm	Made ground (sandy till)
A_0	0–14 cm	Blackish-brown humus
A_0	14–20 cm	Blackish-grey sandy humus
A_1	20–32 cm	Blackish-grey sandy till
A_2	32–37 cm	Grey sandy till
B	37– cm	Rust-coloured sandy till
		–A 13, N4, E2
A_0	0– 7 cm	Light-brown humus
A_0	7–23 cm	Blackish-brown humus
A_{1+2}	23–25 cm	Grey sand
B	25–35 cm	Blackish-grey sand
B	35–50 cm	Greenish-grey sand with humus spots
B	50–70 cm	Greenish-grey sand with rust spots
C	70– cm	Yellowish-grey sand

large. Samples were secured from an excavation in the centre of the hollow. A plantation of *Picea abies* occurs to the west. Three *Fagus sylvatica* and eight *Quercus petraea* trees occur within 30m north, east and south of the hollow. *Molinia caerulea* covers the peat; its rootlets penetrate the peat and the gyttja.

Terrestrial soil sections in the research area in Eldrup Forest

Seven terrestrial soil sections were studied (Fig. 8). Five sections are described in Tables 2-3 (H 16, C 19, -C 9, E 13 and W 14), the other sections in Table 48. The samples were secured by excavation. The sampling was somewhat difficult due to *Fagus* roots and channels dug by mice; it was therefore not possible to take volumetric samples (cp. Aaby 1983).

Sections H 16, C 19, and -C 9 are podzols on sandy till, E 13 is podzol on sorted sand, and W 14 brown earth on sandy till. The results from section W 14 are not reported here, because the pollen spectra were strongly modified (see Andersen 1979a).

Section Ma (Matrikel bank) was excavated beneath the earth wall which delimits the research area to the north (Fig. 8, Plate IX) and marks the border between the Eldrup Farm and Løvenholm properties. The site is located 7m to the north of the section from the Matrikel hollow. The earth wall is located 30m south of the remains of a stone wall which delimited the Løvenholm fields from Eldrup Forest on a map of the Løvenholm Estate from 1788 (found at Løvenholm Castle). The present property boundary is indicated on a surveyor's map of Eldrup Farm from 1814 (at Matrikeldirektoratet), and the earth bank was probably erected some time later. The humus layer beneath the earth bank thus formed before the middle of the 19th century. The section is a podzol on sandy till (Table 48).

At section -A 13, N4, E2, only a thin bleached layer occurred beneath the humus (Table 48). The sand below had a very high aluminium content (3%) and ferrous iron was dominant. The surface of the sand was near the former ground water level (Fig. 54). The section is thus podzol-gley on sorted sand.

POLLEN ANALYSIS

Identifications of pollen and Pteridophyte spores

Identifications were based on comparison with the reference collection rather than on published keys and illustrations. The nomenclature follows *Flora Europaea* (1964-1980).

The identifications of pollen from Cyperaceae are in accordance with Fægri & Iversen (1975). *Scirpus lacustris* -type thus includes *S.lacustris* and *Eleocharis palustris*. The identifications of Poaceae pollen were discussed in Andersen (1979b). Poaceae pollen with annulus diameters smaller than 8μm were considered wild-grass pollen. Among pollen with larger annulus diameters, the following taxa were identified: *Glyceria fluitans* -type (including *G. fluitans* and *G. plicata*), *Hordeum* -type (including *Hordeum vulgare* and *Elymus repens*), *Secale cereale*, *Avena sativa* and *Triticum* sp. A majority of the pollen grains referred to *Glyceria* belong to that genus; some of them, however, may belong to other wild grasses.

Groupings of taxa

The taxa identified were divided into the following categories: trees, vines and epiphytes, shrubs, Ericales, and herbaceous plants. The herbaceous plants were divided into the following groups: open ground, forest brown earth, acid humus, uncertain, wet ground, and aquatics. The taxa included in the various categories are shown in Table 49, where the notations follow the principles advocated by Birks (1973). These notations are somewhat simplified on the pollen diagrams.

TABLE 49. Categories of taxa identified by pollen and spores. Conventions according to Birks (1973), nomenclature for genera and species after *Flora Europaea* (1964–80).

- Trees
  - *Acer*
  - *Alnus glutinosa*
  - *Betula*
  - *Populus tremula*
  - *Carpinus betulus*
  - *Corylus avellana*
  - *Fagus sylvatica*
  - *Fraxinus exelsior*
  - *Picea abies*
  - *Pinus sylvestris*
  - *Populus tremula*
  - *Quercus*
  - *Tillia cordata*
  - *Tilia plathyphyllos*
  - *Ulmus*

- Vines or epiphytes
  - *Hedera helix*
  - *Lonicera periclymenum*
  - *Viscum album*

- Shrubs
  - *Crataegus*
  - *Frangula alnus*
  - *Hippophaë rhamnoides*
  - *Ilex aquifolium*
  - *Juniperus communis*
  - *Myrica gale*
  - *Prunus*
  - *Salix*
  - *Sambucus*
  - *Sorbus aucuparia*
  - *Taxus baccata*
  - *Viburnum opulus*

- Ericales
  - *Calluna vulgaris*
  - *Empetrum nigrum*
  - *Vaccinium*-type

- Herbaceous plants: Open ground
  - *Ambrosia*
  - *Armeria maritima*
  - *Artemisia*
  - *Botrychium*
  - *Campanula*
  - *Centaurea cyanus*
  - *Centaurea* undiff.
  - Chenopodiaceae
  - *Dianthus*
  - *Dryas octopetala*
  - *Helianthemum*
  - *Hypericum*
  - *Jasione montana*
  - *Plantago lanceolata*
  - *Plantago major*
  - *Plantago maritima*
  - *Plantago media*
  - *Polygonum aviculare*
  - *Polygonum persicaria*-type
  - *Rumex acetosella*-type
  - *Rumex acetosa*
  - *Sagina* cf. *S. procumbens*
  - *Saussurea alpina*
  - *Saxifraga oppositifolia*
  - *Scleranthus annuus*
  - *Scleranthus perennis*
  - *Sedum*
  - *Spergula arvensis*
  - *Trifolium* cf. *T. medium*
  - *Trifolium* cf. *T. pratense*
  - *Trifolium* cf. *T. repens*

- Cultivated
  - *Avena sativa*
  - *Fagopyrum*
  - *Hordeum*-type
  - *Secale cereale*
  - *Triticum*

- Forest, brown earth
  - *Anemone*
  - *Mercurialis perennis*
  - *Stellaria holostea*

- Acid humus
  - *Gymnocarpium dryopteris*
  - *Lycopodium alpinum*-type
  - *Lycopodium annotium*
  - *Lycopodium clavatum*
  - *Melampyrum*
  - *Oxalis acetosella*
  - *Polypodium vulgare*
  - *Pteridium aquilinum*

- Uncertain
  - *Achillea*-type
  - *Allium*
  - Apiaceae undiff.
  - *Arctium* cf. *A. tomentosum*
  - Asteraceae, Liguliflorae
  - Brassicaceae
  - Caryophyllaceae undiff.
  - *Cerastium*-type
  - *Cirsium*-type
  - *Epilobium angustifolium*
  - *Epilobium* undiff.
  - *Filipendula*
  - *Galium*-type
  - *Gentiana*
  - *Geum*
  - *Humulus*-type
  - *Knautia arvensis*
  - Lamiaceae undiff.
  - *Lathyrus*-type
  - Liliaceae undiff.
  - *Lotus*
  - *Mentha*-type
  - *Ophioglossum vulgatum*
  - *Parnassia palustris*
  - *Potentilla*
  - *Ranunculus acer*-type
  - *Rhinanthus*-type
  - *Rubus*
  - Scrophulariaceae undiff.
  - *Selaginella selaginoides*
  - *Senecio*-type
  - *Solanum dulcamara*
  - *Succissa pratensis*
  - *Thalictrum*
  - *Trollius europaeus*
  - *Urtica dioica*
  - *Valeriana*
  - *Veronica*

- Wet ground
  - *Alisma*
  - *Caltha palustris*
  - *Carex*-type
  - *Glyceria fluitans*-type
  - *Hydrocotyle vulgaris*
  - *Lysimachia*
  - *Menyanthes trifoliata*
  - *Osmunda regalis*
  - *Peplis portula*
  - *Polygonum amphibium*
  - *Scirpus lacustris*-type
  - *Sparganium*-type
  - *Sphagnum*
  - *Typha latifolia*

- Aquatics
  - *Callitriche*
  - *Pogamogeton*
  - *Hottonia palustris*
  - *Lemna*
  - *Littorella uniflora*
  - *Myriophyllum alterniflorum*
  - *Myriophyllum spicatum*
  - *Nymphaea*
  - *Ranunculus trichophyllus*-type

The divisions in Table 49 are not unambiguous in all cases. *Corylus avellana*, for example, may exhibit shrub-like characteristics. But, as the species formed a canopy at certain times, it was included with the trees in accordance with the decision of Fægri & Iversen (1975). *Sorbus aucuparia* may be considered a tree; as no correction factor was available, however, it was considered more practical to exclude it from the trees.

The groups within the herbaceous plants are broad ecological categories. "Open ground" thus includes plants which occur in vegetation with little or no tree vegetation and on well-drained ground without a humus layer. Apophytes, anthropochores and cultivated plants are included. No attempt was made to distinguish *a priori* plants related to arable farming and plants related to pastoral farming. The difficulties of such a procedure were discussed by Behre (1981).

The "forest brown earth" group includes shade-tolerant species found mainly on brown earths in forests; and the "acid humus" group includes species occurring particularly on a terrestrial acid humus layer within or outside forest. *Gymnocarpium dryopteris* was included in this group, although the species may also occur on acid brown earths.

The group "uncertain" includes taxa which comprise a range of species and species considered to be ambiguous in their requirements of the habitat (cp. Rybníčková & Rybníček 1971). These plants occur mostly in open vegetation; dry-land and wet-ground habitats may be represented, however.

The "wet ground" group includes plants which occur mainly or exclusively on soils with a high ground water table for at least part of the year. Telmatophytes and Amphiphytes, in the sense of Iversen (1936), and some Terriphytes are included.

"Aquatics" includes Limnophytes as defined by Iversen (1936). *Ranunculus trichophyllus* -type was included because this taxon comprises mainly aquatic species (Andersen 1961).

Wild grasses (Poaceae pollen with annulus diameters smaller than 8μm) and *Dryopteris* -type were assigned to various groups. Both categories are ambiguous with respect to wetness of the habitat. In the terrestrial soils, nearly all pollen and spores can be supposed to derive from plants growing on dry land. The wild grass pollen was therefore included in the open-ground group, and *Dryopteris* -type in the acid-humus group in pollen spectra from soils. The wild grasses do include species from the field layer in forests. These species flower rarely in shaded habitats, and it can therefore be assumed that most of the wild grass pollen derived from plants growing in open habitats.

In the sections from peats and gyttjas, wild grasses show affinities to open-ground herbs in some cases, and no definite affinities in other cases. *Dryoperis* -type was assigned to the wet-ground group in these sections, because the spores are believed to derive mainly from *Thelypteris palustris*.

The construction of the pollen diagrams

Ideally, the pollen diagrams should reflect changes in the abundance of plants. Due to the method of construction, the percentage diagrams should include all plants which were reciprocal - that is, plants which replaced each other on the same area in the course of succession. These goals are, however, difficult to achieve, because it is difficult to distinguish the dependant variables in the vegetation from independant variables. The pollen diagrams must therefore, by neccessity, remain compromises, which achieve their purpose with varying degrees of success.

The abundance of plants is best expressed by their areal projection on the surface, because the pollen productivity of a species can be supposed to reflect more or less directly the size of the area which it occupies. This, however, is not always the case. Plants shaded by others may thus fail to flower, or may flower with reduced intensity. In multi-layered vegetation, therefore, pollen analyses are likely to reflect mainly the uppermost vegetation surface (cp. Fægri & Iversen 1975). Furthermore, young trees that form a canopy may fail to flower.

Fægri and Iversen (1975) advocated the inclusion of all non-aquatic plants in the pollen total. Hence, plants from dry and wet habitats should be included. In pollen spectra from moderately-sized or large lakes, the land plants can be supposed to be reciprocal - that is to have competed with each other on the same land area. In the case of peat bogs, it is difficult to distinguish the dependantly variable land plants from independantly variable plants which grew on the peat surface. Distinction of "upland types" from "local types", as done by van Leeuwaarden (1982), for instance, is problematic in such cases, because of the ambiguity of many taxa.

In the present investigation, various situations exist. At Elsborg Bog, which had a large surface with few trees, regionally derived pollen (*sensu* Janssen 1973) was important; it was, however, difficult to distinguish regionally derived non-tree pollen from locally derived non-tree pollen in the peat layers. Hence, the tree pollen total (AP) was used as a calculation basis.

Neither is the calculation of pollen percentages from small wet hollows totally without problems, as conceded by Birks (1982). Difficulties in separating dry-land herbs from herbs which grew within the hollows may thus arise because of the ambiguity of many taxa. Initially, diagrams based on all pollen and spores, excluding only aquatics, were calculated. As the curve for open-ground herbaceous plants was generally low in these diagrams, it was concluded that the tree canopy was fairly dense. Hence additional diagrams based on the tree pollen sum were calculated. In this way difficulties in distinguishing dry-land plants from local plants do not affect the percentage calculations.

As nearly all pollen and spores in the soil sections can be assumed to derive from dry-land plants, a total comprising all pollen and spores was used. Iversen (1964, 1969) used a similar procedure. Besides, diagrams of tree pollen percentages are shown. Vegetation poor or lacking in trees is recorded at certain times in these sections.

Taxa not shown in the pollen diagrams are indicated in Tables 64-70.

Reconstruction of the former vegetation

A primary purpose of the present investigation was to reconstruct the past vegetation in Eldrup Forest and its changes. The degree of resolution with which past vegetation types can be reconstructed from pollen spectra varies according to the nature of the sampling site (cp. Webb *et al.* 1978, Jacobson & Bradshaw 1981, Janssen 1981).

The pollen analyses from Elsborg Bog reflect regional as well as local vegetation. Several tree communities are probably represented but cannot be distinguished, and treeless vegetation is difficult to characterize because of the difficulty of differentiating upland non-tree pollen from locally produced pollen in the peat layers. Hence, it was not considered possible to reconstruct the former vegetation at a low level of resolution.

In contrast to the sections from Elsborg Bog, the pollen spectra from the terrestrial soil sections in the research area in Eldrup Forest can be assumed to reflect single plant communities, at least at times when the sites were wooded. Pollen analyses of surface samples from Danish forests have shown that the tree pollen assemblages deposited under the tree canopy mainly reflect the tree community found within a short distance (20-30m) from the sampling site, whereas pollen and spores from field-layer plants is of even more narrowly localized origin than the tree pollen (Andersen 1970). Raynor *et. al.* (1976) thus found maximum deposition of *Ambrosia* pollen and *Dryopteris* spores released 1.4m above the ground inside a forest at 10m distance. This distance would be even smaller for sources placed nearer to the ground. Pollen diagrams from soil sections therefore reflect single upland forest communities. At times when trees were scarce or absent at a soil site, pollen transported from some distance may be present, and distinguishing between plant communities becomes more difficult. The interpretation of pollen diagrams from the mineral soils is hampered somewhat by the fact that temporally discrete pollen assemblages become mixed during their incorporation in the soil (Andersen 1979a). Pollen analysis from soils is further limited by the fact that only vegetational stages from periods with acid soil conditions are preserved.

Temporal sequences of single tree communities may also be recorded in the small wet hollows. These sites have the additional advantage that they may record long spans of time - in favourable cases, the entire Holocene - providing insight into the composition of the forest on upland sites at various points of time. As the gyttja layers were more or less sandy, tree pollen may have been transported from terrestrial soils by slope-wash. It can be assumed, however, that most of the tree pollen was transported directly through the air. Pollen and spores derived from plants that grew in the field layer of the forest must have had a small chance of dispersal to the hollows through the air, because of their short ranges and because vegetation around the hollows may have acted as filters (Birks 1982). Such pollen and spores may have been transported to the hollows by slope-wash. It may be difficult to separate plants from the forest field layer from plants that grew within a hollow, due to the ambiguity of many pollen and spore taxa.

Pollen from vegetation on treeless areas, specially from anemophilous plants, may be transported to a forest site and occur there in low percentages, which may depend somewhat on the distance from the site and the extension of the open areas.

The interpretation of the pollen spectra in terms of vegetation communities may be hampered by differential pollen representation and preservation, which are discussed in the following chapters.

Differential pollen and spore representation

Due to variations in pollen productivity and dispersial opportunity, various plants are very unequally represented in pollen spectra. Anemophilous plants thus usually have higher pollen productivity than entomophilous plants, plants exposed to winds have a better opportunity for dispersing their pollen than plants that grow at sheltered sites, and plants that grow at or near a sampling site have the best opportunity for being represented in a pollen spectrum. These problems are as old as pollen analysis itself and have been discussed widely.

For a description of former vegetation, it is not sufficient to know its floristic composition; insight into its quantitative composition is also necessary. It is therefore desirable to transform pollen frequencies to areal frequencies.

Trees

It was found (Andersen 1970) that the pollen frequencies of tree species in surface samples from forest ground (moss humus accumulated on tree stumps) were quantitatively related to the areal frequencies of the same species within 20-30m from the sampling site. It was possible in these cases to transform the pollen frequencies found in individual samples to semi-quantitative figures. It was later proved that the basis for this transformation was sound (Andersen 1974). A formula for pollen deposition of a tree species thus could be calculated,

$$p = Pxa + p_o$$

where p equals the pollen deposition of the species at a site, a is the total crown area of the species within a specified distance, p_o is that part of the pollen deposition which derived from trees of the same species occurring outside the chosen distance, and P is a factor which determines the slope of the regression line. As p could be measured as relative pollen deposition and a as the crown area of the species, for individual samples, P and p_o could be calculated using linear regression analysis. When distances equalling 20 or 30m were used, it was possible to calculate satisfactory correlations and regressions where p_o was low, indicating that nearly all the pollen deposited was derived from trees standing within the chosen distances. Among the advantages of the method were that the area of origin of the pollen could be determined and, hence, the tree areas measured exactly, and that a simple linear model could be used.

P indicates the intensity with which pollen is deposited and varies for the species examined. As pollen is transferred directly to the sampling sites from the trees (cp. Raynor et al. 1975), the differences between the P-values calculated for various species were assumed to indicate differences in pollen productivity. The pollen productivity of the various species was calculated in relation to that of a common reference species (P_{rel}), in the present cases, *Fagus sylvatica*, and the relative pollen productivity of the same species in various tree stands could be compared. Relative pollen-representation values (R_{rel}-values, cp. Davis 1963) were shown to resemble the P_{rel}-values under certain conditions. Based on this material, Andersen suggested correction factors, which were rounded figures in order to simplify the calculations. These were used to correct the pollen spectra from the moss humus with satisfactory results. Additional correction factors for tree species not represented in the Danish tree stands were based on R_{rel}-values calculated by means of published data from foreign tree stands.

Andersen (1970) showed that tree basal areas could be used as substitutes for crown areas in tree stands with a closed crown canopy. The ratios of crown areas to basal areas differed somewhat in stands with a discontinous tree canopy.

Andersen (1974) calculated similar figures for tree pollen collected in Tauber pollen traps over a period of six years. Although this sampling period was rather brief, the P_{rel}-values found by means of the traps resembled those based on moss humus samples.

Birks & Birks (1980) calculated R_{rel}-values for various trees based on pollen collections from Bialowieża Forest in Poland but, as the pollen collections were from three years only, and young non-flowering trees were frequent, these R_{rel}-values are unreliable (cp. Andersen 1980b).

Bradshaw (1981a) used methods similar to those used by Andersen (1970) for three British woodlands. He used he living parts of moss polsters, which may record rather too brief a period (perhaps five years, Bradshaw 1981a) and he relied on tree basal areas alone. Bradshaw noticed that one of the woodlands (Bradfield Woods) was coppiced and consisted of young trees. The P_{rel}-values found by Bradshaw for the two other woodlands differ somewhat from those found by Andersen (1970).

Andersen's (1970) correction factor for *Quercus* was based on *Quercus robur*, while Bradshaw (1981a) pooled data for *Quercus robur* and *Q.petraea* in his calculation. He noticed some discrepancies in the results of various authors for *Quercus*, as did Andersen (1970). His own P_{rel}-value for *Quercus* is, however, the same as found by Andersen, relative to *Fagus sylvatica*, and, hence, confirms Andersen's result that *Quercus* should be considered a high pollen producer.

Bradshaw (1981a) also pooled data for *Betula pubescens* and *B.pendula*, whereas Andersen (1970) considered *B.pubescens* alone. The high P_{rel}-value found for *Betula* by Bradshaw is not quite comparable with that of Andersen, as the ratios of the tree basal areas to the crown areas may vary (cp.above). *Betula* may have particularly slender trunks, as also noticed by Bradshaw.

The low pollen deposition rates found for *Fraxinus excelsior* by Bradshaw (1981a) were ascribed by him to bad preservation. His P_{rel}-values are slightly higher than those found by Andersen (1970). The low figures found in Denmark are consistent for two woodlands and were confirmed by the data from pollen collectors (Andersen 1974). The low figures found for the moss humus samples by Andersen cannot have been due to bad preservation, as the *Fraxinus* pollen was better preserved than other tree pollen, and because only well-preserved samples were studied (Andersen 1970).

Bradshaw (1981a) calculated additional correction factors for *Taxus baccata* and *Salix*.

Webb *et al.* (1981, p. 271) stated that Andersen (1970) "pooled his samples before calculating correction factors from his pollen and tree percentages and did not use regression analysis directly on percentage data". Only the second part of this statement is true. Webb *et al.* failed to mention that Andersen's correction factors were based on linear regression analysis of semi-quantative data. Webb *et al.* (1981 p. 294) also stated that the ranking of taxa found by Pohl (1937) differs from the ranking found by Andersen (1970). This statement is correct (Andersen 1970, p. 78). It should be remembered, however, that Pohl's figures are based on gross extrapolations from the numbers of pollen found per stamen on to a calculation of the pollen productivity of a whole tree stand, and therefore are extremely unreliable (cp. Andersen 1970, pp. 12 and 78). The statement of Webb *et al.* (1981) that Andersen's correction factors do not reflect pollen productivity is therefore unsupported.

For sampling sites on soils and in small wet hollows covered by trees, the mode of tree pollen transfer can be assumed to have been the same as for the surface samples from forests. In the study of Raynor et al. (1975), the main trajectory (highest pollen concentration) for pollen released at crown level is very steep, nearly at a 45° angle. In Draved Forest, where the main part of the surface samples were derived, 70-90% of the tree pollen was transferred during the flowering seasons, and dry deposition of pollen prevailed (Andersen 1974). Some of this pollen may have been caught on understorey vegetation during the transport (Tauber 1965, 1977). Such pollen becomes washed down by rain during the remainder of the year (Andersen 1974, Tauber 1977) and thus will reach a sampling site on the ground. On soils, similar transport processes can be assumed to prevail. In a wet hollow, the tree pollen may be transported directly to the surface without passing possible understorey vegetation. The receptive surfaces of moss cushions, soil, and wet hollows may differ; however, as the transport directions are very steep, or vertical, the effect of such differences is probably small.

The incorporation of pollen into a soil is direct. The hollows with shallow ponds are so sheltered from winds that the problems concerning redeposition as found by Davis (1968) for larger lakes can be assumed not to occur.

Andersen (1980b) found, by means of measurements of pollen concentration in sediments from a small wet hollow, nearly the same pollen productivity rates in the early Holocene as found to-day for *Betula*, *Pinus*, *Quercus*, *Alnus*, *Ulmus* and *Tilia* ; and the relative productivity of *Corylus* was found to have been the same as that of *Betula*, *Pinus*, *Quercus* and *Alnus*, as indeed assumed earlier by Fægri & Iversen (1975) with the exception of *Quercus*. Hence the correction factors suggested by Andersen (1970, 1978a) for tree pollen may be used with some confidence for pollen spectra from soils and small wet hollows.

The tree pollen from the sites in Eldrup Forest was in some cases indentified at the generic level alone. Two *Betula* species, *B.pubescens* and *B.pendula*, may have occurred. The pollen productivity of the two species does not seem to differ in the investigation of Bradley (1981a). The *Tilia* pollen was almost exclusively *T.cordata*, and the *Ulmus* pollen is most likely to belong to *Ulmus glabra*, the same species as investigated by Andersen (1970).

As for the *Quercus* pollen, it can be assumed that *Quercus petraea* occurred alone in Eldrup Forest for a considerable time; however, the occurrence of *Q. robur* at some earlier time cannot be excluded. As mentioned above, the correction factor calculated by Andersen (1970) was based on *Q. robur*, whereas the two species were considered together in the investigation by Bradshaw (1981a).

No moss humus samples from Eldrup Forest have yet been examined. The percentages of *Fagus sylvatica* and *Quercus petraea* pollen in the topmost samples from five soil sections and one section in peat (-A 12) were compared with the percentages of the tree basal areas in cirlular plots with radii at 20m and 30m. The crown canopy was dense in

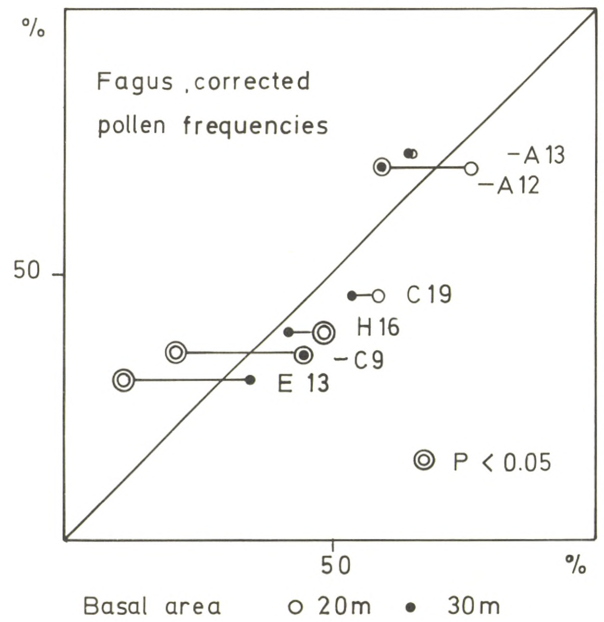


Fig. 55. Corrected pollen frequencies for *Fagus sylvatica* (% APc) at surface level of six sections, compared with basal area percentages in circular plots with radii 20 m and 30 m. Significance tests by the chi-squared method (cp. Table 50).

TABLE 50. *Fagus sylvatica*. Pollen frequencies (% APc) at surface level of six sections, and differences from basal area percentages in circular plots with radii 20m and 30m. Significance tests by chi-squared method and t-test (paired samples).

	Pollen correc- ted (%)	Difference from basal areas 20m (%)	30m (%)	20m (P)	30m (P)	20m Significance	30m
E 13	30.3	19.8	– 5.16	<0.001	0.352	+ + +	
–C 9	34.5	13.3	–10.6	<0.001	0.016	+ + +	– –
H 16	39.4	– 8.8	– 2.5	0.037	0.525	–	
C 19	45.7	–12.9	–10.5	0.056	0.110		
–A 12	69.9	– 6.4	10.4	0.086	0.002		+ + +
–A 13	73.4	7.3	8.3	0.268	0.195		
Total diff.		12.2	–10.1	<0.001	0.001	+ + +	– – –
Correlation, r		0.874	0.917	0.023	0.010	+	+ +

+,–: P<5%; + +,– –: P<1%; + + +,– – –: P<0.1%.

these cases. Hence, the basal area percentages can be assumed to equal the crown area percentages. *Fagus* pollen-frequencies after correction (*Fagus* xl, *Quercus* xl/4) and differences from the measured basal area percentages are shown in Table 50 and Fig. 55. The corrected pollen percentages were correlated to the basal area percentages. The pollen percentages were larger than the basal area percentages for the 20m plots in two cases, and smaller in one case; and they were larger than the basal area percentages for the 30m plots in one case, and smaller in one case. The total difference was +12% for the 20m plots and -10% for the 30m plots. Hence, the differences between the corrected pollen frequencies and the basal area frequencies are accidental. The correction factor used for *Quercus robur* (xl/4), is, therefore, also valid for *Q. petraea*.

Some difficulties may arise with regard to *Corylus avellana*. This species has a high pollen productivity when forming the topmost canopy (Birks 1973, Andersen 1980b). However, when shaded, the pollen productivity of the species is low, as assumed by Fægri & Iversen (1975) and other authors, and is similar to that of *Fagus sylvatica*, as proved by Andersen (1970). Bradshaw (1981a) found a similar situation with regard to *Taxus baccata*. Hence, the use of varying correction factors would be preferable in the case of *Corylus*, but simply not practicable in a diagram covering a major part of the Holocene. *Corylus* pollen was therefore corrected with xl/4. An additional curve for *Corylus*, uncorrected and calculated outside the tree pollen total, is shown for a case where *Corylus* is less than 10% (*Molinia* hollow).

No correction factor is available for *Populus tremula*. Pollen of this species is abundant (10% of the tree pollen) for a short period of the early Holocene at one of the sites (*Glyceria* hollow). *Populus* pollen is often abundant (10-20%) in other pollen diagrams from the early Holocene in Denmark (Krog 1959, Jørgensen 1963, Fredskild 1975, K. Andersen *et al.* 1982), a time in which only trees with a high pollen production (*Betula*, *Pinus*, *Corylus*) were present. As argued by Andersen (1978a), the *Populus* pollen must be corrected by a factor which is similar to that of trees with high pollen produtivity as otherwize the tree would become dominant in the corrected pollen spectra.

The correction factors used for the tree pollen spectra in Eldrup Forest thus were as follows, in accordance with Andersen (1970, 1978a, 1980b): *Pinus*, *Betula*, *Corylus*, *Quercus*, *Alnus*, *Populus* : xl/4; *Carpinus* : xl/3; *Ulmus*, *Picea* : xl/2; *Fagus* : xl; *Tilia*, *Fraxinus* : x2.

These are rounded figures. It will be noted that small changes in one species do not materially change the results (cp. Andersen 1980b).

The tree pollen spectra from Eldrup Forest corrected in this manner may be assumed to reflect the true areal composition of the tree canopy, and the pollen diagrams to reflect changes in the crown area. Great precision should not be expected due to uncertainties in the method. For the same reason no statistical treatment of the data has been attempted. It may be noticed that stands of young trees which have not reached flowering age are not represented in the pollen spectra. Baker *et al.* (1978) and Birks (1982) used the correction factors suggested by Andersen (1970, 1978a) for pollen diagrams from small hollows in the British Isles. Bradshaw (1981b) used his own correction factors (Bradshaw 1981a) for a transformation of tree pollen percentages from a small basin in East Britain to basal area perentages. The present author considers tree areas to be more relevant for a reconstruction of forest composition than the areas of the tree trunks. The differences may, however, be irrelevant in relation to other uncertainties of the methods.

The pollen percentages for trees with zero area percentages were less than 10% in the corrected pollen spectra from the moss humus samples (Andersen 1970). The woodlands examined were heterogeneous, and the pollen deposited at zero area (p_o in the formula on p. 93) derived mostly from trees found just outside the plots measured (extra-local pollen *sensu* Janssen 1973). Tree pollen found with low frequencies in corrected pollen spectra from a homogeneous forest probably derived from trees found at still greater distances (regional or extra-regional pollen, Janssen 1973). At times when human activity caused localized changes in tree composition some distance from a site, one expects to find slightly increased percentages of those trees, which were favoured by the human activity.

AP (*Arboris Pollen*) is used for the tree pollen sum, and APc for the corrected tree pollen sum. The deposition of tree pollen will have varied considerably according to variations in tree coverage and in tree composition. Andersen (1980b) showed that the ratio AP/APc expresses the same variations in total tree pollen output as did the measured deposition of total tree pollen at times where the tree cover was continuous. A curve for the AP/APc ratio is shown on some of the pollen diagrams. These ratios can vary from 0.5 to 4.0 according to the correction factors used.

The pollen countings were ajusted in such a way that the corrected tree pollen total (APc) was approximately the same for all samples within a particular section. The APc thus was approximately 500 in the sections from two wet hollows (*Glyceria* hollow and *Molinia* hollow), and 250 in one wet hollow (Matrikel hollow) and the soil sections. In this manner the numbers of tree pollen actually counted could vary between 250 and 2000 in the former, and between 125 and 1000 in the latter cases.

Non-tree vegetation

Whereas the quantative composition of the tree canopy at the sites in Eldrup Forest can be reconstructed with some confidence, it is difficult to reconstruct quantative relationships for the other plants.

Numerous studies of pollen assemblages in surface samples exist, but results from lowland areas in northwestern Europe are particularly relevant for the present work. These studies, especially those of Jonassen (1950), Bastin (1964), Birks (1970, 1973), Andersen (1970), Heim (1971) and Damblon (1979), deal with surface samples from woodlands, fields, pastures, heaths and bogs and were based on percentage analyses. Bastin (1964), Heim (1971) and Damblon (1979) calculated the frequencies for various plants as percentages of all pollen and spores, and compared average percentages with average cover percentages in vegetion plots varying from 100 to 10.000m^2 (R-values in the sense of Davis 1963). Birks (1970, 1973) compared pollen percentages with cover percentages in 25m^2 plots. Andersen (1970) calculated frequencies for herbaceous plants in woodlands in percentages of the corrected tree pollen sum (APc), i.e. corresponding to a *Fagus* woodland, and compared them with cover percentages in lm^2 vegetation plots from the immediate vicinity of the sampling sites.

Transects through woodlands, glades and treeless vegetation in Heim (1971) and Damblon (1979) show that the NAP percentages increase strongly immediately outside forests, even in small glades. Heim (1971), who surveyed results of earlier authors, found that the average NAP percentages in dense forest varied between 10 and 30%. The NAP includes pollen transported from treeless areas around the forests as well as pollen and spores from the field layer. The NAP perentages depend highly on the pollen productivity of the forest itself in these cases.

Bastin (1964) and Heim (1971) found that *Hedera helix*, *Ilex aquifolium*, *Salix* and wild grasses were under-represented in the samples from forests. Ferns were variously represented, but their spores were common only in open situations, and Cyperaceae were under-represented. *Sorbus aucuparia*, *Salix cinerea* and *Juniperus communis* were under-represented as understory species, according to Birks (1973); ferns were variously represented, and other field layer plants from forest were under-represented. Andersen (1970) found that *Filipendula ulmaria* was well-represented and -dispersed, and that *Dryopteris austriaca*, *Rubus fruticosus* and *Crepis paludosa* were locally well-represented. *Anemone nemorosa* was also well-represented on neutral soils, but the pollen was scarce on acid humus. Most other pollen, including that of *Carex*, was scarce.

Heim (1971) found an average percentage for NAP of 66% in forest clearings, predominantly from wild grasses or Ericales. The average NAP frequencies in heaths, grasslands and fields were 68%, 78% and 84%. Wild grasses were well-represented in grasslands and slightly under-represented in heaths, whereas cereals were strongly under-represented, even in cultivated fields (it was not stated which cereals were cultivated). *Calluna vulgaris* was slightly, and species of *Vaccinium* strongly, under-represented. *Plantago* species were found to be well-represented in grasslands, whereas other herbaceous plants (*Galium*, Cyperaceae, Ranunculaceae) were under-represented in the pollen spectra from treeless areas. *Sphagnum* was slightly over-represented in peats. Birks (1973) found abundant *Juniperus communis* pollen in pollen spectra from tall-growing scrub.

Damblon (1979) found 55-75% NAP in pollen spectra from treeless peatlands. *Carex rostrata* was well-represented, whereas other *Carex* species were under-represented. *Molinia*, *Galium* and ferns were well-represented in such pollen spectra. Birks (1970) found that Cyperaceae were over-represented, and *Rumex acetosa*, *Ranunculus acris* and *Taraxacum officinale* were well-represented, whereas other herbaceous species were under-represented, in surface pollen spectra from Scottish peats.

The representation of plants other than trees in surface samples thus varies considerably, and differs for the same plants in various situations in some cases. Iversen (1969) corrected the pollen frequencies of various herbaceous plants in pollen diagrams from terrestrial soils. He considered that if herb pollen is included in the pollen total in pollen spectra where the tree pollen had been corrected, then pollen from the highly productive herbs should be corrected as well. The correction factors used by

Iversen were, however, arbitrary, and no reliable correction factors for non-tree pollen and spores can be suggested.

Non-tree pollen prevailed at certain times in the pollen spectra from soil sections from the research area in Eldrup Forest, as mentioned above. Hence, the NAP had to be included in the pollen totals in these cases. The NAP percentages may vary due to differences in tree cover, tree composition, and pollen productivity; the quantative composition of the vegetation can therefore only be estimated in a general way. Besides uncorrected percentages, curves for total NAP x 1/4 in percentages of APc + NAPc are shown on these diagrams. These curves are usually parallel with the curves for the uncorrected percentages. The curves for non-tree plants thus can be assumed to reflect changes in area in a general way.

As discussed above, various discrete non-tree communities can be supposed to be represented in the pollen spectra from the three wet hollows that were studied. These communities include field vegetation of the upland forest and vegetation from the hollows themselves. In addition, non-tree pollen derived from open vegetation outside the forest may ocur at times when the regional forest cover was discontinuous. As the tree cover can be supposed to have been fairly dense at these sites, the NAP frequencies were calculated as percentages of the AP. Changes in these percentages may, however, reflect changes in total tree pollen output due to changes in tree composition (AP/APc ratio). The NAP frequencies were therefore calculated additionally as percentages of the corrected tree pollen sum (APc), which can be supposed to have been the same throughout the sections (Andersen 1980a, Birks 1982). In this way, changes in NAP percentages can be assumed to indicate true changes in pollen deposition. It is, however, difficult to interpret these percentages in terms of areal frequencies due to differential pollen produtivity and dispersal opportunity. Plants from the forest field layer may be scarcely represented, and local plants with a high pollen or spore productivity strongly overrepresented.

It may become difficult to decide whether non-tree plants that occur occasionally or with very low frequencies in the pollen spectra from the soils and the small wet hollows, were present near the site or at some distance. Pollen from wind-pollinated plants thus may have derived from more or less distant sources in such cases, especially at times when Man had created areas with tree-less vegetation outside the forest. Pollen from insect-pollinators may, however, also occur in non-local pollen rain; pollen from insect pollinated field or pasture plants thus was not infrequent in the surface pollen spectra from Draved Forest (Andersen 1970). Pollen and spores which occur only occasionally or in very low quantities in the pollen spectra from Eldrup Forest are, therefore, somewhat difficult to interpret in terms of presence or absence at a site.

The observations on pollen preservation serve a twofold purpose: to evaluate the possible effect of differential elimination of taxa on the composition of the pollen assemblages, and to draw possible conclusions about their depositional environment. The former goal may be pursued by observations on the state of preservation in individual taxa and by comparisons of pollen spectra from assemblages in varying states of preservation, the second by observations on the general state of preservation.

Terminology

Observations on pollen preservation were greatly neglected during earlier stages of pollen analysis. Fægri & Iversen (1975) state that pollen analysis should simply be restricted to deposits with good pollen preservation. Such stringent requirements, however, would mean that valuable information on former vegetation and environments would be lost. Pollen preservation has therefore received increased attention in recent years.

A terminology for various states of pollen preservation has developed gradually, and some confusion has developed simultaneously. One may here distinguish observable features which indicate processes that remove pollen grains from the assemblages from features which obscure the pollen grains and make identification difficult. In the present investigation, identification was in some cases hampered, but not made impossible, by bad pollen preservation.

Troels-Smith (1941) calculated a degree of destruction for each pollen spectrum, which indicated the total percentage of tree pollen grains with etchings. At the same time it became a common practice at his laboratory to notice the frequency of pollen grains, which were unidentifiable due to etching, crumpling or concealment (used, for example, by Jørgensen 1963).

Havinga (1964, 1967) distinquished two types of corrosion features - thinning and perforation. Cushing (1967) distinguished six preservation categories - corroded, degraded, crumpled, crumpled and thinned, broken and concealed. He termed Havinga's perforated grains "corroded", and noticed that ectexine elements were removed in such cases, whereas "thinning" consisted of a gradual removal of the endexine. The term "perforated", as used by Havinga, thus is not ideal, as the endexine elements are not removed by the etching. Both authors agreed that it is very difficult to recognize the initial stages of thinning, particularly in thin-walled grains. The other categories of Cushing (1967) mentioned above rather describe mechanical influences that do not remove pollen grains from the assemblages.

Delcourt & Delcourt (1980) united degraded and thinned grains in a degradation class, broken and crumpled grains in a mechanical damage class, and they distinguished yet another class called concealment by authigenic detritus. Birks (1982) classified perforated and thinned grains as corroded, whereas Aaby (1983) united corroded and thinned grains in a deterioration group.

Corroded, thinned and degraded grains are thus rather ill-defined groups. The present author, like Havinga (1967) and Cushing (1967), has found it difficult to distinguish grains in the initial stages of thinning from unaffected grains - especially in genera such as *Betula*, *Corylus* and *Quercus*, which have very thin endexines. As thinning, furthermore, can be provoked by chemical oxidation (Havinga 1967), artificial thinning cannot be distinguished from natural thinning in acetolyzed samples. In severely affected grains, it is difficult to decide whether the thin membrane present was originally the tectum or the endexine, and, hence, to distinguish the perforation type from the thinning type (cp. Havinga 1967, Andersen 1970). In the present

TABLE 51. Correlation of the frequencies of corroded grains with average corrosion in samples from gyttja and peat (GP; K 17, –A 12, Mah) and from mineral soil (MS; –C 9, –A 13, H 16, E 13, C 19, Ma), and calculated frequencies of corroded grains at average corrosion 50%.

	GP	MS	GP		MS		Corroded grains at av. corr. 50%			
	(n)	(n)	(r)	(P)	(r)	(P)	GP (%)	MS (%)	GP Sequence	MS
Tilia	46	46	0.565	<0.001	0.917	<0.001	58.8	65.3	(1)	(1)
Corylus	67	46	0.973	<0.001	0.892	<0.001	58.6	53.2	(2)	(2)
Ulmus	26	9	0.613	<0.001	0.834	0.005	52.0	42.8	(3)	(6)
Betula	71	49	0.938	<0.001	0.895	<0.001	45.7	49.9	(4)	(4)
Quercus	71	69	0.951	<0.001	0.923	<0.001	43.8	44.6	(5)	(5)
Alnus	63	46	0.887	<0.001	0.902	<0.001	43.6	37.8	(6)	(7)
Fagus	36	31	0.706	<0.001	0.953	<0.001	43.1	50.7	(7)	(3)
Pinus	53		0.692	<0.001			19.4		(8)	
Poaceae	70	21	0.763	<0.001	0.890	<0.001	17.6	28.1	(9)	(9)
Calluna	21	17	0.578	0.006	0.838	<0.001	16.9	20.2	(10)	(10)
Dryopt.–type[1])	67	50	0.530	<0.001	0.335	0.017	8.4	4.6	(11)	(11)
Average difference							–0.87	P=0.687		

1) including *Gymnocarpium*

investigation, therefore, corroded grains include both types of etching - in agreement with Birks (1982). Other types of preservation have been ignored.

Aaby (1983) distinguished corroded, thinned, and corroded and thinned grains. This procedure may be an improvement over the one adopted in the present investigation. It requires minute study of each single pollen grain. Aaby, however, restricted his observations to *Tilia*, *Alnus*, *Corylus* and *Betula*, omitting *Quercus* and *Fagus*, which were important tree constituents. His total deterioration percentage does not, therefore, refer to the entire tree pollen assemblage.

Differential corrosion

Corrosion features were scarce in the pollen assemblages from Elsborg Bog and have been disregarded there. In the pollen analyses from Eldrup Forest, the number of corroded grains of each taxon were noted and calculated for each level as percentage of the total number of grains of that taxon, if ten or more grains were found. Average corrosion was calculated for each pollen spectrum as an average of the corrosion percentages found for each tree taxon. *Pinus* and non-tree pollen and spores were excluded from the calculation of the average corrosion, because the frequencies of corroded grains were substantially lower for these taxa than for the trees other than *Pinus* (see below). Similar procedures were used by Andersen (1970, 1978a, 1983).

The vertical variations in average corrosion are shown in Figs. 56 and 57. The average corrosion depends somewhat on the lithology. It is variable in the gyttjas (0-70%), low in the peats (0-30%, Fig. 56), variable in the mineral soils (5-60%), and low in the humus layers (0-20%, Fig. 57).

Correlations of the percentage frequency of cor-

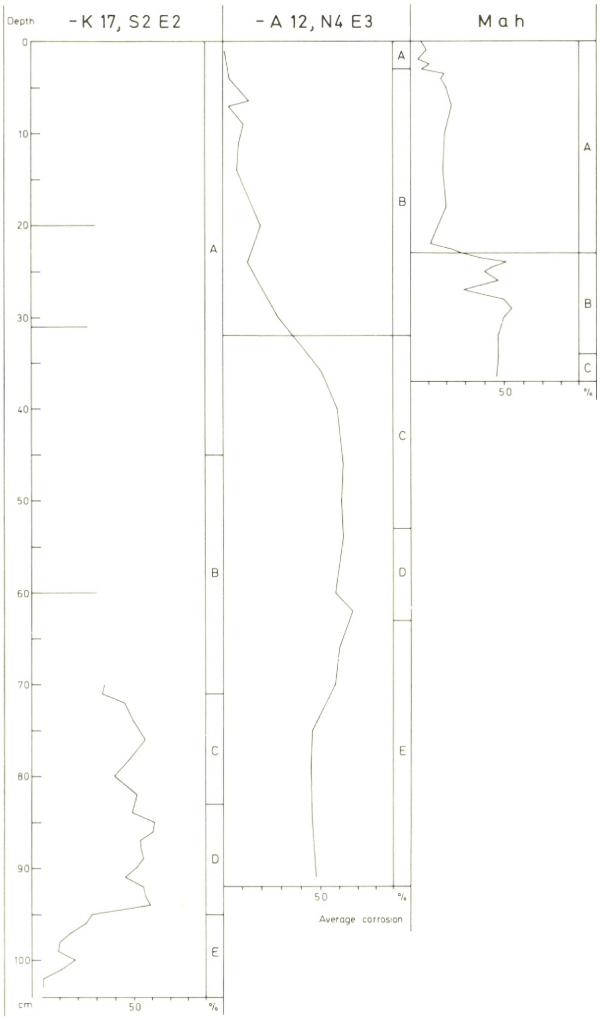


Fig. 56. Average frequency of corroded tree pollen in sections from the *Glyceria* (K 17), *Molinia* (-A 12) and Matrikel (Mah) hollows. the letters refer to sediment units described in Tables 45-47.

roded pollen grains in various taxa with the average corrosion percentages in the three sections from hollows with water-logged soils (gyttja and peat), and in six mineral soils, are shown in Table 51. No correlation was calculated for *Pinus* in the mineral soils - nor any for non-tree plants other than Poaceae, *Calluna* and *Dryopteris* -type, because the pollen frequencies were too low. The percentages of corroded grains found were strongly correlated to the average corrosion. Calculated percentages of corroded grains at average corrosion 50% were nearly the same in the gyttja and peat samples as in the mineral soils, and the average difference was insignificant (Table 51). Regression lines for samples from the two kinds of deposit calculated together are shown in Fig. 58. The regression lines fall into three distinctive groups: (l) trees other than *Pinus*, (2) *Pinus*, Poaceae and *Calluna*, and (3) *Dryopteris* -type. The regression line for *Ulmus* is the steepest in Fig. 58. the *Ulmus* pollen grains were apparently attacked more slowly than the grains of the other taxa, but corrosion then proceeded more quickly than in the other grains.

The sequences of decreasing corrosion frequency in Table 51 are nearly the same in the two types of deposit, and also resemble the sequences found by Havinga (1971) for samples exposed in biologically active soils, those found by Andersen (1970) for moss humus samples, and by Aaby (1983) for perforated (corroded) and thinned grains in soil samples.

One may conclude from Table 51 and Fig. 58 that the same taxa were attacked to the same degree in the water-logged deposits and in the mineral soils. Conclusions as to resistance to corrosion would, however, be doubtful. Due to the large differences, one may conclude that *Pinus*, *Calluna*, Poaceae and *Dryopteris* -type are less susceptible to corrosion than the other taxa shown - a conclusion which has been reached by other authors with respect to *Pinus* pollen and Pteridophyte spores (cp. Havinga 1967).

In samples where corrosion has induced loss of pollen, one may expect to find especially large numbers of strongly corroded pollen grains which are on their way out of the assemblages. For that reason, the frequencies of unaffected pollen, intermediately affected pollen (less than 50% of the surface), and severely affected pollen (more than 50% of the surface) were determined in selected samples with contrasting low and high average corrosion. A similar procedure was used by

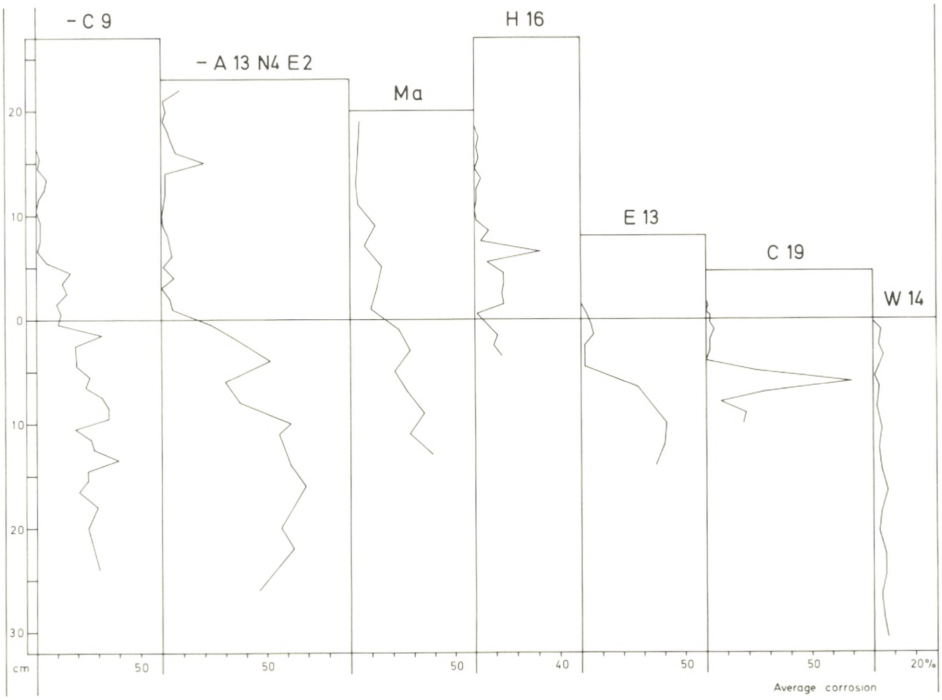


Fig. 57. Average frequency of corroded tree pollen in seven soil sections, at levels above and beneath the surface of the mineral soil (horizontal line).

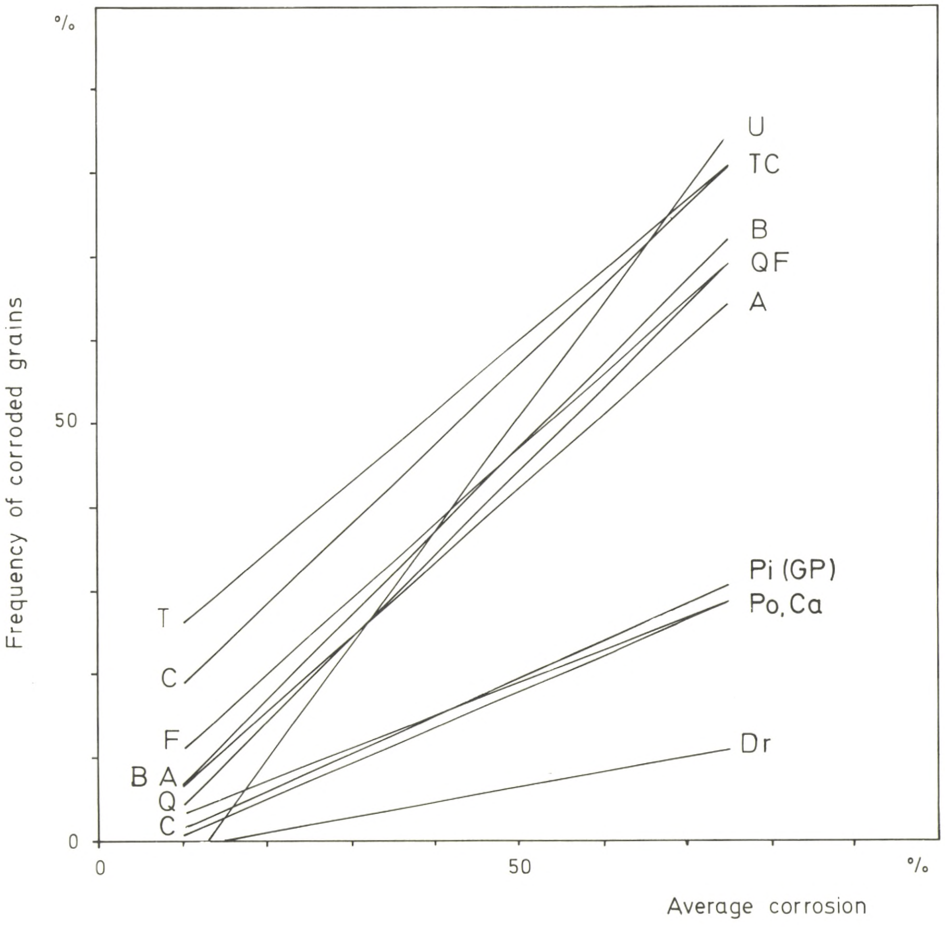


Fig. 58. Calculated regression lines for the frequency of corroded pollen and spores in relation to the average frequency of corroded tree pollen, in samples from gyttja, peat and mineral soils (cp. Table 51). U, *Ulmus;* T, *Tilia;* C, *Corylus;* B, *Betula;* Q, *Quercus;* F, *Fagus;* A, *Alnus;* Pi, *Pinus* (only in gyttja and peat samples, GP); Po, *Poaceae;* Ca, *Calluna,* Dr, *Dryopteris*-type.

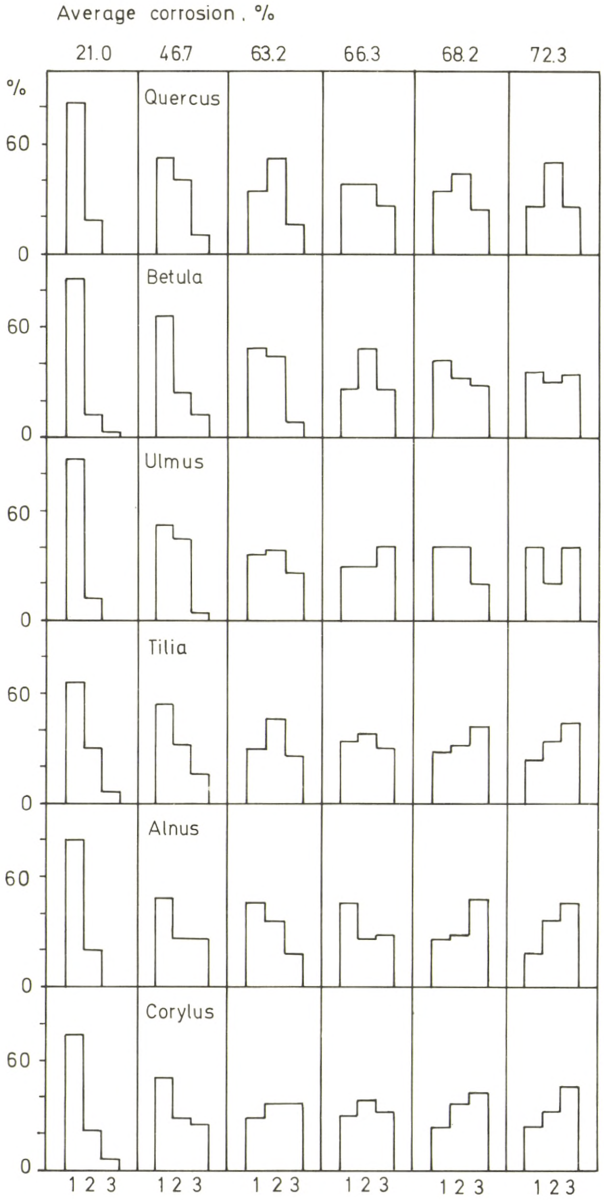


Fig. 59. Frequencies of uncorroded (1), slightly corroded (2, less than 50% of the surface), and strongly corroded (3, more than 50% of the surface) pollen grains, in gyttja samples with increasing average frequency of corroded tree pollen (46.7-72.3%), compared with a soil sample with low average frequency of corroded pollen (21.0%).

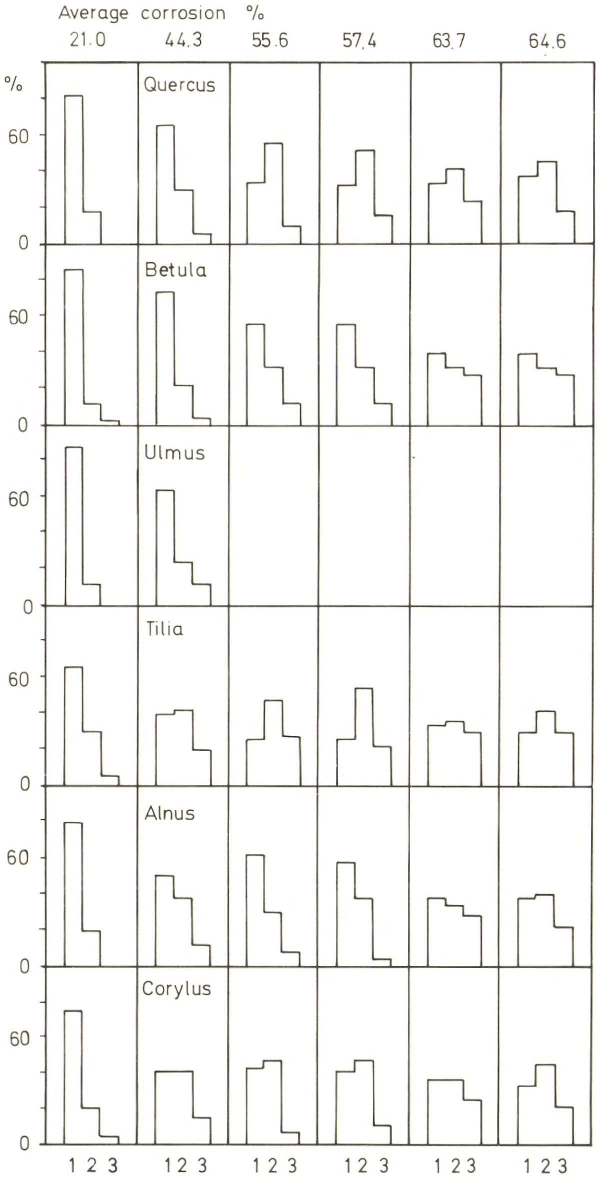


Fig. 60. Frequencies of uncorroded (1), slightly corroded (2), and strongly corroded (3) pollen grains, in samples from mineral soils with increasing average frequency of corroded tree pollen (44.3-64.6%).

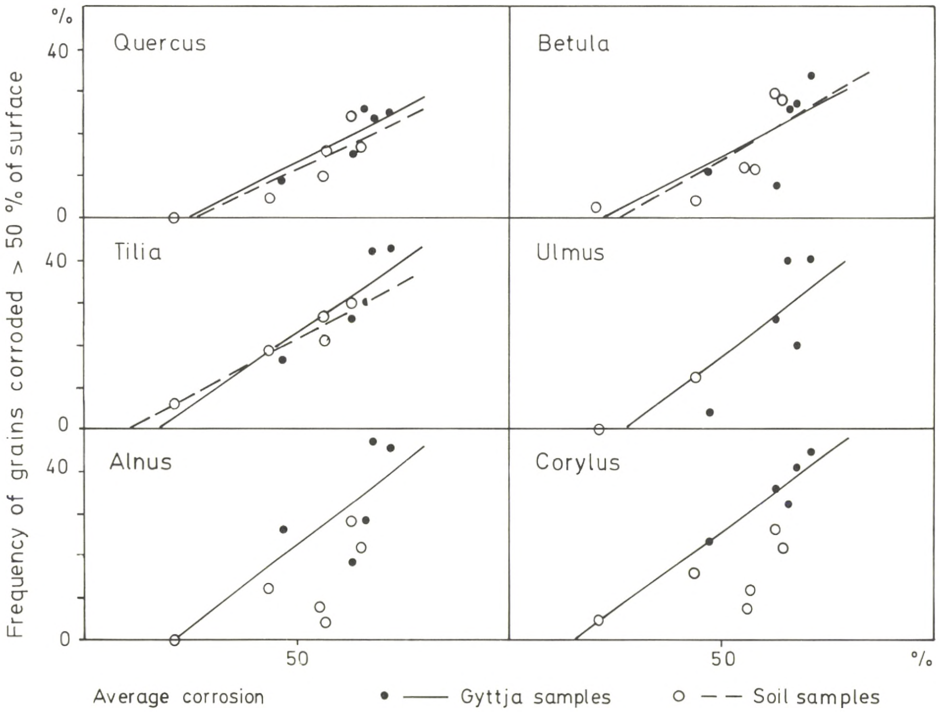


Fig. 61. Frequencies of strongly corroded pollen grains, compared with the average frequency of corroded tree pollen, and calculated regression lines, in samples from gyttja and mineral soils (cp. Table 52).

Havinga (1971) and Aaby (1983). Samples from gyttjas and mineral soils were compared separately with a sample from a mineral soil with low average corrosion (21.0%) in Figs. 59 and 60. It can be seen on these diagrams that the frequencies of severely affected grains are still low at average corrosion less than 50%, and then increase and become highest when the average corrosion exceeds 65%.

TABLE 52. Correlation of the frequency of severely corroded pollen grains (>50% of the surface) with average corrosion in samples from gyttja (G; K 17, –A 12) and mineral soil (MS; –C 9, –A 13), and calculated frequencies of severely corroded grains at average corrosion 70%.

	G		MS		Sev. corr. grains at av. corros. 70% G	MS
	(r)	(P)	(r)	(P)	(%)	(%)
Corylus	0.978	0.001	0.712	0.112	40.4	(21.5)
Alnus	0.844	0.034	0.708	0.116	38.1	(21.1)
Tilia	0.926	0.008	0.964	0.002	36.7	32.0
Ulmus	0.853	0.031			32.0	
Betula	0.817	0.047	0.823	0.044	25.3	25.4
Quercus	0.948	0.004	0.893	0.017	23.5	21.0

Correlations of the severely corroded pollen grains with the average corrosion are shown in Table 52, and regression lines in Fig. 61. Correlations of varying significance were found, and no correlation was found for *Alnus* and *Corylus* in the soil samples. The latter result may be due to observational difficulties. The figures in Table 52 show that *Corylus* and *Alnus* were the most severely corroded genera in the gyttjas and *Quercus* the least, and that the figures for the mineral soils were rather similar to those found for the gyttjas, except for *Alnus* and *Corylus*, which had the lowest percentages of severely corroded grains.

The results stated above indicate that the flow from unaffected to severely affected pollen grains is slow at an average corrosion of less than 50%, and then accelerates, so that one may expect that significant amounts of pollen have been lost in samples

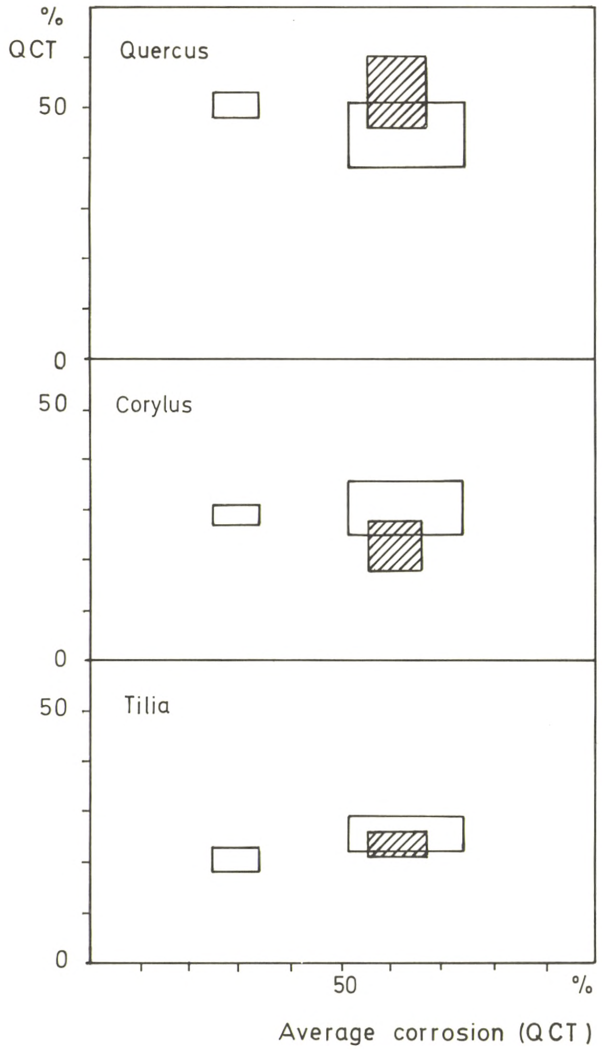


Fig. 62. 95% confidence intervals for the average frequencies of *Quercus, Corylus* and *Tilia* (% QCT) and the average frequencies of corroded pollen (QCT), in samples from gyttja (hatched) and mineral soils (white, cp. Table 53).

where more than 50% of the grains show signs of corrosion. The effect of the observed differences between individual genera on the composition of the pollen assemblages is, however, difficult to evaluate, because it is impossible to estimate the length of time the individual grain remained in the severely attacked stage. Thick-walled grains such as those of *Tilia* may pass more slowly through this stage than thin-walled grains such as *Corylus* and *Quercus* ; thick-walled grains may therefore accumulate in the deposit relatively to other grains.

A better way to estimate a possible differential removal of pollen grains in corroded samples is a comparison of contemporaneous pollen spectra in varying states of preservation, a method which has been utilized in some cases (Havinga 1967, Andersen 1970, 1978a, Aaby 1983). Another method was used by Birks (1982), who correlated pollen frequencies in a sequence of spectra with the percentages of corroded and unidentifiable grains.

Pollen spectra comprising the trees with frequencies above 5% (*Quercus*, *Corylus* and *Tilia*) from gyttja samples and mineral soils from Eldrup Forest dating from late Atlantic time were compared in Andersen (1978a). It was found by correlation that the *Tilia* percentages increased slightly at increased average corrosion. The same samples were compared in Tables 53 and 54, and Fig. 62. Here average pollen percentages of the three tree genera in the highly corroded gyttja samples and soil samples (average corrosion more than 50%) were compared with the slightly corroded soil samples (average corrosion less than 50%). The *Quercus* pollen-frequencies decreased significantly in the highly corroded soil samples (-6.1% AP, -4.9% APc), the *Corylus* pollen-frequencies decreased in the gyttja samples (-5.7% AP, -3.3% APc), and the *Tilia* frequencies increased in both kinds of deposit (3.3% AP, 4.3% APc and 5.0% AP, 6.1% APc, respectively). These results indicate that the *Quercus* and the *Corylus* pollen pass more rapidly through the severely attacked stage in, respectively, soil and gyttja samples than do the *Tilia* pollen. The numerical changes in the pollen percentages are small, however, and may be considered irrelevant compared with other uncertanties inherent in the quantitative reconstruction of tree communities.

Birks (1982) found significant decreases in the pollen percentages of *Quercus* and *Ulmus* in peats with highly corroded pollen, and none for *Tilia*, *Fraxinus* and Poaceae. It is interesting to note that

TABLE 53. Average frequencies of *Quercus, Corylys* and *Tilia,* uncorrected (% QCT) and corrected (% QCTc), in slightly corroded samples (– C9) and in highly corroded samples from gyttja (G; K 17, –A 12) and mineral soils (MS; –A 13).

	–C9 (n=9)		G (n=6)					MS (n=5)				
av. corr., range %	22.5–41.8		56.4–71.6		Difference (–C9)			47.6–72.5		Difference (–C9)		
	x̄ (%)	s (%)	x̄ (%)	s (%)	s (P)	x̄ (%)	(P)	x̄ (%)	s (%)	s (P)	x̄ (%)	(P)
pollen fr., % QCT												
Quercus	50.6	±3.4	53.0	±6.3	0.05	2.3	0.287	44.5	±5.3	0.13	–6.1	0.002
Corylus	29.0	±2.7	23.3	±4.9	0.06	–5.7	<0.001	30.0	±4.5	0.10	1.1	0.491
Tilia	20.4	±2.8	23.7	±2.3	0.32	3.3	0.001	25.5	±2.5	0.42	5.0	<0.001
Pollen fr., % QCTc												
Quercus	21.0	±2.9	20.1	±3.4	0.32	–1.0	0.419	16.1	±2.7	0.46	–4.9	0.002
Corylus	12.0	±1.8	8.8	±1.7	0.43	–3.3	0.001	10.8	±1.7	0.43	–1.2	0.169
Tilia	66.9	±4.1	71.2	±2.7	0.15	4.3	<0.001	73.1	±2.8	0.20	6.1	<0.001

Havinga and other authors (see Havinga 1967) have found selective removal of *Quercus* pollen from pollen assemblages from the mineral soils in podzols. In these cases the corrosion effect was thus much stronger than in the cases examined above. Aaby (1983) found a slight increase in *Tilia* (7%) and only insignificant changes in *Quercus*, *Alnus*, *Betula* and *Corylus* in his comparison of tree pollen percentages from podzols.

Fagus and *Quercus* pollen predominates in some of the mineral soils from Eldrup Forest. The average corrosion in these soils varies 5-69% (Fig. 57). The *Fagus* pollen is somewhat more corroded than the *Quercus* pollen in these samples (Table 51). Selective removal of *Quercus* pollen might be expected in the highly corroded samples, as the *Quercus* pollen grains are smaller and thinner-walled than the *Fagus* pollen. The *Quercus* pollen percentages did not decrease, however, in a highly corroded sample from section C 19 compared with the lesser coroded samples above and beneath (Fig. 63, n=11, r=0.014, P=0.967).

TABLE 54. Significance of differences found in Table 53.

	G	MS
Quercus	0	––
Corylus	–––	0
Tilia	+++	+++

0: P>0.05; ++,––: P<0.01; +++,–––: P<0.001.

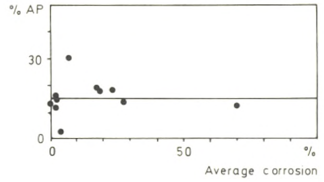


Fig. 63. Frequencies of *Quercus* pollen (% of *Quercus* + *Fagus*) compared with the average frequency of corroded pollen (FQ), in samples from mineral soil from section C 19. The horizontal line indicates the average frequency of *Quercus* pollen.

Pinus pollen generally is very scarce in the pollen diagrams from Eldrup Forest, and erichment of *Pinus* pollen due to differential pollen removal is not in evidence. One exception is levels from the early Holocene at the *Glyceria* hollow (section -K 17). *Populus* pollen found at the same levels were only slightly corroded as well (3-15%), a result which is in accordance with Cushing (1967). Possible enrichment of these taxa at the section mentioned will be discussed later.

The observations on corrosion features of pollen of *Calluna* and Poaceae, and *Dryopteris* -type spores, indicate that these plants may become overrepresented in samples with high average corrosion. This may also apply to other Pteridophyte spores (*Lycopodium*, *Pteridium*, *Polypodium*) found in the same samples. Generally, corrosion features also were scarcer in other non-tree taxa than in the trees.

All the features mentioned above must be taken into account in reconstructions of the former vegetation in Eldrup Forest by pollen spectra with high average corrosion.

Depositional environments

Depositional environments in the gyttja layers

It is a common observation that pollen corrosion is scarce in limnic sediments. Havinga (1971) found only slight pollen corrosion in water-logged alluvial clay, and strong corrosion in a well aerated part of the same sediment with pH 7.2 and high biological activity. Lack of oxygen thus seems to be a main reason for the absence of corrosion in limnic sediments with high pH.

Corrosion features were scarce or absent from the pollen found in the gyttja layers at Elsborg Bog. The high frequencies of corroded pollen grains noticed for some of the gyttjas from the three wet hollows in Eldrup Forest (Fig. 56) are unusual for aquatic sediments. Bradshaw (1981b) and Birks (1982) also found many corroded pollen grains in deposits from small wet hollows. Bradshaw (1981b) ascribed this phenomenon to periodic desiccation of the hollow. The present author has monitored water-level changes at similar sites in forests and found seasonal changes of the water level up to 1.5m. The low water levels occurred during the summer and autumn and were mainly due to consumption of water by the trees. The high pollen corrosion found for the gyttja deposits in Eldrup Forest may thus have been caused by biological activity, which was stimulated by aeration due to desiccation in dry summers. This result is in accordance with the observation by Bradshaw (1981b) mentioned above.

Pollen grains and spores, particularly from field layer plants, were possibly transported to the gyttja layers in the three wet hollows by slope-wash of terrestrial soils (p. 93). Such pollen grains and spores are likely to have been corroded on their arrival at the site (cp. Birks 1970).

It may be concluded that the high corrosion of tree pollen in the gyttja layers from the three wet hollows under consideration here indicates periodic dessication and high pH at the time of deposition. The low values found in the lowermost gyttja layer at section K 17 (unit E, Fig. 56) indicate continuous water cover at the time of deposition.

Depositional environments in the peat layers

Pollen preservation in peats is variable. Troels-Smith (1941) and Cushing (1967) found evidence of strong corrosion in well aerated peats. In his experiments, Havinga (1971) found slight corrosion on pollen exposed in *Sphagnum* peat with pH 4.1 for five years, and stronger corrosion on pollen exposed in *Carex* peat with pH 6.2. High acidity thus seems to hamper pollen corrosion in peats which have been desiccated temporarily.

The low incidence of corroded pollen in the peat layers from Elsborg Bog, and the moderate or low corrosion found in the peat layers from Eldrup Forest (sections -A 12 and Mah, Fig. 56), indicate high or increasing acidity at the time of deposition of these layers, which have been desiccated and aerated periodically.

Depositional environments in the terrestrial soils

Dimblely (1957) compared the pollen contents of terrestrial soils. He found that soils with pH 6.5-8.1 contained practically no pollen, soils with pH 5.2-

5.5 had intermediate pollen contents (1700-4000g^{-1}), and soils with pH 3.1-5.0 high contents of pollen (more than 21000g^{-1}). Havinga (1971) found that 69% of the pollen exposed in well aerated river clay with pH 7.2 was lost in five years, and 56% of the pollen exposed in leaf mould with pH 6.5 had vanished. No calculations were made for pollen exposed in podzolized sand with pH 4.6, but it was noticed by Havinga that the pollen there was less corroded after five years than the pollen exposed in the river clay and the leaf mould. High acidity thus slows down pollen corrosion in well aerated soils. Andersen (1983) found a low frequency of corroded pollen (5%) in a brown earth with pH 5.0 from Eldrup Forest (W 14, Fig. 57), and corrosion was absent in the humus layers where pH was about 4 (Fig. 57).

Havinga (1964, 1967) discussed the various agents which may cause corrosion of pollen. He found that the perforation type prevailed in biologically active soils with high pH (6.5-7.2), and that oxidation produced thinning similar to that observed in podzols. Havinga (1967) made the important observation that perforation corrosion prevailed in a podzol which had been submerged by the sea, whereas thinning prevailed in other podzols. He concluded that the pollen assemblages present in the first mentioned podzol had been buried during a former brown earth stage and had remained unchanged due to the submergence, whereas the assemblages found in the other podzols had been transformed later. Pollen assemblages in soils which were originally attacked by biological activity may thus be subsequently transformed by a diagenetic process which is similar to oxidation.

Aaby (1983) noticed that the perforation and thinning types of corrosion (in Havinga's terminology) both occurred at the initial stage of pollen deposition. He found perforated and thinned pollen grains in podzols. These pollen assemblages thus apparently were not as strongly transformed as the assemblages from podzols mentioned by Havinga (1967) where thinning prevailed.

Andersen (1984) found that the moderate or high average corrosion percentages (20-70%) found in the mineral soils of podzols from Eldrup Forest (Fig. 57) indicated that these pollen assemblages had been buried during former brown earth stages with moderate or high biological activity at pH levels above 5. Pollen with low average corrosion (less than 5%) found in the topmost part of the mineral soil in podzols derived from a former podzoloid stage with increased acidity (pH below 5) and decreased biological activity. Moderate and low pollen corrosion in the humus layers superposed on the mineral soils of the podzols indicated increased acidity, from pH about 5 to about 4.

Aaby (1983) noticed decreasing pollen degradation in lumbricid humus, arthropod humus and raw humus.

As post-depositional degradation of pollen grains in podzols (thinning due to diagenetic oxidation?) results in the removal of *Quercus* pollen (Havinga 1967, cp. p. 107), it can be concluded that the pollen assemblages in the podzols from Eldrup Forest, where the *Quercus* pollen was removed only to a slight degree (p. 106, Fig. 62), were subjected to only slight post-depositional diagenesis. The reason may be that these podzols either are young, or, if older, are covered by deep humus layers.

TEMPORAL DIVISION OF THE VEGETATIONAL SUCCESSIONS

The temporal changes in the pollen diagrams may be used for subdivisions into units which may serve for a correlation of sequences from different sites, or for a description of vegetational development.

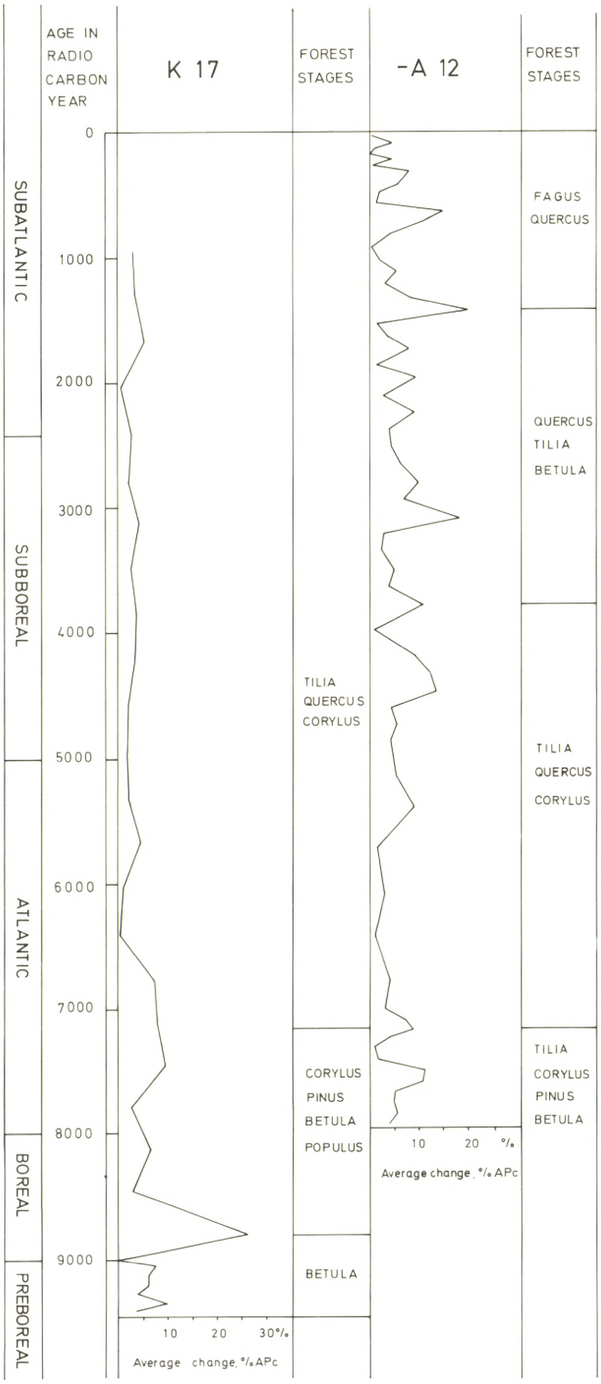


Fig. 64. Average changes for corrected tree pollen frequencies larger than 5% at the *Glyceria* (K 17) and *Molinia* (-A 12) hollows, shown on synchronized time scales.

The classical Danish pollen zones were at least originally delimited by changes in pollen assemblages and can therefore be considered biostratigraphic units (Mangerud *et al.* 1974). The tree pollen assemblages from Elsborg Bog were sufficiently regional in character to justify application of the Danish pollen zones as originally described by Jessen (1935) and modified by various authors (see Andersen 1978a).

A temporal subdivision of the vegetational sequences from the research area in Eldrup Forest raises some problems. The tree assemblages found there at a given point in time do not include the entire tree assemblages represented in the contemporaneous pollen spectra of regional significance. Thus, regional pollen zones cannot be applied, and local pollen assemblage zones would have to be defined. As individual pollen diagrams will differ even within these small areas, pollen assemblage zones would differ from site to site and would therefore be meaningless. Hence, local pollen assemblage zones have not been defined here; the vegetational sequences were instead divided into broad forest stages which could be recognized and compared at the various sections. A survey of the Holocene forest stages is shown in Table 61 (p. 142).

Watts (1973) advocated that periods of stability and periods of change should be distinguished as separate units in vegetational history. In natural successions, periods of change are intervals during which a newly arived species expands and attains full population size. In order to delimit periods of change from periods of stability, the average changes in the corrected tree pollen frequencies were calculated for the sections from the *Glyceria* hollow (K 17) and the *Molinia* hollow (-A 12), and are shown on synchronized time scales in Fig. 64. Average changes greater than 5% predominated in the early Holocene (Preboreal, Boreal and early Atlantic). A long stable period then occurred in one of the diagrams (K 17), whereas changes greater than 5% prevailed again from the late Atlantic to the present in the second diagram (-A 12) Hence, it was difficult to distinguish stable and unstable periods in some parts of the diagrams. Instead, forest stages - where the same tree species predominated to varying degrees - were distinguished. It can be seen in Fig. 64 that the limits between these forest stages coincide with particularly large average changes.

SOIL EVOLUTION IN ELDRUP FOREST

Five soil sections were examined for content of fungal hypha fragments, organic matter and pollen (-C 9, C 19, E 13, H 16, W 14), and two for pollen content alone (-A 13, N4, E4; Ma). One of the sections (W 14) was brown earth, and the others podzols. Vertical variations in hypha fragment length, organic content, pollen corrosion and pollen assemblages, and their significance for the distinction of soil evolutionary stages were discussed by Andersen (1979a, 1984).

As described by Andersen (1984) fungal mycelium is produced in the litter layer. At rapid litter decomposition, the hyphae disintegrate quickly, whereas resistant melanized hyphae increase in numbers if litter decomposition is retarded. The dark-coloured, melanized hyphae are fragmented first by macroarthropods such as Diplopoda (millipeds) and Isopoda (woodlice) and later by Cryptostigmata (oribatids). The various animals produce hypha fragments of characteristic length variation. Hypha fragments produced at the surface are transported downwards in mineral soil by earthworms or arthropods, and may become further comminuted within the soil; or they may become incorporated in accumulating humus layers. Distribution curves for fragment length indicate the degree of comminution of the fungal hyphae. The influence of oribatids is indicated by the frequency of fragments shorter than 21 μm.

Andersen (1984) noticed that hypha fragments were scarcer in soils where *Tilia* leaves had predominated in the litter, than in soils where *Quercus* or *Fagus* leaves had predominated, presumably due to a more rapid disintegration of *Tilia* leaves and, hence, a lower productivity of dark hyphae. Aaby (1983) measured total hypha length in soils and found that the productivity of dark hyphae had depended on the composition of the leaf litter.

Organic matter is likewise transported downward in mineral soils or is accumulated in humus layers. The total organic content was determined as loss on ignition.

Pollen deposited on the soil surface is destroyed at pH levels higher than 6. At lower pH, the pollen is transported downward in mineral soils by soil fauna, or is incorporated in accumulating humus layers. The frequency of corroded pollen grains depends on the acidity of the depositional environment (p. 109). Discrete pollen assemblages which have been incorporated in mineral soils are more or less homogenized due to the activity of the soil fauna.

Four soil evolution stages were distinguished in Eldrup Forest (Andersen 1979a, 1984, Figs. 65-66). Aaby (1983) used different names for identical stages.

Neutral brown earth stage

The soils in Eldrup Forest are assumed to have been neutral originally, and to have developed into neutral brown earth. Dark-coloured fungal hypha fragments were presumably scarce, and pollen disintegrated rapidly. Hence, no traces of former neutral brown earth stages exist in the soils. The humus was lumbricid humus.

Oligotrophic brown earth stage

The present oligotrophic brown earth in Eldrup Forest is moderately acid (pH 5.0). Hypha production in the former oligotrophic brown earth stages varied with the composition of the leaf litter. The relative frequency of short hypha fragments increased with depth due to the activity of oribatids. The humus was a lumbricid humus, and the origi-

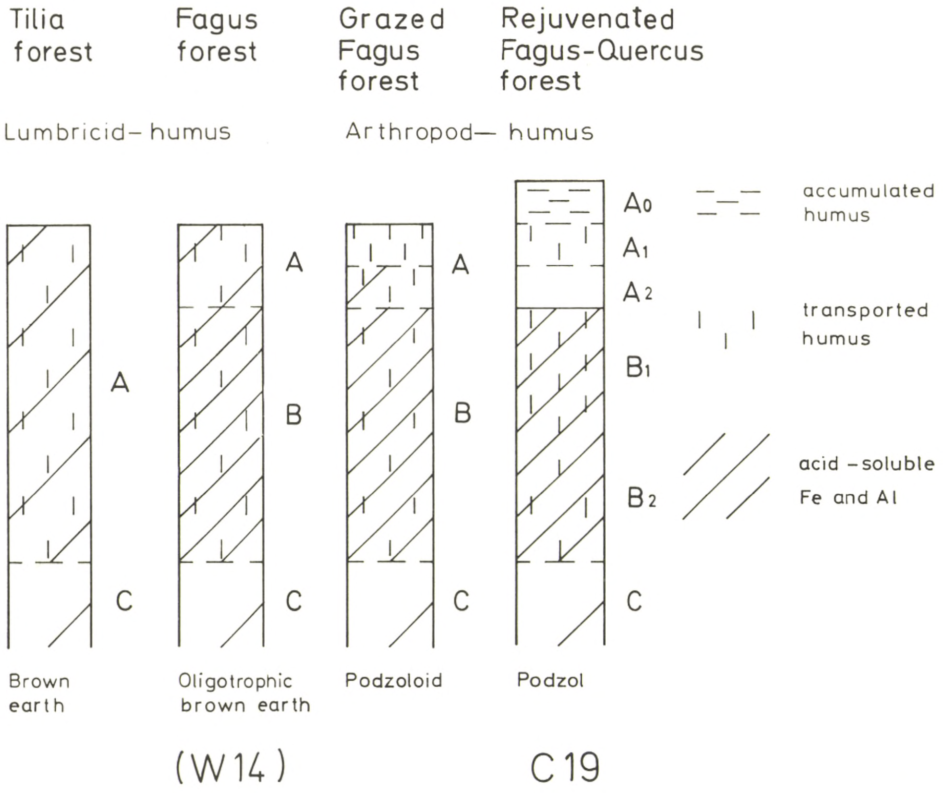


Fig. 65. Soil development in Eldrup Forest, schematic (from Andersen 1979a).

nal organic content was low. Pollen corrosion was moderate or high, and the original pollen assemblages were strongly homogenized.

Former oligotrophic brown earth stages were traced in the A_2 and B horizons of podzol profiles by increasing frequencies of short hypha fragments with depth, moderate or high pollen corrosion and homogeneous pollen assemblages.

Podzoloid stage

Burrowing earthworms were absent in the podzoloid stage, and organic material was transported downward to a shallow depth by arthropods. Hypha fragments were strongly comminuted by oribatids. The humus was an arthropod humus. Pollen corrosion was low due to increased acidity, and the original pollen assemblages were only slightly mixed.

Former podzoloid stages were traced in the A_1 horizons of podzol profiles by high frequencies of short hypha fragments, higher organic content than in the subjacent soil, low pollen corrosion, and fairly well-differentiated pollen assemblages. The former podzoloid stage was differentiated to varying degrees in the soil sections (Fig. 66).

Humus accumulation (podzol) stage

Organic debris was no longer transported downward into the mineral soil and accumulated on the mineral surface. The humus is arthropod humus. Dark-coloured hypha fragments are frequent and are more or less strongly comminuted by oribatids. The soil is strongly acid (pH about 4), and pollen corrosion is scarce. The original pollen assemblages are preserved. The humus accumulation still continues.

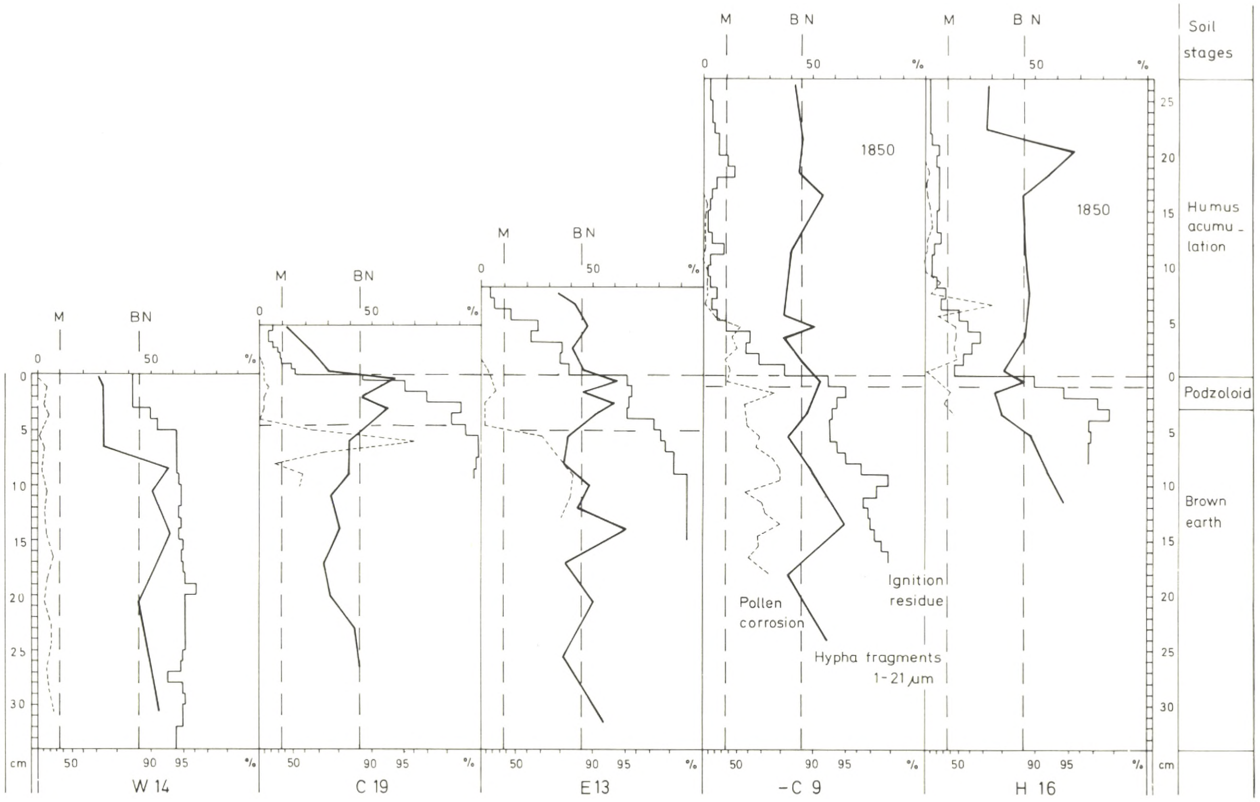


Fig. 66. The frequencies of hypha fragments 1-21 μm long, average pollen corrosion (uppermost percentage scale), and ignition residue (lowermost percentage scale, cp. Andersen 1979a), in humus layers above, and in mineral soils below, the mineral surface (at 0 cm) in five soil sections. M indicates the frequency of short hypha fragments in macroarthropod pellets (10%) and BN the lower limit for oribatid pellets (45%, *Belba* and *Nothrus*, from Andersen 1984), reproduced with permission of the Leicester University Press).

The humus accumulation stage was recognized as the A_0 horizon of the soil profiles by high organic content, fragmentation of hyphae to varying degrees, scarce pollen corrosion and well-differentiated pollen assemblages.

Podzolization was completed during the humus accumulation stage.

RADIOCARBON DATES

Radiocarbon dates from Elsborg Bog and sites within the research area in Eldrup Forest are shown in Tables 55-56.

From Elsborg Bog there are 4 datings of gyttja deposits, 11 datings of peats and 3 datings of wood. The gyttja samples were non-calcareous. *Myriophyllum alterniflorum* and *Isoetes* were present, and it was therefore assumed that the water was poor in bicarbonate. The ^{13}C deviations measured (Table 55) are normal for terrestrial plants and floating pond weeds (Olsson & Osadebe 1974, Stuiver 1975). The organic material is thus probably mainly of terrestrial origin. It is assumed that the dates are correct.

TABLE 55. Radiocarbon dates from Elsborg Bog, sections 1972 and 1974, in conventional radiocarbon years before 1950. *, date corrected according to ^{13}C-content.

1972	290±80	70–72.5 cm. Light-brown weakly humified *Sphagnum* peat. Loss on ignition 99%. Rootlets removed, 1.2%. K–2278.
	880±80	78–80 cm. Reddish-brown humified peat. Loss on ignition 95%. Rootlets removed, 1.9%. K–2216.
	1010±80	88–120 cm. Trunk of *Quercus* sp. The outermost part was rotted away. Outermost wood infected by white fungal mycelium was removed. The sample dated consisted of the outermost 2.9 cm of uninfected wood, which comprised about 60 year-rings. K–2279.
	560±70	103–105 cm. Wood with bark of *Alnus* sp., 2 cm thick. Wood infected by white fungal mycelium was removed. K–2221.
	1520±80	105–107 cm. Reddish-brown humified peat. Loss on ignition 96%. Rootlets removed, 1.0%. K–2217.
	310±60	109–114 cm. Wood of *Populus* sp. Wood infected by white fungal mycelium and fine rootlets was removed. K–2222 (average of two dates).
	3140±70	120–122.5 cm. Reddish-brown humified peat. Loss on ignition 96%. Rootlets removed, 0.1%. K–2348 (average of 2 dates).
	2930±70	122.5–125 cm. Reddish-brown humified peat. Loss on ignition 96%. Rootlets removed, less than 0.1%. K–2302 (average of 2 dates).
	3940±60	125–127.5 cm. Reddish-brown humified peat. Loss on ignition 98%. Rootlets removed, 1.1%. K–2218 (average of 3 dates).
	4350±70	127.5–130 cm. Reddish-brown humified peat. Loss on ignition 99%. Rootlets removed, less than 0.1%. K–2303 (average of 2 dates).
	4390±90	130–132.5 cm. Reddish-brown humified peat. Loss on ignition 99%. Rootlets removed, 0,1%. K–2349.
	4680±90	160–162.5 cm. Reddish-brown humified telmatic peat. Loss on ignition 98%. Rootlets removed, 0.1%. K–2219.
	5160±80	184–188 cm. Greyish-brown non-calcareous gyttja. Loss on ignition 98%. K–2220 (average of 2 dates).
	*5400±75	188–192 cm. Greyish-brown non-calcareous gyttja. Loss on ignition 97%. ^{13}C–26.4‰. K–2420.
	*7100±115	194–200 cm. Greyish-brown non-calcareous gyttja. Loss on ignition 67%. ^{13}C–26.7‰. K–2421.
	*7440±115	202–208 cm. Greyish-brown non-calcareous gyttja. Loss on ignition 65–47%. ^{13}C–27.4‰. K–2422.
1974	1680±60	37.5–40 cm. Dark-brown humified peat. Rootlets removed 0.8%. K–2393 (average of 3 dates).
	*1840±55	45–47.5 cm. Dark-brown humified peat. Rottlets removed, 1.4%. ^{13}C–27.4‰. K–2423 (average of 2 dates).

The peat samples from Elsborg Bog derived from a 30-years old exposed section which was partly overgrown by vegetation (p. 84). 30cm peat was removed before the samples were extracted. Rootlets removed from the samples amounted to less than 2% (Table 55). Hence, it can be assumed that contamination by modern material is insignificant. Humus was extracted from the samples before dating (p. 83) in order to avoid infiltrated young humus. Birks (1982) has shown, however, that the humus fraction in peat samples may in fact be slightly older than the bulk samples. The age differences found by Birks were 100-250 years and were insignificant at the 1% level.

Five samples from a narrow depth interval at Elsborg Bog (120-132.5cm) differed more than 1000 years in age (3140-4390 years). A hiatus may be present at this level and, as will be discussed later, the samples may have been mixed by human activity.

Two wood samples from Elsborg Bog (K-2221 and K2222, *Alnus* and *Populus*) were considerably younger than the peat above them. The wood apparently consisted of roots that had penetrated into the peat. Hence, these dates were disregarded. The *Quercus* trunk dated (K-2279) was so thick (80cm) that it does not yield a precise date of a definite level.

The gyttjas from the hollows in Eldrup Forest had low organic content, a part of which may be humus infiltrated from above. Some of them were, furthermore, penetrated by modern rootlets. They were, accordingly, unsuitable for radiocarbon dating. The peat layers were also unsuitable for dating, as they were likewise penetrated by modern root-

TABLE 56. Radiocarbon dates from Eldrup Forest, in conventional radiocarbon years before 1950. *, date corrected according to ^{13}C content. Soluble humus was not removed from K–3792.

*11020±155	Section K 16, N0, W5, 125–130 cm. Brown gyttja. ^{13}C–31.4‰. K–3792.
5340±120	Section –A 12, N4, E3, 57–60 cm. Wood of *Quercus* sp. Rootlets removed, 0.3%. K–1421.

lets. Hence, only two samples were dated (Table 56). One (K-3792) was from a gyttja layer intercalated in clay deposits from the *Glyceria* hollow, in a core taken 3m east of section K 17, S 2, E 2, and corresponds stratigraphically to the disturbed gyttja at 175cm depth at that section (Table 46). The low ^{13}C deviation (-31.4 ‰) indicates that the organic material was not of aquatic origin. The other sample from the research area was *Quercus* wood from the *Molinia* hollow (K-1421). The wood cannot have derived from a root in this case, as the hollow was too wet for the growth of *Quercus*. The wood was penetrated by modern rootlets which were removed before the dating and the wood was subjected to a rigorous pre-treatment. Hence, it was assumed that the date is reliable. The terrestrial humus layers were not dated. Charcoal, which can provide a reliable date, was not found in quantities sufficient for dating.

Ages are stated in conventional ^{14}C-years before 1950, or in calender years (BC/AD), corrected according to Clark (1975).

THE VEGETATIONAL SEQUENCE AT ELSBORG BOG

A pollen diagram from Elsborg Bog is shown in Plate X. The diagram shows the trees and selected herbaceous plants as percentages of the tree pollen sum (AP) for the section from 1972. In addition, a *Fagus* curve is shown for the uppermost part of the section from 1974.

Only features of regional significance and a few local features will be duscussed in the present article.

Open-ground herbs and wild grasses are scarce at 130-210cm, a fact which indicates that the region was densely forested. The herb pollen frequencies increase in the samples beneath 210cm (not shown in Plate X) indicating Late Weichselian age. Open-ground herbs increase again above 130cm and remain at 10-20%. The wild grasses (Poaceae, anl-D smaller than 8µm) are correlated with this curve; they can therefore be assumed to have occurred in open dry-land vegetation as well. Treeless vegetation, presumably fields or pastures, thus was a significant landscape-element at the time. The extent of the upland treeless vegetation cannot be determined, however, as non-tree taxa in addition to those mentioned above may comprise plants that have grown on dry land and locally on the peat.

The samples from 130-210cm comprise the pollen zones IV-VIII (Jessen 1935, Andersen 1978a). The lowermost part of the diagram is strongly compressed. The oldest sample thus belongs to zone IV, and the next sample, 2cm above, to zone VI. It is not possible to say whether there is a hiatus between these two samples, or whether the sedimentation was extremely slow.

The pollen spectrum from zone IV at Elsborg Bog shows 80% *Betula* and 20% *Pinus* pollen. These figures are typical for other Danish pollen diagrams.

Other pollen diagrams from Djursland covering zones VI, VII and VIII were constructed by Iversen (1937, 1941, Korup Sø, 15km, to the southeast) and Troels-Smith (1942, Dyrholmen, 10km to the west). The pollen spectra from zone VI at Elsborg Bog show low values for *Quercus*, *Ulmus* and *Tilia* as do the pollen spectra from Korup Sø. The percentages for *Betula* and *Corylus* are similar to Korup Sø, and *Alnus* and *Pinus* are somewhat lower at Elsborg Bog than at Korup Sø. The radiocarbon date from zone VI (7440 BP) is nearly the same as a date from zone VI in Fredskild (1975, 7660 BP).

The *Ulmus* and the *Tilia* percentages are slightly lower at Elsborg Bog than at Korup Sø and Dyrholmen in zone VII, the *Pinus*, *Alnus* and *Corylus* percentages are nearly the same, and the *Betula* percentages at Elsborg Bog are slightly higher than at Korup Sø and at Dyrholmen. An increase in *Quercus* from about 5% to nearly 30% began shortly after 7100 BP. Similar increases in the *Quercus* percentages can be seen in the diagrams from

Korup Sø and Dyrholmen. The level of the *Quercus* curve is somewhat higher at these two sites than at Elsborg Bog. Hence, the pollen spectra from zone VII from Elsborg Bog differ only slightly from those from the other two sites in Djursland.

The decline of *Ulmus*, which marks the transition from zone VII to zone VIII, is dated at 5160 BP. The *Ulmus* decline probably indicates human activity, as suggested by Troels-Smith (1960); it is, however, not possible to localize such activities, as the *Ulmus* pollen may have derived from a distant source. Changes similar to those noticed by Iversen (1941) at Korup Sø: minima for *Quercus* and *Tilia* and maxima for *Betula*, *Corylus* and *Alnus*, occur at between 140 and 160cm at Elsborg Bog. These changes indicate neolithic forest clearance in Iversen's (1941) interpretation. They were dated at Elsborg Bog at between 4680 and 4390 ^{14}C-years ago (3500 and 3200 BC). The herb pollen frequencies are low, and *Plantago lanceolata* pollen is scarce. Hence, the forest clearance was probably of limited extent. A neolithic barrow occurs near the present Eldrup Farm 1.5km northwest of the site (Fig. 7); the clearance may have occurred in that area. An increase in herb pollen, as noticed by Troels-Smith (1942) at Dyrholmen just after the neolithic forest clearance, is absent at Elsborg Bog.

The transition to zone IX is marked by a steady increase in the *Fagus* pollen frequencies. The radiocarbon dates around this level indicate a hiatus at the section from 1972 (p. 114). The *Fagus* increase was dated at between 1890 and 1680 ^{14}C-years (AD 130 and 325) in the section from 1974 (Plate X). This level is 120cm higher than at the section from 1972. The bog surface was thus very uneven at that time. The contemporaneous increase in pollen from open-ground plants and wild grasses indicates human activity in the region. Traces of peat-digging in the Pre-Roman Iron Age have been found elsewhere in Denmark (Becker 1948, Jørgensen 1956, A. Andersen 1975). Hence it can be suggested that the bog surface at section 1972 was disturbed by peat-digging, and that the sediment was mixed due to the human activity. The dates for the *Fagus* increase at the section 1974 (AD 130 and 325) can therefore be deemed more reliable than the dates from section 1972.

In section 1972, the *Fagus* frequencies increase strongly and reach 40% shortly after AD 450. At 95cm *Fagus* pollen is absent and *Corylus* is high (40%). This spectrum obviously belongs to zone VIII. Contamination during the sampling can be excluded; hence, it must be assumed that the sample contains a lump of old peat that was probably brought to the site by human traffic. The *Fagus* pollen is dominant throughout the uppermost part of the section and reaches frequencies up to 70%, indicating that *Fagus* was dominant in the woodlands around the bog.

At 74cm there is an abrupt change from strongly- to weakly-humified peat. The radiocarbon dates below and above this horizon differ by 600 years. Hence, a hiatus may be present at that level. There is no evidence of peat-digging since the surface of the strongly-humified peat rises gradually between the sections from 1972 and 1974. It can therefore be assumed that peat growth had stagnated and resumed again shortly before 290 ^{14}C-years (AD 1590) due to increased moisture. While the horizon coincides with a period of increased humidity (Aaby 1976), it seems unlikely that this radical change in the sediment was due to a climatic change alone, as no earlier changes in moisture are recorded. It therefore seems possible that the change to increased moisture was due to a local hydrological change due to human activity.

The samples above 7cm have low *Fagus* pollen percentages, high *Pinus* and *Corylus*, and *Tilia* pollen is recorded. These features indicate contamination, and it may be concluded that the deposit was mixed with old peat during the recent peat-digging.

Cultivation of *Cannabis sativa* at Elsborg bog

Pollen of *Cannabis* or *Humulus* occur in large quantities (up to 40%) slightly above the *Fagus* rise at section 1972 (Plate X). *Cannabis* / *Humulus* pollen was absent at section 1974; hence, it can be assumed that the pollen was not transported to the site through the air, but rather in an artificial manner. The oldest maximum of *Cannabis / Humulus* pollen was dated at 1520 ^{14}C-years (AD 450) and maxima occur up to near-surface-levels.

Bradshaw *et al.* (1981) have discussed evidence for the cultivation of *Cannabis* in Britain and elsewhere in Europe back to about the time of the Birth of Christ. They also mention the former practice of retting of *Cannabis* stems in lakes or pools, and evidence of this procedure found in Finland and Britain. Bradshaw *et al.* (1981) explained maxima of *Cannabis / Humulus* pollen (up to 50% of the total land plant pollen) in small pools or bog pools in Britain as due to pollen which had adheared to *Cannabis* stems deposited for retting. In one case, achenes of *Cannabis* were also found. A. Andersen (1954) mentioned evidence of the cultivation of *Cannabis* in Denmark in the early Subatlantic (in Jessen 1948), and he ascribed a maximum of *Cannabis / Humulus* pollen from the 17th century (up to 20%) at Bundsø, southern Denmark, to the cultivation of *Cannabis*. In Sweden *Cannabis* had a similar history (Påhlsson 1981). In view of these results, it seems likely that the depression present at section 1972 in Elsborg Bog was used intermittently for the retting of *Cannabis* from the centuries after the Birth of Christ up to the 18th or 19th centuries. A main road to Randers passed just north of the bog, and this city has a famous rope factory. Production of hemp for rope may thus have been an ancient industry in the area around Elsborg Bog. The cultivation of *Cannabis* in Denmark declined in the 19th century (Brøndegaard 1979). No traces of this former practice are left in the area around Elsborg Bog today.

THE VEGETATIONAL SEQUENCES AT THE WET HOLLOWS IN ELDRUP FOREST

A survey of the Holocene forest stages is shown in Table 61 (p. 142). Taxa not shown on the pollen diagrams are indicated in Tables 64-66.

Glyceria hollow

Pollen diagrams from core K 17, S2, E2 are shown in Plates XI-XIII (cp. Table 64). Additional pollen spectra from section K 16, N0, W5, are shown in Table 57.

As mentioned on p. 88 the *Glyceria* hollow lies in an erosional gully which traverses the enclosure from southwest to northeast (see Fig. 52). The surface around the hollow is rather even.

The sediments are aquatic throughout the sequence, and the hollow still contains a pool (Table 46 and Plate VIII).

Late Weichselian

Pollen spectra from the disturbed gyttja layer enclosed in the lowermost clay layers at section K 16 are compared with the lowermost Holocene sample from section K 17 in Table 57. Tree pollen dominates, except for the sample from 130cm at K 16; shrubs range from 5 to 9%, Ericales, open-ground and acid-humus herbs are scarce; uncertain and wet-ground herbs are 4-25%; aquatics are scarce; and *Pediastrum* colonies are abundant. *Betula* dominates among the trees, *Salix* among the shrubs, and Poaceae and *Carex*-type dominate among the uncertain and the wet-ground herbs. The pollen spectra from the disturbed gyttja are thus very similar to the early Holocene sample, except for the lowermost level, where the percentage for *Betula* is lower, and the percentages for Poaceae and *Carex*-type higher, than in the other samples.

As the open-ground herbs are very scarce, and *Salix* and *Carex*-type frequent, it can be concluded that the vegetation recorded was *Betula* woodland, and that the hollow contained marginal swamp vegetation of *Salix* and *Carex* species, and probably some wet-ground Poaceae.

TABLE 57. *Glyceria* hollow, Pollen spectra from the lowermost Holocene sample at section K 17, S2, E2 (*Betula* stage) and from gyttja enclosed in clay at section K 16, N0, W5 (Allerød chronozone).

	K 17	K 16		
Depth, cm	103	120	126	130
Trees	61.0	73.2	85.9	41.5
Betula	57.9	70.7	85.2	38.0
Pinus	2.7	2.4	0.7	3.3
Populus	0.1	–	–	–
Shrubs	7.9	9.3	5.1	6.2
Juniperus	–	–	0.5	1.0
Salix	7.9	9.3	4.6	5.2
Ericales	0.9	0.7	0.2	–
Empetrum	0.9	0.7	0.2	–
Herbaceous plants				
Open ground	1.2	1.0	0.2	1.5
Artemisia	0.8	–	0.2	0.3
Botrychium	0.1	–	–	–
Chenopodiaceae	–	–	–	0.5
Dryas	–	0.2	–	–
Helianthemum	–	–	–	0.3
Plantago media	–	–	–	0.3
Rumex acetosella-type	0.3	0.2	–	0.3
Saussurea	–	0.5	–	–
Acid humus	0.1	2.0	0.4	0.3
Gymnocarpium	0.1	2.0	0.4	0.3
Uncertain	15.4	5.6	3.7	25.8
Poaceae	14.2	5.1	3.2	24.0
Achillea-type	–	–	–	0.8
Apiaceae	–	–	0.2	–
Caryophyllaceae	0.1	–	–	–
Epilobium	0.1	–	0.2	–
Filipendula	0.1	0.2	–	–
Galium-type	0.1	–	–	–
Geum	–	0.2	–	–
Liguliflorae	0.1	–	–	–
Potentilla	0.1	–	–	–
Senecio-type	0.1	–	–	–
Thalictrum	0.3	–	–	0.3
Urtica dioica	–	–	0.2	0.8
Wet ground	13.6	8.3	4.6	24.7
Carex-type	12.6	7.6	4.4	24.0
Glyceria-type	0.3	–	–	–
Menyanthes	0.1	0.7	–	–
Spharganium-type	–	–	–	0.3
Sphagnum	0.4	–	0.2	0.5
Dryopteris-type	0.3	–	–	–
Pollen and spores totals	748	410	566	388
Aquatics	0.4	1.0	0.4	0.5
Myriophyllum spic.	0.4	–	–	–
Potamogeton	–	1.0	0.4	0.3
Ranunculus trich.-type	–	–	–	0.3
Pediastrum colonies	+	+	+	+

Potamogeton, *Myriophyllum*, *Ranunculus* and *Pediastrum* indicate a pond at the centre of the hollow.

The low tree pollen percentage in the lowermost samples from the gyttja layer is thus due mainly to a higher amount of locally produced pollen and does not indicate scarcity of trees at that time.

As the pollen spectra from the disturbed gyttja layer are very similar to the lowermost Holocene pollen spectrum, they are inconclusive regarding the age of the deposit. They might belong either to the Allerød Chronozone or to the early Holocene. The radiocarbon date at 11.020 BP (Table 56) indicates Allerød age. It can therefore be assumed that the gyttja layer was covered by clay and disturbed by solifluction during the Younger Dryas.

The *Betula*-woodland from Allerød time contained a few calciphilous pioneer plants such as *Dryas*, *Helianthemum* and *Plantago media*. Hence the soils were probably neutral. The swamp vegetation was rich in *Salix*, Poaceae and *Carex* species; and *Menyanthes*, *Sparganium* and *Sphagnum* were scarce. The presence of *Pediastrum* indicates eutrophic conditions in the pond. The presence of an aquatic deposit from Allerød time shows that the *Glyceria* hollow was already a kettle in the late Weichselian.

The clays washed into the pond contain no calcium carbonate. The soils in Eldrup Forest were thus poor in lime.

Holocene

The pollen diagram on Plate XI shows that pollen and spores from Ericales and several herbaceous plant groups (open-ground, acid-humus, and uncertain) are scarce throughout the sequence. Poaceae pollen is frequent at 95-98cm, wet ground herbs are frequent throughout the sequence (except for a minimum at 90-94cm), and aquatics are present at all levels. As the dry-land plants thus were scarce, it can be assumed that forest prevailed around the *Glyceria* hollow. The abundance of wet-ground plants indicates local swamp vegetation, and the presence of aquatics indicates a pool in its centre. The maximum water depth was 1.5m in the Early Holocene, and 0.5m at present.

The curves for tree pollen as percentages of AP initially show high percentages for *Betula* ; then for *Pinus*, *Populus* and *Corylus* ; for *Quercus* and *Tilia* ; and finally, for *Fagus*.

Corroded tree pollen is scarce below 95cm, and frequent above that level (average corrosion about 50%, Fig. 56). The *Pinus* and the *Populus* pollen is distinctively less corroded than the *Betula* and *Corylus* pollen. The *Pinus* and *Populus* percentages at levels 89-94cm may therefore be somewhat excessive, but it is not possible to estimate the magnitude of overrepresentation. Above these levels, the *Tilia* percentages may be slightly elevated, and *Corylus* slightly depressed, due to differential preservation (p. 106). Poaceae pollen, fern spores and other non-tree pollen may be slightly overrepresented in the pollen spectra above 95cm due to differential preservation.

The pollen spectra above 72cm do not differ; hence it was assumed that the deposit was homogenized to that depth due to the trampling of the red deer (see p. 88). The sample at 72cm differs from the spectrum above by a very low *Fagus* percentage. Hence, this sample and the samples below it were not contaminated.

Reconstruction of the past vegetation

A curve for the AP/APc ratio is shown on Plate XI; it varies from 1.5 to 4.0 due to variations in tree composition. Changes in non-tree pollen percentages based on the corrected tree pollen sum can therefore be assumed to be more real than changes in percentages based on a sum of uncorrected tree pollen.

Pollen curves calculated as percentages of the corrected tree pollen sum are shown in Plates XII-XIII. Only the two lowermost pollen spectra from the contaminated deposit above 70cm are shown.

As non-tree pollen was not corrected, an overrepresentation of non-tree plants with a high pollen production can be expected.

The vegetational sequence was divided into three forest stages based on the corrected tree pollen curves: *Betula*-stage, *Corylus- Pinus- Betula- Populus* stage, and *Tilia- Quercus- Corylus* stage. The two uppermost samples reflect a *Fagus- Quercus* stage, which cannot be described in detail, as the samples derive from the contaminated deposit.

Betula stage

Betula was the only tree present at the beginning of the sequence. The species indentity is unknown; it can be assumed that *Betula pendula* and *B.pubescens* occurred. Later, *Pinus* and *Corylus* appeared with 10-20% and had therefore probably immigrated to the forest. The *Betula* stage terminated at the expansion of *Corylus*, *Pinus* and *Populus*.

The curves for the non-tree plants, here calculated as percentages of the corrected pollen sum, differ somewhat from the same curves based on the pollen total. Shrubs, open-ground and uncertain herbs thus have distinctive maxima at 96-99cm. Hence it is indicated that the tree cover was more open during the late part of the *Betula* stage than during its early part.

Among the shrubs, *Salix* pollen is abundant throughtout the *Betula* stage. Most of the pollen probably derived from *Salix* scrub around the site. *Juniperus* pollen is scarce in the early part of the stage and frequent in its late part; a few *Hippophae* occur.

Among the Ericales, *Empetrum nigrum* pollen is present throughout the stage. Pollen from open-ground herbs, in particular *Artemisia* and *Rumex acetosella*-type, is frequent, especially in the late part of the stage; *Botrychium*, *Polygonum aviculare*, *Saxifraga oppositifolia*, Chenopodiaceae, *Campanula*, *Sedum* and *Armeria maritima* are represented.

Gymnocarpium and *Lycopodium annotinum* represent the acid-humus herbs.

Several herbs of the uncertain and the wet-ground groups are represented. The most frequent taxa are Poaceae and *Carex*-type. Among the aquatics, *Myriophyllum spicatum*, *Ranunculus trichophyllus*-type and *Callitriche* can be mentioned. *Pediastrum* colonies were abundant.

It is rather difficult to reconstruct the plant communities of the *Betula* stage quantitatively, due to the lack of experience with sites similar to the *Glyceria* hollow. Dry-land plants such as *Juniperus*, *Artemisia*, *Rumex acetosella* and *Gymnocarpium* produce pollen and spores abundantly if well illuminated; their dispersal may, however, have been hampered by low wind speeds near the ground and filtering by swamp vegetation around the hollow. Some of the Poaceae and plants from the uncertain group - such as *Epilobium*, *Thalictrum*, *Potentilla*, *Geum* and *Filipendula*- probably also occurred in the field layer. It may be concluded that the *Betula* forest was fairly open during the *Betula* stage, particularly during the late part: abundant ground vegetation apparently occurred. There was also a rich swamp vegetation around the hollow - with *Salix*, *Carex*, *Selaginella*, *Menyanthes*, *Caltha* and *Glyceria* and, probably, Poaceae and some of the herbs classified as uncertain, as well.

As *Sphagnum* spores were scarce in the *Betula* stage, it can be assumed that the swamp vegetation at the *Glyceria* hollow was eutrophic. *Empetrum nigrum* does not belong to such plant communities today; hence, it can be assumed that the species occurred in the dry-land field layer. The presence of *Empetrum*, *Gymnocarpium* and *Lycopodium annotium* indicates initial acidification of the soils at the time of the *Betula* stage.

TABLE 58. Average frequencies from the *Betula*-stage at the *Glyceria* hollow (K 17) and in surface samples from Scottish lowland birch-woodland (in Birks 1973). Cyperaceae were calculated outside the pollen total at the *Glyceria* hollow, and *Dryopteris*-type in the surface samples. +: less than 2%.

	Glyceria hollow		Birks 1973	
	99–103 cm	95–98 cm		
n	(5)	(4)	(2)	(3)
Betula	65	33	62	61
Pinus	4	6	3	+
Corylus	5	6	2	+
Salix	8	6	+	+
Juniperus	+	2	+	2
Empetrum	+	+	+	–
Artemisia	+	2	–	–
Rumex acetosella-type	+	+	–	–
Gymnocarpium	+	+	–	+
Poaceae	13	36	18	22
Geum	+	+	+	+
Filipendula	+	+	3	+
Potentilla	+	+	+	3
Cyperaceae	(15)	(24)	6	3
Dryopteris-type	+	+	(9)	(31)
Sphagnum	+	+	+	+

Average pollen spectra from the *Betula*-stage at the *Glyceria* hollow are compared with surface pollen spectra from Scottish lowland *Betula*-woodlands containing scattered *Corylus* (in Birks 1973) in Table 58. Pollen from the wet-ground plants was excluded from the pollen totals at the *Glyceria* hollow, and *Dryopteris*-type spores from the surface spectra. The *Betula* crown cover varied 40-70% in the Scottish woodlands and the *Betula* pollen percentages 26-81%. Hence, the forest of the *Betula* stage, with *Betula* percentages at 65 and 33, at the *Glyceria* hollow was fairly dense at the older part of the stage, and fairly open at its younger part. The *Salix* and Cyperaceae pollen, which probably had derived from wet-ground vegetation, is more common at the *Glyceria* hollow than in the modern pollen spectra. The *Juniperus* percentages were 1-3 at the younger part of the *Betula* stage at the *Glyceria* hollow, and 7 in one of the surface spectra with abundant *Juniperus* scrub (30% cover). The Poaceae pollen is more common at the *Glyceria* hollow than in the surface spectra and may thus to some degree have derived from wet-ground grasses, whereas *Dryopteris*-type spores are nearly absent at the *Glyceria* hollow, in contrast to the surface spectra.

The pollen spectra from the *Betula* stage are thus similar to pollen spectra from present more or less open *Betula* woodlands with a rich herbaceous vegetation. They differ somewhat from these woodlands by the lack of fern spores of *Dryopteris*-type and higher proportions of wetland plants. The crown cover was distinctively more open during the later part of the *Betula* stage, and the wet-ground vegetation richer. There was, at the same time, a minimum for *Corylus*. As the dissolution of the crown cover occurred after the immigration of *Corylus*, it cannot be correlated with the Rammelbeek cold phase (Behre 1978); it is, however, impossible to decide whether the dissolution of the crown cover and the decrease in *Corylus* were general and due to another temperature decrease, or were local events - due, for example, to disturbance of the land surface by the melting of buried ice.

High percentages for ignition residue (Plate XII) indicate low organic content, especially in the late part of the *Betula* stage, where the sediment was nearly pure clay. The organic material was nearly completely distintegrated, and no plant remains were present in the acetolyzed samples, except for pollen grains, Pteridophyte spores and *Pediastrum* colonies. Hence, organic debris such as leaves and the branches and trunks of trees that had fallen into the pond were mineralized almost completely, indicating strong biological activity within the pond. In the upper part of the *Betula* stage, increased influx of mineral matter due to a more open vegetation or soil disturbance can be suggested.

The low pollen corrosion (Fig. 56) indicates continuous water cover (p. 108) during the *Betula* stage. The absence of dessiccation during the summer may be explained by low water consumption in the fairly open *Betula* woodland.

Corylus- Pinus- Betula- Populus stage

The *Corylus- Pinus- Betula- Populus* stage was initiated by an abrupt decrease for *Betula* and increase in *Corylus*, *Pinus* and *Populus*. *Tilia* appeared at the middle part of the stage, and *Quercus* pollen is present. The stage terminated at the expansion of *Tilia*.

Corylus was dominant within the tree vegetation, and *Betula* obviously was suppressed by *Corylus* due to shade. The survival of *Betula* and expansion of *Pinus* and *Populus* do suggest, however, that the *Corylus* canopy was sufficiently open to permit scattered *Betula*, *Pinus* and *Populus* trees to penetrate. *Corylus avellana* is known only as a low tree today, and hence it appears that scattered tall specimens of *Betula*, *Pinus* and *Populus* towered above the *Corylus* canopy.

There is a peak of *Pinus* at the beginning of the stage. *Pinus* thus expanded together with *Corylus*, but its regeneration was apparently hampered later due to increasing density of the *Corylus* woodland. The expansion of *Corylus*, *Pinus* and *Populus* succeeded a stage where the tree canopy was rather open for reasons which are not fully explained.

Tilia immigrated during the *Corylus- Pinus- Betula- Populus* stage, but this tree apparently did not expand immediately after its arrival. The very low frequency of *Quercus* may be explained as pollen transported from a great distance. Long-distance transport is an obvious explanation for the small amounts of *Ulmus*, *Alnus* and *Fraxinus* pollen.

Hedera is represented during the stage, and *Viscum* in its latest part. *Viscum* thus appeared together with *Tilia*, one of its preferred host plants.

The non-tree categories decrease at the beginning of the *Corylus- Pinus- Betula- Populus* stage and were much scarcer than during the preceding *Betula* stage.

Among the shrubs, *Juniperus* nearly disappeared, and *Salix* became much rarer than in the preceding stage. *Viburnum opulus*, *Sorbus aucuparia* and *Frangula alnus* are represented at low frequencies.

Empetrum also disappeared, but *Calluna*, which was not represented earlier, was present.

The open-ground herbs became very scarce: *Campanula*, *Sedum*, *Plantago lanceolata* and *Jasione* are represented by a few pollen grains.

Gymnocarpium was still present, and *Pteridium* and *Melampyrum*, also indicative of acid soil, appeared.

Poaceae and herbs classified as uncertain became scarcer, as did *Carex*-type and other wet-ground plants, except for *Dryopteris*-type, which is represented at increasing frequencies.

Among the aquatics, *Callithriche*, *Lemna* and *Myriophyllum alterniflorum* may be mentioned. The *Pediastrum* colonies became scarce.

Clearly, there was no well-developed shrub layer beneath the *Corylus* trees. There was apparently a scarce field layer with *Calluna*, *Gymnocarpium*, *Pteridium* and *Melampyrum* and probably some Poaceae, near the site or at some distance. Hence, the soils were somewhat acid. The presence of *Sedum*, *Campanula*, *Plantago lanceolata* and *Jasione* point towards a few sunny spots, probably at places where occasionally trees had fallen causing temporary disruptions of the tree canopy.

The presence of *Plantago lanceolata* pollen is noticeable. These pollen grains may have been transported from sources some distance away; however, the species must be considered a member of the natural flora at the time. Iversen (1941, 1954) considered *Plantago lanceolata* an introduced species and regarded a few Late Weichselian finds from Denmark as redeposited or transported from a far distance. *Plantago lanceolata* has proved to have been a member of interglacial floras (Reich 1953, West 1956, Andersen 1961) and was present in the British Isles during the Weichselian and the early Holocene (Godwin 1975). A few pollen grains were recorded from pollen zone VII in eastern Denmark by Jørgensen (1963). Hence, *Plantago lanceolata* was a member of the natural Holocene flora before the time when the species expanded due to Man's forest clearences.

The swamp vegetation around the *Glyceria* hollow also became less abundant in the *Corylus- Pinus- Betula- Populus* stage than it had been before. The *Dryopteris* spores belong most likely to *Thelypteris palustris*, which apparently became prominent at that time.

The scarcity of shrubs and field vegetation and the decrease in the abundance of the local swamp vegetation indicate that the amount of light that penetrated the tree cover had decreased considerably. This change was obviously caused by the expansion of *Corylus*. The decrease in *Pediastrum* was probably also due to decreased light; the persistence of *Callitriche* and *Lemna* indicate, however, that the central pool in the hollow still received a fair amount of light.

The percentages for ignition residue are somewhat lower than in the preceding *Betula* stage, probably due to decreased influx of mineral matter.

The average pollen corrosion increases from about 20% to more than 50% at the transition to the *Corylus- Pinus- Betula- Populus* stage (Fig. 56). Hence, the pond dried out during dry summers, as it does today. This development was probably due to increased water consumption by the then dense tree vegetation. The maximum water depth was 1.45m at that time.

Tilia- Quercus- Corylus stage

The *Tilia- Quercus- Corylus* stage was initiated by increases in *Tilia* and, somewhat later, *Quercus*, as well as decreases in *Corylus*, *Pinus*, *Betula* and *Populus*. *Betula*, *Pinus* and *Populus* nearly vanished. *Corylus* decreased to about 10%. *Tilia* became dominant and constituted up to 65% of the tree canopy, and *Quercus* increased from 5 to 20% in the lowermost part of the stage and thus expanded somewhat later than *Tilia*.

The canopy of the *Tilia- Quercus* forest around the *Glyceria* hollow became thus so dense that the rejuvenation of *Pinus*, *Betula* and *Populus* was impossible, and *Corylus* was suppressed. When growing in pure stands, *Tilia cordata* casts a deep shade (Iversen 1960, Pigott 1975). *Quercus robur* and *Q.petraea* demand less light than *Pinus*, *Betula* or *Populus* (Lyr *et al.* 1967); the species do need some light however, for a vigoruos height growth at a young age (p. 57, Penistan 1974), so the presence of

Quercus in the *Tilia* forest indicates that disruptions of the tree canopy occurred. (Such gaps can have been caused by the felling of individual mature trees by storms). *Corylus* may also have utilized openings in the tree canopy and may have flowered profusely there, whereas specimens covered by tree canopy flowered scarcely.

The *Tilia* percentages decrease gradually from around 65 at the early part to 30 at the topmost level, and *Quercus* increases from around 20% to about 30%. There is also a slight increase in *Corylus*. These changes may indicate a gradual decline in the competitive ability of *Tilia*.

Betula, *Pinus* and *Populus* are so scarcely represented throughout the *Tilia- Quercus- Corylus* stage that it can be assumed that these trees were not present or were very scarce. The *Betula* percentages increase slightly in the later part of the stage. *Ulmus*, *Alnus*, *Fraxinus*, *Acer* and *Carpinus* are also scarcely represented, and it may be assumed that all or most of the pollen was derived from other sites. There is a slight decline in *Ulmus* and increase in *Fraxinus* at 84-85cm, which reflect the border between pollen zones VII and VIII in the regional pollen diagrams. *Fagus* is scarcely represented from about the same level, and increases somewhat in the late part of stage. *Hedera* and *Viscum* are scarcely represented throughout the stage. As these plants are likely to be underrepresented, it can be assumed that they occurred frequently in the tree tops as a climber and a parasite, respectively.

Shrubs, Ericales, open-ground and uncertain herbs, Poaceae, and aquatics become extremely scarce at the transition to the *Tilia- Quercus- Corylus* stage, but increase slightly in the later part, whereas acid-humus herbs are unchanged. Wet-ground herbs increase somewhat at the beginning of the stage and are nearly unchanged in its later part.

Among the shrubs, *Salix* and *Sorbus aucuparia* increase somewhat in the upper part of the stage. *Frangula* and *Ilex* are represented by scattered finds.

Calluna among the Ericales, and *Artemisia*, *Rumex acetosella* and *Plantago lanceolata* among the open-ground herbs increase slightly in the later part of the stage. *Chenopodiaceae*, *Campanula*, *Jasione* and *Hypericum* occur sporadically.

Anemone and *Mercurialis* on neutral humus are represented in the later part of the stage, whereas the acid-humus plants *Gymnocarpium*, *Pteridium*, *Melampyrum* and *Polypodium* are constant throughout. Poaceae and several herbs of uncertain significance increase in the later part.

Dryopteris-type increases at the beginning of the stage and *Carex*-type and *Dryopteris*-type, both assigned to wet-ground vegetation, are rather common throughout the stage; *Sphagnum* and *Glyceria* increase slightly in the later part.

Among the aquatics *Callitriche* and *Lemna* increase in the later part of the stage.

It is somewhat difficult to say which of the non-tree plants with low frequencies occurred near the site, and which of them are represented by pollen transported from other sites.

The *Tilia* and *Quercus* tree canopy certainly was very dense during the early part of the stage; *Corylus* formed an understorey, but shrub- and field-layer plants were very scarce. The spores of *Gymnocarpium*, *Pteridium* and *Polypodium*, and pollen of *Melampyrum* were dispersed to the site in low frequencies. *Salix* and Poaceae, which occurred near the hollow in the previous stage, were apparently suppressed by shade.

The expansion of *Dryopteris*-type probably indicates that the swamp vegetation around the hollow moved nearer to the site due to filling-in of the hollow by sediments.

As *Callitriche* and *Lemna* within the pond were not suppressed, light apparently still penetrated to the hollow through an opening in the tree canopy.

The presence of *Calluna*, open-ground herbs and Poaceae pollen in the upper part of the stage may have been due to transport from fields or pastures some distance away. The increase coincides with the zone border VII-VIII, from which time forest clearances occurred in the area. The increase in *Salix*, *Sorbus aucuparia*, some of the uncertain and wet-ground herbs (*Sphagnum*, *Glyceria*), and the aquatics (*Callitriche*, *Lemna*) may indicate a slightly more open tree canopy around and over the hollow.

The *Tilia- Quercus- Corylus* forest thus was initially very dense, but it appears that along with the decrease of *Tilia* and increase of *Quercus*, there was a slight decrease in the density of the canopy. At the same time, the effect of distant forest clearences can be seen. The dominance of *Tilia* and presence of *Corylus* indicate brown earth. The field layer plants point to neutral and acid brown earth and, possibly, some acid-humus sites.

High percentages for ignition residue persist throughout the *Tilia- Quercus- Corylus* stage. The large amounts of leaf litter, tree branches and probably some tree trunks that must have fallen into the hollow have thus disintegrated completely.

The average pollen corrosion remains about 50% during the *Tilia- Quercus- Corylus* stage. Hence the pond was dessicated periodically throughout the stage.

(*Fagus- Quercus* stage)

The *Tilia- Quercus- Corylus* stage is terminated by abrupt decreases in *Tilia* and *Corylus* and an increase in *Fagus*. The deposit above that level was homogenized. The sequence was thus truncated, but no lithological change could be observed, except for a slight change in colour (Table 46).

Fagus clearly became a dominant tree but, due to the disturbance, it is not possible to follow the transition from the *Tilia- Quercus- Corylus* stage to the *Fagus- Quercus* stage and events which caused this change. *Tilia* and *Corylus* occurred throughout the deposit up to the present surface, an indication of the thoroughness of the homogenization.

Shrubs and wet-ground herbs are somewhat more frequent in the disturbed deposit than they were in the *Tilia- Quercus- Corylus* stage, whereas other non-tree categories are unchanged. Mainly *Salix* in the shrub category and *Dryopteris*-type in the wet-ground herb category increased, indicating increased illumination at or around the hollow. Today there is no *Salix* or swamp vegetation around the hollow, which is in deep shade, and only a few *Glyceria fluitans* are present.

The soils around the *Glyceria* hollow today are podzolized and are covered by an acid humus layer with a poor field flora.

Molinia hollow

Pollen diagrams from section -A 12, N4, E3 from the centre of the *Molinia* hollow are shown on Plates XIV-XVI (cp. Table 65).

The *Molinia* hollow lies just east of an eastward slope, whereas the surface east of the hollow is rather even (Figs. 52 and 53). The sediments are peaty at 0-32cm and aquatic at 32-92cm; beneath is sandy till (Table 45). The original maximum water depth was 1.2m; the hollow was artificially drained by the middle of the 19th century (p. 87). *Fagus sylvatica* predominates around the hollow to-day (Figs. 52 and 55).

Only Holocene sediments are present in the *Molinia* hollow, so it did not exist in the late Weichselian.

The pollen diagram on plate XIV shows that dry-land non-tree plants are scarce throughout the sequence. It can be assumed that the area around the *Molinia* hollow was continously covered by trees. Wet-ground plants are commonly represented in the peat at 7-29cm, and aquatics are represented beneath 7cm.

The curves for tree pollen as percentages of AP first show high percentages for *Pinus*, *Betula*, and *Corylus* ; then for *Quercus* and *Tilia* ; for *Quercus* and *Betula* ; and finally for *Quercus* and *Fagus*.

Corroded tree pollen is frequent in the aquatic sediments (average corrosion 50-60%, Fig. 56), and scarce in the peat (average l-30%). The *Corylus* percentages can be assumed to be somewhat depressed and *Tilia* somewhat elevated in the pollen spectra with high corrosion; and *Pinus*, Poaceae, *Dryopteris*-type and other non-tree pollen somewhat elevated (p. 108). The curves for corroded pollen of individual tree genera in plate XIV show no relationship to the changes in the percentage curves.

A pollen spectrum at 49cm (indicated by black bars on plate XIV) differs distinctively from the pollen spectra above and beneath. The sample has higher percentages for *Pinus*, *Betula* and *Corylus*, and lower percentages for *Quercus*, and obviously belongs to an older part of the sequence (at about 78cm). A sampling error can be excluded; the occurrence of the aberrant pollen spectrum is thus mysterious and unexplained. This pollen spectrum was disregarded in the description of the vegetational sequence.

Reconstruction of the past vegetation

The AP/APc ratio varies l-3; hence, the changes in non-tree pollen percentages based on the corrected tree pollen sum are assumed to be more real than changes in percentages based on a sum of uncorrected pollen.

Pollen curves based on percentages of the corrected tree pollen sum are shown in plates XV-XVI. The vegetational sequence was divided into a *Tilia- Corylus- Pinus- Betula* stage, a *Tilia- Quercus- Corylus* stage, a *Quercus- Tilia- Betula* stage, and a *Fagus- Quercus* stage.

Tilia- Corylus- Pinus- Betula stage

In the *Tilia- Corylus- Pinus- Betula* stage, *Tilia* increases from 20 to 50%, and *Corylus*, *Pinus* and *Betula* decrease 20-10%. *Quercus* occurs at low frequencies and *Populus*, *Ulmus*, *Alnus* and *Acer* are scarce. This stage reflects the expansion of *Tilia* in the uppermost part of the *Corylus- Pinus- Betula- Populus* stage at the *Glyceria* hollow but, due to a higher sedimentation rate, the *Tilia* expansion (20-50%) which occupied only 2cm at the *Glyceria* hollow covers 10cm at the *Molinia* hollow. The sediment at the *Molinia* hollow has a very high ignition residue (Plate XV), indicating an influx of mineral matter, and a strong mineralization of organic matter.

The *Tilia* curve is somewhat unsteady with slight minima which correspond to slight maxima for *Corylus* and *Betula*. The expansion of *Tilia* was thus hampered by slight set-backs.

Hedera and *Viscum* are represented throughout the *Tilia- Corylus- Pinus- Betula* stage. The shrubs have decreasing frequencies; Ericales, the herbaceous land plants, and the aquatics have rather low frequencies.

The shrubs were similar to those found in the *Corylus- Pinus- Betula- Populus* stage at the *Glyceria* hollow, *Salix* being most frequent. *Calluna* and *Empetrum* represent the Ericales. Within the open-ground plants, *Artemisia*, *Rumex acetosella*, *Jasione* and *Sedum* are represented; *Anemone* was present on neutral forest soil, and *Pteridium*, *Gymnocarpium* and *Polypodium* on acid humic soil. Poaceae were rather frequent, and several herbs of uncertain significance are represented. *Carex*-type, *Dryopteris*-type and *Glyceria* were the most frequent wet-ground plants, *Lemna* was present, and *Pediastrum* colonies were frequent in the pond.

The *Tilia- Corylus- Pinus- Betula* stage thus had a fairly well developed field layer with acid-soil plants, neutral-soil plants and some heliophilous plants near the site or at some distance; *Salix*, Poaceae and swamp vegetation occurred around the pond; and the pond itself was fairly illuminated.

The minima in the *Tilia* curve are reflected by maxima in several of the non-tree plants, particularly *Salix*, Poaceae and *Carex*-type, and in *Pediastrum*, whereas *Pteridium* and *Gymnocarpium* are unchanged. The set-backs in the expansion of *Tilia* are thus reflected by increases in *Corylus* and *Betula*, and in the vegetation at the hollow.

As mentioned above, there are no Late-Weichselian sediments in the *Molinia* hollow, and it appears that early Holocene sediments are missing too. The hollow was thus dry during both the Late Weichselian and the early Holocene, and apparently did not come into existance until some point in time corresponding to the late part of the *Corylus- Pinus- Betula- Populus* stage at the *Glyceria* hollow. The collapse of buried ice does not seem a highly likely explanation; however, one still wonders whether such a process could have been responsible. The set-backs in the *Tilia* expansion, one of which can also be seen at the *Glyceria* hollow, point to disruptions of the *Tilia* canopy, and hence, to an unstable soil surface. However, the possibility of the persistence of ground ice buried in the moraines of the area cannot be satisfactorily evaluated from the vegetational data alone.

As *Pteridium* and *Gymnocarpium* do not reflect the minima in the *Tilia* curve, sites with acid soil were unaffected by possible land-slides.

The high pollen corrosion indicates periodic desiccation of the pond in the *Molinia* hollow.

Tilia- Quercus- Corylus stage

The *Tilia- Quercus- Corylus* stage at the *Molinia* hollow is very similar to the lower part of the *Tilia- Quercus- Corylus* stage at the *Glyceria* hollow.

The *Tilia* curve initially has a peak at 70%, is rather constant at around 60% in the lower part of the stage, and somewhat irregular in the upper part. Initial *Quercus* values are around 5%, then increase to 20%, with irregular peaks in the upper part. *Corylus* is rather low and probably occurred under gaps in the tree canopy and under the trees. If unchanged and calculated outside the pollen sum, the frequencies are around 30%. *Corylus* understorey was thus scarce. *Pinus* and *Betula* nearly vanished during this stage, and *Populus*, *Ulmus*, *Alnus*, *Fraxinus* and *Alnus* are very scarce. One seed of *Alnus* (Table 45) indicates that this tree occurred at the site. There is a slight increase in *Fraxinus* at the middle part of the stage, which is radiocarbon-dated at 5400 ^{14}C years ago (Table 56), and thus corresponds to the zone border VII/VIII in the regional pollen diagrams. *Fagus* and *Carpinus* are scarcely represented above that level.

Hedera and *Viscum* were present throughout the *Tilia- Quercus- Corylus* stage. Shrubs and herbaceous plants were very scarce. There is a slight increase for wet-ground plants and aquatics in the upper part of the stage.

Salix and *Sorbus aucuparia* are represented within the shrubs, *Calluna* within the Ericales, and *Pteridium*, *Gymnocarpium*, *Polypodium* and *Melampyrum* on acid humic soil. *Sedum*, *Artemisia*, *Jasione*, *Rumex acetosella*, Chenopodiaceae and *Plantago lanceolata* from open-ground vegetation are represented. The pollen from some of these plants may have derived from distant sites. *Plantago lanceolata* pollen occurs below the zone border VII/VIII, but becomes slightly more common above that level. *Plantago lanceolata* was thus present within the region before the neolithic clearences and increased slightly at the zone border.

Poaceae and plants of the uncertain category are scarce. *Carex*-type within the wet-ground group is also scarce, whereas *Dryopteris*-type, *Sphagnum* and *Glyceria* increase somewhat in the upper part of the stage - so do the aquatics *Lemna* and *Callitriche*.

As at the *Glyceria* hollow, the *Tilia- Quercus* canopy around the *Molinia* hollow was dense, the shrub and field vegetation was scarce, and the hollow itself was shaded. *Pteridium*, *Gymnocarpium*, *Polypodium* and *Melampyrum* indicate somewhat acid soil, the herbs from open-ground a few sunny spots at more or less distant sites.

The increase in the wet-ground plants may have been due to expanding swamp vegetation due to the formation of peat around the hollow; the ignition residue decreases simultanously and indicates a decreased influx of mineral matter. The occurrence of *Sphagnum* and *Osmunda* shows that the peat was somewhat acid. The increase of *Lemna* and *Callitriche* may imply better illumination of the pond in the upper part of the stage.

Two or three minima in the *Tilia* curve in the upper part of the stage, and corresponding maxima for *Quercus*, have no counterparts in the lower part of the stage. The *Tilia* minima occur from 5400 ^{14}C years ago (4300 BC) and later. There are no distinctive indications of human activity at the site; the changes in the *Tilia* and *Quercus* curves may, however, be interpreted as traces of intermittant human activity at the cost of *Tilia*.

Quercus- Tilia- Betula stage

The *Quercus- Tilia- Betula* stage at the *Molinia* hollow is initiated by a distinctive decrease in *Tilia*, and increases in *Quercus* and *Betula*. The curves are somewhat unsteady. *Tilia* decreases to less than 10% during the stage, *Quercus* has frequencies around 50% and one distinctive minimum, *Betula* has one large peak, at 50%, and several minor peaks, and *Corylus* has one minor peak. *Fagus* increases in the upper part of the stage. Other trees are very scarce.

Hedera and *Viscum* are slightly less frequent than in the preceding stage. The shrubs have maxima in the upper part of the stage, and Ericales, open-ground herbs, Poaceae and the uncertain group are slightly more frequent than in the preceding stage. The wet-ground plants are unchanged, and there are slight peaks for aquatics.

Salix is most important among the shrubs with one high, and a few moderate peaks. *Sorbus aucuparia* is frequent, with at least one minor peak, and *Frangula* and *Juniperus* are scarce.

Calluna increases slightly throughout the stage, whereas the acid-humus herbs are unchanged and similar to the preceding stage. *Anemone* and *Stellaria holostea* from neutal forest soil are steadily represented.

Artemisia, *Jasione*, *Rumex acetosella*-type and *Plantago lanceolata* are slightly more frequent than in the preceding stage, and *Plantago major*, *Trifolium* cf. *repens*, *T.* cf. *pratense*, *Hypericum* and *Scleranthus perennis* have appeared among the open-ground plants. *Secale* pollen occurs sporadically in the upper part of the stage.

Poaceae have increased somewhat, and *Apiaceae* and *Galium*-type are particularly frequent within the uncertain category. *Carex*-type, *Sphagnum* and *Glyceria* increase during the stage, *Glyceria* having one pronounced peak. There are also some minor peaks for the aquatics *Lemna* and *Callitriche*, and *Potamogeton* appeared within the pond.

The *Quercus- Tilia- Betula* stage at the *Molinia* hollow has no counterpart at the *Glyceria* hollow, where the *Tilia- Quercus- Corylus* forest, - except for the steady decrease of *Tilia* and increases in *Quercus*, *Corylus* and *Betula*- was essentially unchanged at the levels below and above the appearance of a continuous *Fagus* curve. The events that lead to the abrupt decrease in *Tilia* were thus concentrated around the *Molinia* hollow. Hence, the abrupt changes in the tree pollen curves there cannot have been due to natural causes, and indicate the intervention of Man. *Tilia* apparently was felled selectively in favour of *Quercus*. The various peaks on the *Betula* curve indicate the removal of trees; *Corylus* was also favoured somewhat by the felling of trees. The *Fagus* curve increases somewhat in the upper part of the stage, but with several set-backs, which indicate that this tree was also checked by intermittant felling.

Sorbus aucuparia and *Frangula* were apparently favoured by better illumunation. The pronounced peaks for *Salix* indicate fair light conditions, which allowed *Salix* scrub to develop intermittantly around the hollow, as was also the case for herbaceous vegetation around and within the hollow. The frequencies of *Juniperus*, *Calluna* and the herbs from open ground remain low; their slight increase may thus be due to an expansion of field or pasture areas outside the forest. This is true too for the Poaceae pollen, whereas the herbs from acid humus do not increase. Hence, there is no indication that the forest was cleared or that grazing by cattle occurred.

There is, accordingly, evidence that *Tilia* was felled around the *Molinia* hollow in favour of *Quercus*, and that the felling of trees occurred repeatedly. This was probably a continuation of similar activity initiated in the later part of the *Tilia- Quercus- Corylus* stage at about 5400 ^{14}C years ago (4300 BC). The presence of *Fagus* and *Secale* indicates that human intervention persisted throughout Subboreal and early Subatlantic time. The forest was thus exploited locally for millenia, but Man did not settle down and clear the area.

The purpose of the human activity around the *Molinia* hollow is somewhat difficult to see. Both exploition of *Tilia* for leaf-fodder and slash-and-burn cultivation have been mentioned (Andersen 1978); however, such activities are difficult to prove, and raise the question of why *Quercus* should have been left unscathed, since it would have been useless for leaf-fodder, and should have been felled along with the other trees if slash-and-burn cultivation was carried out. One possible explanation for the preference for *Quercus* at the cost of *Tilia* is a wish to produce mast for the foddering of pigs. The bones of pigs are very frequent in Neolithic, Bronze Age and Early Iron Age settlements (Winge 1919, Higham 1967, 1970), and rearing of swine in woodlands was important (Higham 1967). It may be assumed, accordingly, that peasants who lived in settlements near the forest cleared *Tilia* around the *Molinia* hollow in order to promote the browsing of swine on the mast of *Quercus*.

Fagus - *Quercus* stage

The *Fagus* - *Quercus* stage was initiated by a steep increase in *Fagus* and decreases in *Quercus*, *Tilia*, *Corylus* and *Betula*. *Fagus* remained dominant until the present day, at around 70-80%, with two pronounced minima - at 22-26cm and 12-16cm. *Quercus* is around 10-20% with two peaks, and increases to 30% at the topmost part of the stage. *Tilia* nearly vanishes. *Betula* decreases to around 5%, has two maxima at about 10%, and nearly vanishes at the topmost part of the stage. The other trees are very scarce. *Picea* has a low, but continuous curve at the topmost part.

Hedera is represented by a few finds, whereas *Viscum* has disappeared. The shrubs become very scarce, and Ericales, open-ground and acid-humus herbs are scarce. These plants have a few low maxima. Poaceae and the uncertain group are scarce in the lower part of the stage and increase in the upper part; the Poaceae have a pronounced maximum and then decrease. The wet-ground herbs increase strongly at the beginning of the *Fagus* - *Quercus* stage. They have three maxima, and then decrease abruptly at the topmost part. Aquatics are present for most of the stage, and disappear at the uppermost part.

Among the shrubs, *Salix* is low, and has a slight peak at 21cm. *Sorbus aucuparia* and *Frangula* occur sporadically, and *Juniperus* is represented by low frequencies at 5-14cm. *Calluna* also increases slightly at 5-14cm. The acid-humus herbs *Pteridium*, *Gymnocarpium*, *Polypodium* and *Melampyrum* occur sporadically at below 5cm. *Anemone* and *Stellaria holostea* from neutral soil have a few occurrences. Several open-ground herbs are scattered throughout the stage. *Rumex acetosella* -type shows a low maximum at 5-14cm. *Centaurea cyanus* appears at 24cm and is represented by scattered finds. Among cultivated plants, *Secale* is constantly present, *Fagopyrum* occurs above 25cm, and there are a few finds of *Avena*. Among the uncertain group, *Galium* is rather frequent below 4cm, and *Ranunculus acer* -type has a pronounced maximum at 6-14cm.

Carex-type, *Dryopteris*-type and *Sphagnum* on wet ground increase strongly at the beginning of the stage, and both curves show two distinctive minima. They nearly disappear at 6cm. *Glyceria* is scarcer than in the preceding stage and also vanishes at 6cm. *Schoenoplectus* (*Scirpus lacustris*) is present at 6-14cm.

The aquatics *Lemna* and *Callitriche* are still frequent in the lower part of the *Fagus*- *Quercus* stage, and disappear at the upper part.

The area surrounding the *Molinia* hollow was thus covered by *Fagus* forest during the *Fagus*-*Quercus* stage, as it is today, and *Quercus* occurred with scattered specimens. The two distinctive minima in the *Fagus* curve correspond to maxima for *Quercus* and, less pronounced, for *Betula*. These minima in the *Fagus* tree cover were probably due to felling of *Fagus* trees. The abrupt disappearance of *Betula* at 6cm coincides with the apperance of *Picea* in low, but constant frequencies. Hence, it falls within the time of modern forest management. It can therefore be supposed that the *Betula* trees were removed artificially at that time.

Tilia and *Corylus* vanished at the expansion of *Fagus* ; their occurrences at the level of the first *Fagus* minimum may indicate that they were still present in the vicinity. The uppermost *Tilia* occurrences are probably due to redeposition during human disturbance of the deposit (se below).

The *Fagus*- *Quercus* forest was initially very dense. The herbs on acid-humus are similar to the preceding stage. Hence, there was a scarce field layer. Shrubs and open-ground herbs were very scarce.

During the first *Fagus* minimum at 22-26cm, there was a slight increase of *Salix* and open-ground herbs; however, there is no indication that the tree canopy was less dense.

During the second *Fagus* minimum, at 12-16cm, there are slight increases in *Juniperus*, *Calluna* and the open-ground herbs - particularly *Rumex acetosella*, *Plantago lanceolata*, and the cultivated *Secale*- and there are several finds of *Fagopyrum*. This pollen probably derived from field and pasture areas somewhere in the region.

The sediment of the *Fagus*- *Quercus* stage was peat, and wet-ground vegetation near the site was recorded. Seeds of *Carex rostrata* and *C.caespitosa* were recorded (Table 45). The swamp vegetation in the hollow was somewhat acidophilous. *Galium*-type and *Ranunculus acer*-type probably represent plants that grew in the hollow. Achenes of *Ranunculus flammula* were recorded (Table 45). The presence of *Callitriche* and *Lemna* indicate that there were small pools in the swamp. The high pollen and spore production of the swamp vegetation indicates that there was a small opening in the tree canopy above the hollow.

The two minima for wet-ground plants correspond to the minima in the *Fagus* curve, but a likely explanation is not immediately obvious. The wet-ground plants and the aquatics decrease abruptly at 6-7cm where a dark-coloured horizon with sand lenses occurs (Table 45). This level coincides with the appearance of *Picea* pollen and the felling of *Betula*, and it can be assumed that the ditch which drains the hollow today (p. 87) was established at that time, causing the swamp vegetation to disappear. The sand lenses are probably material derived by the digging of the ditches. The *Tilia* pollen, and a slight maximum for *Quercus* at the same level, may derive from such material dug up from the bottom of the hollow.

The curve for Poaceae pollen is uncorrelated with the curves for open-ground plants and wet-ground plants. It is difficult to say whether the pollen in the lower part of the *Fagus*- *Quercus* stage was derived from dry-land or from wet-ground vegetation. The maximum at 5-9cm was probably due to wet-ground species, which succeeded the *Carex*- *Dryopteris*- *Sphagnum* swamp; *Molinia coerulea* thus occupies the hollow today.

The low pollen corrosion in the peat layers (Fig. 56) was probably due to an acid environment.

The influx of mineral matter to the hollow was apparently slight.

Matrikel hollow

The Matrikel hollow occupies a shallow depression at the north-western corner of the research area (p. 88, Fig. 8), and was examined in order to obtain an upward extension of the vegetational sequence at the *Glyceria* hollow, where the youngest deposits were disturbed.

Pollen diagrams from the centre of the Matrikel hollow are shown in Plates XVII-XIX (cp. Table 66).

The silty sand beneath the shallow peat and sandy gyttja layers here corresponds to the sorted meltwater sand which partly covers the sandy till in the research area (fig. 10). The pollen spectra from the lowermost centimeters of the sandy gyttja were mixed with pollen of early Holocene age (*Pinus*, *Betula*, *Corylus*). These pollen spectra were disregarded. The samples above 33cm contained pollen of middle or late Holocene age, hence continuous sedimentation began at that time.

The tree pollen spectra in the continuous sequence (Plate XVII) are dominated at first by *Quercus* and *Corylus* ; then by *Quercus*, *Corylus* and *Betula*, and, finally, by *Quercus*, *Fagus* and *Betula*. Shrubs, Ericales, open-ground and acid-humus herbs, and the uncertain group, are scarce in the lowermost part, and there is a maximum for Ericales and the open-ground herbs at 3cm below surface. The Poaceae are correlated with the open-ground herbs, hence it may be concluded that a major part of this pollen derived from vegetation on dry and open sites. Wet-ground plants are frequent, and aquatics present, except in the uppermost centimeters.

It may be assumed that the tree cover was fairly dense throughout the sequence, except for the 3cm level, where an open tree vegetation may be indicated.

The pollen spectra from the peat at 4-21cm do not vary at all, whereas there are well-differentiated pollen assemblages above and below these. Hence, the peat between 4 and 21cm has been homogenized. The forest was grazed by cattle in the 18th century, and the grazing ceased in the early 19th century (p. 8). It can be assumed, therefore, that the peat layers at 4-21cm were trampled by cattle searching for drinking water and that the pollen spectra above 4cm derive from the time after the cattle grazing had ceased. The disturbed pollen spectra are indicated by bars on the pollen diagrams.

The average pollen corrosion (Fig. 56) is about 50% in the gyttja deposit, and 10-20% in the peat, indicating periodic desiccation of the hollow, and fairly acid condition during the formation of the peat.

Reconstruction of the past vegetation

The AP/APc ratio varies 2-3 (Plate XVII). Pollen diagrams based on the corrected tree pollen sum are shown on Plates XVIII-XIX. It can be assumed that the tree cover was discontinuous at the 3cm level, and that the non-tree pollen percentages are therefore somewhat exaggerated at that level.

The vegetational sequence was divided into a *Quercus- Tilia- Corylus* stage, a *Quercus- Tilia- Betula* stage, a *Fagus- Quercus* stage, and a *Fagus- Quercus- Betula* stage.

Quercus- Tilia- Corylus stage

The *Quercus- Tilia- Corylus* stage at the Matrikel hollow has about 50% *Quercus*, 30% *Tilia*, 10% *Corylus*, and 5% *Betula*, whereas the other trees are insignificant. *Fagus* occurs at low percentages. The pollen spectra thus reflect undisturbed *Quercus- Tilia* forest with *Corylus* understorey. The forest composition differs from the *Tilia- Quercus- Corylus* stage at the *Molinia* hollow, where *Tilia* was dominant (around 60%), *Quercus* was less important (20%), and *Fagus* was absent; and rather, resembles the uppermost part of the *Tilia- Quercus- Corylus* stage at the *Glyceria* hollow (*Tilia* 30%, *Quercus* 30%, *Fagus* low).

Viscum is represented; the non-tree plants are scarce except for the wet-ground plants.

There are a few finds of *Sorbus aucuparia* and *Salix*, and *Calluna* ; *Plantago lanceolata* and Poaceae are scarce. There is one find of *Fagopyrum*. *Gymnocarpium* and *Pteridium* have low percentages. Abundant *Carex*-type pollen and *Dryopteris*-type spores indicate swamp vegetation within the hollow. There is no indication that the forest around the Matrikel hollow was exploited during the *Quercus- Tilia- Corylus* stage.

As mentioned above, the Matrikel hollow had been wet at certain times in the early Holocene; it is, however, difficult to say why the continuous sedimentation began at such a late time.

Quercus- Tilia- Betula stage

Betula expands in the *Quercus- Tilia- Betula* stage from 5% in the preceding stage to nearly 20%, and *Quercus* decreases somewhat, whereas *Tilia* and *Corylus* are unchanged.

Hedera and *Viscum* are represented and the non-tree plants are nearly unchanged except for the wet-ground group, which decreases slightly. Aquatics are represented.

Sorbus aucuparia and *Salix*, *Calluna*, and open-ground herbs such as *Plantago lanceolata*, *Artemisia*, *Rumex acetosella*-type and Poaceae are scarce. *Spergula* is recorded. *Anemone* is represented, and *Gymnocarpium*, *Pteridium*, *Polypodium* and *Melampyrum* from acid humus are recorded. *Dryopteris*-type is dominant on wet ground, and *Glyceria* and *Sphagnum* are represented. *Callitriche* and *Lemna* were present in the hollow.

The increase in *Betula* indicates human activity. *Quercus* trees were apparently felled - giving *Betula* an opportunity to replace *Quercus* ; the forest was, however, not strongly disturbed by man in the *Quercus- Tilia- Betula* stage.

Quercus- Betula stage

There is a *Betula* maximum at the beginning of the *Quercus- Betula* stage and an increase of *Quercus* at the end of the stage. *Tilia* and *Corylus* decrease, and *Fagus* begins to increase at the end of the stage.

The *Quercus- Betula* stage thus witnessed a decrease of *Tilia* in this part of the forest. *Tilia* was apparently felled or exploited and *Betula* expanded. Later *Quercus*, and then *Fagus*, expanded at the cost of *Tilia*, *Corylus* and *Betula*.

Hedera and *Viscum* are still represented in the *Quercus- Betula* stage. Shrubs, Ericales, open-ground herbs and Poaceae increase somewhat. The wet-ground plants decrease slightly, and the aquatics are frequent.

Sorbus aucuparia and *Salix* were present, and *Calluna* increased slightly. *Plantago lanceolata*, *Rumex acetosella*-type and Poaceae increase distinctively and there are a few finds of *Trifolium* cf. *repens*, *Scleranthus annuus*, *Fagopyrum* and *Secale*. *Anemone* and *Stellaria holostea* from neutral soil, and *Gymnocarpium*, *Pteridium*, *Polypodium* and *Melampyrum* from acid soil are represented. *Dryopteris*-type and *Carex*-type from wet ground are scarcer, and *Glyceria* increases somewhat. *Callitriche* from the pond is rather frequent.

The open-ground herbs and Poaceae increase to so high frequencies that some grazing activity by cattle can be assumed. The changes in the local vegetation may indicate a somewhat higher water level which may have been due to a scarcer tree cover.

It thus appears that the forest around the Matrikel hollow was exploited somewhat in the *Quercus-Betula* stage. *Tilia* was felled and was succeded by *Betula* and, later, by *Quercus* and *Fagus*, and there was some grazing by cattle. As these events succeded a primeval forest where *Tilia* occurred at about 30% and *Fagus* was continuously represented, they must be considerably younger than the clearances of *Tilia* at the *Molinia* hollow, and slightly younger than the latest part of the undisturbed sequence at the *Glyceria* hollow.

Fagus- Quercus stage

The *Fagus- Quercus* stage at the Matrikel hollow is initiated by a steep increase of *Fagus*, which remains dominant (about 60%) throughout the stage. *Quercus* decreases to about 20%, *Betula* to about 10%, and *Tilia* and *Corylus* to low values.

Hedera and *Viscum* are not recorded. The non-tree categories are mostly low and slightly scarcer than in the *Quercus- Betula* stage. Ericales increase slightly and the wet-ground plants retain moderate values similar to those found for the preceding stage. Aquatics are scarcely represented.

Sorbus aucuparia, *Salix*, *Frangula* and *Juniperus* are scarce. *Calluna* is about 5%, Poaceae are 10-15%, and *Plantago lanceolata*, *Artemisia* and *Rumex acetosella*-type are scarce. There are scattered finds of *Fagopyrum*, *Secale* and *Hordeum*-type. *Anemone* and *Stellaria holostea* are scattered, and *Gymnocarpium*, *Pteridium*, *Polypodium* and *Melampyrum* occur with low frequencies.

Dryopteris-type, *Carex*-type, *Glyceria* and *Sphagnum* are the most frequent wet-ground plants. *Callitriche* is scarce.

Fagus forest thus developed around the Matrikel hollow at the transition to the *Fagus- Quercus* stage, and *Quercus* and *Betula* were suppressed. The tree vegetation shows less influence by human activity than in the *Quercus- Betula* stage. Due to the disturbance of the deposit it is not possible to say whether *Quercus* and *Betula* were favoured by continuous human activity or by intermittant tree fellings, as was the case in the *Fagus- Quercus* stage at the *Molinia* hollow. Neither is it possible to determine whether the *Tilia* and *Corylus* pollen found in low frequencies was derived from contemporaneous trees or was mixed into the deposit. It is not clear whether the forest was grazed in the *Fagus- Quercus* stage; the scattered grains of cultivated plants may have been derived from fields outside the forest. Swamp vegetation and aquatics apparently occurred in the hollow, and the peat was rather acid.

Fagus- Quercus (- *Betula*) stage

The *Fagus- Quercus* (- *Betula*) stage was initiated by a decrease in *Fagus*. There is a *Betula* maximum in the lower part of the stage, and *Quercus* increases somewhat. *Tilia*, *Corylus* and other trees are scarcely represented. *Picea* increases slightly near the top of the deposit.

Shrubs, Ericales, open-ground herbs, Poaceae and herbs in the uncertain category have a maximum in the lower part of the stage, whereas acid-humus plants are unchanged. The wet-ground plants decrease, and aquatics disappear.

There are distinctive maxima for *Juniperus*, *Calluna*, and several open-ground herbs such as *Plantago lanceolata*, *Rumex acetosella* and Poaceae, whereas *Fagopyrum*, *Secale*, *Hordeum*-type and *Avena* are scarcely represented.

Pteridium still occurs, but other acid-humus herbs disappear. *Dryopteris*-type, *Carex*-type, *Glyceria* and *Sphagnum* on wet ground nearly disappear.

The *Fagus- Quercus* (- *Betula*) stage thus shows transition from at first an open tree vegetation to regenerated forest with *Fagus- Quercus- Betula* and then *Fagus- Quercus* forest. The abandonment of cattle grazing in Eldrup Forest in the early 19th century was signified in pollen diagrams from humus layers (Andersen 1979a, and below) by successive maxima of open-ground herbs, *Calluna*, *Juniperus* and *Betula*. *Quercus* regenerated in the grazed areas and reached flowering age about 1850. *Betula* was felled at that time, and planted *Picea abies* began to flower. The same succession is seen in the *Fagus- Quercus* (- *Betula*) stage in the undisturbed topmost peat layer at the Matrikel hollow.

Tilia, *Corylus* and *Hedera* are absent today. The finds in the *Fagus- Quercus*-(*Betula*) stage probably are due to material that was washed into the hollow from soils around the site.

The Matrikel hollow is rather dry and is inhabited by *Molinia caerulea* today. The disappearance of the swamp vegetation and *Callitriche* was probably due to dessication by increased water consumption, and shade, from the now dense tree vegetation.

THE VEGETATIONAL SEQUENCES AT THE SOIL SECTIONS IN ELDRUP FOREST

Pollen diagrams from six soil sections are shown in Plates XX-XXV. Two sections derive from the vicinity of the *Molinia* hollow (-C9, -A 13, N4, E2, Fig. 52), three from the vicinity of the *Glyceria* hollow (H 16, C 19, E 13, Fig. 52), and one from the vicinity of the Matrikel hollow (Matrikel bank, Ma, Fig. 8). The diagrams show non-tree plants in percentages of total pollen and spores, trees in percentages of the corrected tree pollen sum, and curves for non-tree categories and for individual non-tree plants in percentages of total pollen and spores.

Mainly dry-land vegetation is represented at the soil sections; hence, the difficulties in distinguishing dry-land plants from wet-ground plants that were encountered at the wet hollows are avoided.

A survey of forest stages is shown in Table 61 (p. 142). Taxa not shown on the pollen diagrams are indicated in Tables 67-70.

Soil section -C 9

Section -C 9 is situated 35m SE of the *Molinia* hollow (Fig. 52). The section is podzol on sandy till with a deep humus layer (Table 2). The area around the site is rather flat; *Quercus petraea* is more frequent than *Fagus sylvatica* (Figs. 52 and 55).

Pollen corrosion was moderate (average corrosion around 30%) in the mineral soil and low (0-10%) in the humus layer (Fig. 57).

Reconstruction of the past vegetation

The vegetational development at section -C 9 was divided into a *Tilia- Quercus- Corylus* stage, a *Quercus-*

Tilia- Betula stage, and a *Fagus- Quercus* (- *Betula*) stage (Plate XX, Table 67).

Tilia- Quercus- Corylus stage

The *Tilia- Quercus- Corylus* stage is rather homogeneous, probably due to mixing of the pollen assemblages.

Tilia is dominant (50-60%), with less *Quercus* (20%) and *Corylus* (10-15%). There is a slight *Betula* maximum, and *Quercus* begins to increase at the topmost part of the stage. Other trees occur sporadically (Table 67).

Hedera and *Viscum* are represented. Non-tree plants are very scarce except for the acid-humus group.

There are scattered finds of *Sorbus aucuparia*, *Salix* and *Calluna* ; and Poaceae have low frequencies. *Dryopteris*-type and *Gymnocarpium* are frequent, and *Polypodium*, *Pteridium* and *Melampyrum* are scarce. *Carex*-type is scarce.

The forest recorded at the site was very similar to the forest from the *Tilia- Quercus- Corylus* stage at the *Molinia* hollow (Plate XV). Hence, the high Tilia pollen frequencies cannot have been due to stem flow as suggested by Keatinge (1982), as stem flow did not occur at the hollow site. Tree pollen from the preceding *Betula* and *Corylus- Pinus- Betula- Populus* stages is not present and was apparently totally destroyed. The slight *Betula* maximum may indicate traces of human activity, as seen in the upper part of the *Tilia- Quercus- Corylus* stage at the *Molinia* hollow.

Shrubs and field layer plants were scarce, except for the ferns. The *Dryopteris*-type spores represent exclusively dry-land plants, in contrast to the *Molinia* hollow. The *Pteridium* spores are so scarce that it can be assumed that this fern did not occur in the field layer at the site but probably grew elsewhere, on more open sites. Since tree pollen from former vegetational stages is lacking, the abundant *Dryopteris*-type and *Gymnocarpium* spores could possibly have accumulated in the soil due to the destruction of tree pollen, as fern spores are particularly unaffected by corrosion (p. 108). If that had been the case, one would expect the fern spores to increase with depth. This not being the case, the *Dryopteris*-type and *Gymnocarpium* spores are unlikely to be seriously overrepresented. It may be concluded, accordingly, that the field layer of the *Tilia- Quercus- Corylus* forest contained ferns, and that acid brown earth had developed. *Gymnocarpium* and *Dryopteris carthusiana* occur today on acid brown earth and on acid humus layers in Eldrup Forest (pp. 75 and 78).

The productivity of dark fungal hyphae was low because of the prevalance of *Tilia* leaves in the litter fall, and the hyphae were comminuted intensively by oribatids (Andersen 1983, Fig. 66). The moderate pollen corrosion indicates moderately acid soil (ph 5.5-6.0).

Quercus- Tilia- Betula stage

The *Quercus- Tilia- Betula* stage at section -C 9 is initated by a strong increase of *Quercus* and an increase in *Betula*, at the cost of *Tilia*.

Viscum and *Hedera* were still present at the lower part of the stage. The shrubs and the open-ground herbs increase slightly.

Sorbus aucuparia, Poaceae and a few open-ground herbs increase slightly. *Dryopteris*-type is still common, and *Gymnocarpium* is scarce.

The changes that initiated the *Quercus- Tilia- Betula* stage are the same as seen at the *Molinia* holow (Plate XV). *Tilia* thus was cleared by Man and was replaced by *Quercus* and *Betula*. The slight increase in Poaceae and open-ground herbs indicate pastures or fields, however, not at the site itself. The abundant *Dryopteris*-type spores indicate undisturbed field vegetation on acid substrate.

The change from *Tilia*-dominated to *Quercus*-dominated forest coincide with a change from an oligotrophic brown earth stage through an indistinct podzoloid stage to a stage where humus began to accumulate (Andersen 1983, Fig. 66). This change was apparently due to the change from litter fall of *Tilia* leaves to *Quercus* and *Betula* leaves. The soil became more acid, and the soil fauna was impoverished.

The *Quercus- Tilia- Betula* stage at section -C 9 comprises only the lower part of the *Quercus- Tilia- Betula* stage at the *Molinia* hollow. The *Betula* maximum and the *Fagus* increase in the upper part of the *Quercus- Tilia- Betula* stage at the *Molinia* hollow (Plate XV) are thus missing at section -C 9. This hiatus is somewhat difficult to explain. The human activity apparently caused complete disintegration of organic matter.

Fagus- Quercus (- *Betula*) stage

The *Fagus- Quercus* (- *Betula*) stage begins with increasing *Fagus* and decreasing *Quercus*. *Fagus* is generally high (70%). There are two minima in the *Fagus* curve, the first reflected by a maximum for *Betula*, and the second by a *Quercus* maximum. *Fagus* decreases somewhat near the top of the stage and is replaced by *Quercus*. *Tilia* is very low with a few minor peaks.

Viscum has disappeared, and *Hedera* is scarce. Shrubs and Ericales have distinctive maxima near the end of the second *Fagus* minimum. Open-ground plants and Poaceae have a slight maximum during the first, and distinctive maxima at the second *Fagus* minimum. The acid-humus plants decrease in the course of the stage. Wet-ground plants are slightly represented.

Sorbus aucuparia generally is low; *Juniperus* and *Calluna* have distinctive maxima, and *Vaccinium*-type a slight maximum, at the 2nd *Fagus* minimum. The Poaceae have two distinctive maxima, and *Rumex acetosella* one distinctive maximum. *Hordeum*-type, *Secale*, *Avena* and *Fagopyrum* are scattered. *Dryopteris*-type spores are at first abundant, but decrease during the first *Fagus* minimum; they then increase somewhat, and then decrease again during the second *Fagus* minimum. *Gymnocarpium*, *Pteridium* and *Melampyrum* are scarce. *Carex*-type and *Sphagnum* are more frequent than in the preceding stage.

The *Fagus- Quercus* (- *Betula*) stage thus begins with the *Fagus* expansion seen at the *Molinia* hollow and the same two *Fagus* minima are distinguished (Plate XV).

In contrast to the hollow diagram, there is a maximum for *Betula* instead of *Quercus* during the first *Fagus* minimum. *Fagus* trees thus were felled extensively and were replaced by *Betula* at this site. The maximum for Poaceae and *Rumex acetosella*-type indicate open areas near the site.

Calluna, Poaceae and *Rumex acetosella* increase distinctively during the second *Fagus* minimum, and there are maxima for the herbs, *Calluna*, and *Juniperus*, at the end of the *Fagus* minimum. The forest was thus grazed at or near the site, and the final abandonment of grazing was reflected by maxima for *Calluna* and *Juniperus*, before the forest regenerated. *Picea* is continuous from this level; hence grazing was abandoned in the early 18th century, as also seen at the Matrikel hollow.

Some *Fagus* trees were apparently felled some time after the abandonment of grazing, and *Quercus* expanded somewhat.

There are thus traces of two periods of human disturbance of the *Fagus- Quercus* forest at section -C 9, as at the *Molinia* hollow, and some *Fagus* trees were felled in the 19th century.

The slight maxima for *Tilia* may indicate that this tree was still present. The low frequencies of *Tilia* found up to near-surface levels are rather more likely due to inwashing of soil that contained fossilized *Tilia* pollen, as *Tilia* today is absent from Eldrup Forest.

The expansion of *Fagus* promoted the formation of the deep humus layer at section -C 9. Ferns with *Dryopteris*-type spores were at first abundant; they decreased later and were apparently influenced by human activity. The presence of *Carex*-type and *Sphagnum* indicates that the humus was moist. The decrease of *Dryopteris*-type, *Carex*-type and *Sphagnum* at the topmost level can probably be attributed to decreased moisture due to the establisment of ditches in the vicinity in the 19th century.

The podzol at section -C 9 was differentiated during the *Fagus- Quercus* (- *Betula*) stage.

Soil section -A 13 N4, E2

Section -A 13 is situated in a shallow depression on the east slope just west of the *Molinia* hollow (Figs.

52-54), and 11m from the section there (-A 13, N4, E3). It is a podzol-gley with only a thin bleached layer and a deep humus layer (Table 48). *Fagus* predominates around the site (Figs. 52 and 55).

Pollen diagrams are shown on Plate XXI. The bleached sand at 23-25cm contained *Tilia* and *Fagus* in high frequencies (49 and 35% APc), and low *Quercus* (3% APc). No similar pollen spectrum occurs at the *Molinia* hollow. Hence, it was assumed that this spectrum was mixed, and it was omitted. The topmost sample and the samples at 6-8cm contained low quantities of *Tilia* pollen (7-27% APc). It was assumed that these spectra were contaminated with washed soil material; hence, they were also disregarded.

Pollen corrosion is moderate or high in the mineral deposit (20-70%) and low in the humus layer (0-20%, Fig. 57). Hence, the pollen spectra from the mineral deposit may be assumed to be influenced slightly by differential removal of pollen.

Reconstruction of the past vegetation

The vegetational sequence at section -A 13 was divided into a *Tilia- Quercus- Corylus* and a *Fagus- Quercus* stage (Plate XXI, Table 68).

Tilia- Quercus- Corylus stage

Tilia dominates in the lower part of the *Tilia- Quercus- Corylus* stage (around 70%), *Quercus* is about 20% and *Corylus* about 10%. There is a distinctive *Quercus* maximum at the upper part of the stage, at the cost of *Tilia*.

Hedera and *Viscum* are frequent, and non-tree plants are scarce, except for the acid-humus plants.

The *Tilia- Quercus- Corylus* stage corresponds to the lower and middle parts of the *Tilia- Quercus- Corylus* stage at the *Molinia* hollow. Undisturbed *Tilia- Quercus- Corylus* forest, and the first *Quercus* maximum seen at the *Molinia* hollow are recorded.

The non-tree plants are very similar to those from the *Tilia- Quercus- Corylus* stage at section -C 9 (Plate XX). The field plants were, therefore, very scarce, except for the ferns. Among the ferns, *Dryopteris*-type is frequent, but somewhat scarcer than at section -C 9, and *Gymnocarpium* is frequent. Hence, ferns, especially *Gymnocarpium*, occurred in the field layer. *Anemone* is fairly frequent, especially in the upper part of the stage. *Anemone* is better represented on neutral than on acid soil (Andersen 1970). Hence, the soil at section -A 13 was probably less acid than the brown earth at section -C 9. The increase of *Anemone* in the upper part of the stage was probably due to improved illumination during the *Quercus* maximum. The pollen assemblages were presumably buried in the mineral soil during a former brown earth stage. The high corrosion indicates pH at 5.5-6.0.

No *Quercus- Tilia- Betula* stage was recorded at section -A 13. Hence, a hiatus is present here - which comprises the entire *Quercus- Tilia- Betula* stage from the *Molinia* hollow.

Fagus- Quercus stage

A *Fagus- Quercus* stage is recorded in the humus layer at section -A 13. There is a *Fagus* maximum at the beginning of the stage, which is similar to the first *Fagus* maximum at the *Molinia* hollow and section -C 9, followed by two more or less distinctive minima, and accompanied by maxima for *Quercus* as at the *Molinia* hollow.

In the middle part of the stage, shrubs (*Juniperus*), Ericales (*Calluna*) and open-ground herbs have more or less distinctive maxima which resemble the events seen at the *Molinia* hollow and section -C 9. *Dryopteris*-type and *Gymnocarpium* were scarce during the *Fagus- Quercus* stage.

Soil section H 16

This soil section was taken from a shallow depression near the *Glyceria* hollow. There was a deep humus layer and a rather shallow bleached mineral layer (A_{1+2} horizon, Table 2). No pollen was found below 4cm beneath the surface of the mineral soil. The area around the site is rather even. *Fagus* and *Quercus* trees are nearly 50% each around the site (Figs. 52 and 55).

Pollen corrosion was moderate (10%) in the mineral soil and in the lower part of the humus layer, and very low in the upper part of the humus layer (Fig. 57).

Reconstruction of the past vegetation

A *Fagus- Quercus* stage is recorded at section H 16 (Plate XXII, Table 69).

Fagus- Quercus stage

Fagus was probably the only tree present at first; later *Quercus* increased slightly. There is a slight *Betula* maximum at the middle of the stage, and *Quercus* then increases strongly. *Tilia* is represented in the lowermost sample. The *Fagus- Quercus* stage at section H 16 thus records the same *Fagus- Quercus* stage as seen at the Matrikel hollow. The *Tilia* at the lowermost level probably signifies the last *Tilia* occurrence seen at the transition to the *Quercus-Fagus* stage at that site.

There are maxima for shrubs and Ericales at the middle of the stage. Open-ground herbs and Poaceae are initially low, they increase to a maximum at the middle of the stage, and then decrease. Acid-humus plants are low in the lower part, and scarce in the upper part of the stage.

Juniperus is the most important shrub, and *Calluna* and *Vaccinium*-type represent the Ericales. *Rumex acetosella*-type is most frequent within the open-ground plants. *Hordeum*-type, *Secale*, *Fagopyrum* and *Avena* are scattered. *Dryopteris*-type and *Gymnocarpium* were present at the lower part, and there are slight maxima for *Pteridium* and *Melampyrum* at the middle part of the stage. *Sphagnum* and *Carex*-type are scarce.

The area around section H 16 was thus at first covered by *Fagus* forest. A few relic *Tilia* trees disappeared. The increase of Poaceae, *Rumex acetosella*-type and other open-ground herbs was due to grazing by cattle known to have occurred in the 18th century. The percentages for these plants are only moderately high; it may be assumed that the flowering of the grazed plants was reduced. The herbs increase somewhat at the middle part of the stage, *Vaccinium* had a slight peak, and *Calluna* and *Juniperus* became very frequent. Andersen (1979a) interpreted these changes as effects of the abandonment of grazing in the early 19th century. The herbs and *Vaccinium* and *Calluna* apparently began to flower profusely, and *Juniperus* invaded the glades. Slightly later, a few *Betula* trees began to flower. The *Quercus petraea* trees in the area derive from the early 19th century, as shown by tree ring counts (pp. 40-41). *Quercus* apparently invaded the glades when the grazing was abandoned, and the young trees were 6m tall about 1850. The increase in *Quercus* in the upper part of the *Fagus- Quercus* stage thus reflects the onset of flowering by the young trees. The *Fagus* trees, which had survived the grazing period, were cut away and allowed to regenerate by sprouting. The new generation of *Fagus* trees reached flowering age later than *Quercus* and were responsible for the increase in *Fagus* seen in the uppermost part of the pollen diagram. *Fagus* begins to flower at 40-50 years' age in open stands, but flowering maturity is retarded in dense stands (Lyr et.al. 1967). Hence, the increase in *Fagus* pollen probably occurred at about 1900. The few *Betula* trees were apparently cut about 1850, and planted *Picea abies* began to flower at that time.

The pollen diagram at section H 16 thus reflects a development which progressed from *Fagus* forest - to *Fagus* forest with grazed glades - to regeneration in the glades, by *Quercus* and, within the former clumps of *Fagus* trees, by *Fagus*. A similar development was reflected in the diagrams from the *Molinia* and Matrikel hollows and at the soil sections -C 9 and -A 13, described above.

The field layer of the undisturbed *Fagus* forest housed some ferns of *Dryopteris*-type, whereas *Gymnocarpium* was scarce. *Pteridium* and *Melampyrum* increased slightly during the grazing. The grazed glades thus had a rather acid soil. Nearly all field layer plants vanished when the present forest regenerated, presumably due to shade.

The soil at section H 16 developed from oligotrophic brown earth through an indistinctive podzoloid stage to a podzol with humus accumulation in the period when *Fagus* forest prevailed (Andersen 1979a, 1982, Fig. 66).

Soil sections C 19 and E 13

The sections C 19 and E 13 are situated south and southeast of the *Glyceria* hollow (Fig. 52). Section C 19 is podzol on sandy till, and E 13 is podzol on sorted sand (Table 2). The humus layer was 5cm deep at C 19 and 8cm at E 13. The areas around the sites are rather even; *Fagus sylvatica* dominates at C 19 (around 60%) and *Quercus petraea* at E 13 (around 80%, Figs. 52 and 55).

Pollen corrosion generally is moderate in the lower parts, and low or absent in the upper parts, of the mineral soils, and in the humus layers (Fig. 57). Pollen corrosion is high (70%) at 5.5cm depth at section C 19; however, the pollen spectrum from this sample does not differ from the spectra above and beneath (p. 107).

Reconstruction of the past vegetation

The pollen diagrams from the sections C 19 and E 13 are very alike (Plates XXIII and XXIV, Table 69) and will be discussed together. Andersen (1979a) showed that the pollen assemblages from the mineral soils were mixed by bioturbation at the time of incorporation in the soils. Smoothed pollen curves from section H 16 were shown to be similar to the related curves from the upper parts of the mineral soils at C 19 and E 13.

A *Fagus*- *Quercus* stage is present at the two sections.

Fagus- *Quercus* stage

Fagus is dominant at the lower part of the stage; *Quercus* is 5% at C 19 and 10-20% at E 13. *Quercus* increases strongly in the upper part of the stage, and *Fagus* increases slightly in the uppermost samples at C 19. *Picea* is represented in the upper parts of the stage.

Ericales, open-ground herbs,Poaceae and *Dryopteris*-type have high values at the lower part of the stage. This phase is not recorded at section H 16. Ericales and open-ground herbs again reach maxima in the upper part of the stage which are similar to those of section H 16.

The *Dryopteris*-type spores are very frequent (40 and 20% of the total pollen and spores) in the lower parts of the diagrams. These pecentages are much higher than found in the *Fagus*- *Quercus* stage at section H 16 (Plate XXII). *Dryopteris*-type spores are nearly uneffected by corrosion in mineral soils (p. 102, Table 51); hence it was assumed that the spores present in the lowermost parts of the mineral soils at sections C 19 and E 13, or a major part of them, are residual from an earlier forest stage, probably a *Tilia*- *Quercus* stage rich in ferns, which otherwize left no trace in the soil due to elimination of pollen by corrosion. The *Dryopteris*-type spores were, accordingly, excluded from the pollen diagrams and were disregarded.

Calluna, Poaceae, *Rumex acetosella*-type and *Hordeum*-type are particularly frequent in the lowermost samples, and *Spergula*, *Centaurea cyanus* and *Fagopyrum* have low frequencies. The percentages for *Hordeum*-type (5-10%) are higher than found in any other pollen spectra from Eldrup Forest. This pollen may derive from *Hordeum vulgare* or from *Elymus repens* (Andersen 1979b); both plants indicate cultivated fields. Hence, it can be assumed that fields occurred at the two sites. The *Fagopyrum* pollen is in contrast so scarce that cultivation of this plant at the sites is unlikely; the pollen was, rather, tansported from fields outside the forest. Poaceae, *Rumex*, *Spergula* and *Centaurea cyanus* may have occurred as weeds in the local fields. These pollen spectra can be assumed to be so strongly mixed that a detailed vegetational sequence cannot be detected. It is thus impossible to say whether the *Fagus* and *Calluna* pollen was contemporaneous with the pollen from the cultivation phase, or derived from successions that followed after the phase.

Dense forest is recorded above the lowermost phase with high *Calluna* and open-ground pollen at both sectios. *Quercus* was scarce at C 19, as it was at section H 16, and was apparently somewhat more frequent at section E 13. Hence there are indications that the *Fagus* forest was less dense and contained more *Quercus* on the sorted sands at section E 13 than on the sandy tills found at H 16 and C 19.

The vegetational sequences recorded in the upper parts of sections C 19 and E 13 are similar to H 16, but were modified by bioturbation. *Fagus* today is dominant at C 19, and *Quercus* at E 13.

Andersen (1979a, 1983) showed that the pollen assemblages from the lower parts of the mineral soils at sections C 19 and E 13 were buried during former oligotrophic brown earth stages. Brown earth thus still prevailed at the time when *Fagus* forest was dominant, whereas humus accumulation and podzolization were initiated at the same time in the small depression at section H 16. The brown earth changed to podzoloid during the grazing at C 19 and E 13, and humus accumulation and podzolization were initiated at about 1850 - at a time when the present tree generation was about 6m tall, and the open-ground vegetation disappeared due to increased shade. Increased production of leaf litter was presumably the main reason for the initiation of humus accumulation.

The high pollen corrosion at a narrow level at section C 19 (5.5cm, Fig. 57) is unexplained as no changes can be seen in the pollen diagram. A local fire may possible have caused the high pollen corrosion; no traces of charcoal were observed, however.

Soil section Ma (Matrikel bank)

The Matrikel bank section was excavated beneath the earth wall which was erected before the middle of the 19th century (p. 89). The site was located 7m north of the Matrikel hollow section (Fig. 8). The section was a podzol on sandy till (Table 48). The humus layer was 19cm deep.

The average pollen corrosion is moderate (20-40%) in the mineral soil and low (5-10%) in the humus layer.

Reconstruction of the past vegetation

The vegetational sequence was divided into a *Quercus- Tilia- Corylus* stage and a *Fagus- Quercus- Betula* stage (Plate XXV, Table 70)).

Quercus- Tilia- Corylus stage

Quercus and *Tilia* are about 40%, and *Corylus* about 10% in the *Quercus- Tilia- Corylus* stage which occupies the mineral soil at section Ma. *Fagus* pollen occurs continuously; other tree pollen and non-tree pollen are scarce.

There are a few finds of *Viscum* and *Hedera*.

The *Quercus- Tilia- Corylus* stage at the Matrikel bank is very similar to the uppermost part of the *Tilia- Quercus- Corylus* stage at the *Glyceria* hollow (Plate XII), and to the *Quercus- Tilia- Corylus* stage at the Matrikel hollow (Plate XVIII). *Quercus* had gained ground in these stages at the cost of *Tilia*, and the forest was still undisturbed by Man. The *Quercus- Tilia- Corylus* stage at the Matrikel bank thus is younger than the *Tilia- Quercus- Corylus* stage at the soil sections -C 9 and -A 13 (Plates XX and XXI).

The pollen assemblages from the *Quercus- Tilia- Corylus* stage were apparently buried in the mineral soil at the Matrikel bank during a brown earth stage with moderately acid soils (pH 5.5-6.0).

Stages corresponding to the *Quercus- Tilia- Betula* and *Quercus- Betula* stages at the Matrikel hollow (Plate XVIII) are missing at the Matrikel bank section. Organic debris was apparently destroyed due to human activity, as also noticed at sections -C 9 and -A 13 (pp. 134 and 135).

Fagus- Quercus (- *Betula*) stage

The *Fagus- Quercus* (- *Betula*) stage at the Matrikel bank begins with increasing *Fagus* and decreasing *Quercus*, *Tilia* and *Corylus*. These changes are similar to those noticed at the transition from the *Quercus- Betula* stage to the *Fagus- Quercus* stage at the Matrikel hollow (Plate XVIII). *Betula* is about 10%, as at the Matrikel hollow. *Fagus* then becomes dominant (70%) with low *Quercus* and *Betula* (10-20%). There is a maximum for *Betula* at the middle of the stage, which was not recorded at the Matrikel hollow because of the disturbance of the peat. *Tilia* and *Corylus* pollen found in the middle and upper parts of the stage was probably redeposited by influx of mineral soil with fossilized pollen.

Viscum and *Hedera* are absent. Shrubs, Ericales and open-ground herbs increase in the upper part of the *Fagus- Quercus* stage. Acid-humus plants are fairly frequent, and there is a small maximum for wet-ground plants.

Juniperus and *Calluna* have maxima at the uppermost part of the stage. Poaceae are fairly frequent, and *Plantago lanceolata* and *Rumex acetosella*-type increase slightly in the upper part. *Dryopteris*-type spores are fairly frequent at the lower part, and *Melampyrum* at the upper part of the stage.

The *Fagus*- *Quercus* (- *Betula*) stage at the Matrikel bank section thus records the establishment of *Fagus* forest after the destruction of the *Quercus*-Tilia-*Corylus* forest which was recorded at the Matrikel hollow. Ferns were fairly frequent. The *Betula* maximum records the felling of trees, and the forest was influenced by grazing. The earth bank was built during the maxima for *Calluna* and *Juniperus*, which indicate the abandonment of grazing in the early part of the 19th century.

Humus accumulation at this site began simultanously with the expansion of *Fagus*.

SYNCHRONIZATION OF THE POLLEN DIAGRAMS IN ELDRUP FOREST

In order to compare the vegetational sequences at the various sites in Eldrup Forest, an attempt to synchronize them on a common time scale was necessary. Andersen (1978a) synchronized the pollen diagrams from the *Glyceria* hollow (site l) and the *Molinia* hollow (site 2) using ages for specific levels inferred from radiocarbon dates or historical information. Radiocarbon dates used, and ages assumed for various levels at the two sites, are shown in Tables 59 and 60, and sediment accumulation curves in Fig. 67. Ages are stated in conventional radiocarbon years before 1950 and in calendar years (AD/BC), corrected according to Clark (1975).

The first increase of *Corylus* at the *Glyceria* hollow was assumed to signify the immigration of *Corylus*. The *Corylus* curve rises steeply in regional pollen diagrams from Denmark (Mikkelsen 1949, Jørgensen 1963, Krog 1973, Fredskild 1975), and it was assumed that the *Corylus* increase at the *Glyceria* hollow coincided with this general expansion of *Corylus*. The subsequent decrease in *Corylus* there was assumed to be a local event which was not reflected by the regional pollen diagrams. The *Corylus* expansion is dated at about 9400 ^{14}C years in southern Denmark and Sweden, and some centuries later than that date in northern Jutland (B. Aaby, personal communication). The dating used here for the *Corylus* expansion in Djursland (9400 ^{14}C-years) may, accordingly, be slightly too old.

The first increase in *Tilia* at the *Glyceria* hollow was likewise assumed to coincide with the first *Tilia*-increase in regional pollen diagrams from Denmark, an event which was dated at about 8000 ^{14}C-years in southern Denmark and Sweden. *Tilia* increased at about the same time in northern Jutland (B. Aaby, personal communication).

The *Quercus*-increase at the *Glyceria* and *Molinia* hollows was assumed to coincide with the increase of *Quercus* in pollen diagrams from Elsborg Bog and elsewhere in Djursland (p. 115). This event was dated at shortly after 7100 ^{14}C years at Elsborg Bog.

The decrease in *Ulmus* and the nearly simultaneous increase in *Fraxinus* at the *Glyceria* hollow were assumed to reflect similar events at Elsborg Bog, which have been dated at about 5200 ^{14}C-years. This date nearly coincides with the date of *Quercus* wood from the *Molinia* hollow (5400 ^{14}C-years).

The appearance of continuous *Fagus* curves at the *Glyceria* and *Molinia* hollows was assumed to reflect the general appearance of *Fagus* in the area, and hence to be synchronous. The date obtained for this event at the *Molinia* hollow (see below) was therefore assumed to be the same at the *Glyceria* hollow, about 3000 ^{14}C-years (1300 BC).

The expansion of *Fagus* at the *Molinia* hollow was assumed to coincide with the *Fagus*-expansion at Elsborg Bog dated at about 1500 ^{14}C-years (450 BC). This event was slightly later than the appearance of *Secale* pollen at both sites.

The increase of *Picea* at the *Molinia* hollow, finally, can be assumed to be due to the first flowering of the oldest *Picea* plantations in Eldrup Forest, about 1850. At the same level, there is evidence that the hollow was drained artificially, an event which also took place in the middle of the 19th century (p. 129).

Four levels at the *Molinia* hollow can thus be dated approximately. The graphs on Fig. 67 show nearly constant sedimentation rates in the gyttja deposits at the two sites, and somewhat higher rates in the basal clay at the *Glyceria* hollow and in the peat at the *Molinia* hollow. If unchanged sedimemtation rates are assumed for the gyttja layers at the two sites, then the date of the beginning of a continuous *Fagus* curve at the *Molinia* hollow is about 3000 ^{14}C-years (1300 BC), and the topmost part of the undisturbed layers at the *Glyceria* hollow derived from about AD 1000.

Synchronized pollen diagrams from the *Glyceria* and the *Molinia* hollows are shown on plate XXVI. The diagram from the soil section H 16 near the *Glyceria* hollow is inserted above the diagram from that hollow. The gap between the two diagrams covers the period that saw the disappearance of *Tilia* at these sites. The two minima in the *Fagus* curve at the *Molinia* hollow appear at about AD 800-1400 and 1550-1800.

The pollen diagrams from the Matrikel hollow and from humus layers at the soil sections were dated and synchronized relatively to the diagrams from the *Molinia* hollow (Plate XXVII), whereas the mineral soils at the soil sections were disregarded. A generally recognizable level was the decreases in herbs, *Calluna*, *Juniperus* and *Betula*, and the increase in *Picea* which reflect the re-establisment of forest and the first flowering of planted *Picea* at about 1850. The first increase and the first minimum in the *Fagus* curve at section -C 9 near the

TABLE 59. Radiocarbon dates used for age determinations (for dates from Elsborg Bog and the *Molinia* hollow, see Tables 55 and 56).

Event	Source		Radiocarbon years before 1950 T/2=5570	Calendar years AD/BC (Clark 1975)
Fagus expansion	Elsborg Bog	K–2217	1520±80	450
Fagus expansion	Elsborg Bog	K–2393	<1680±60	>310
Ulmus decline	Elsborg Bog	K–2220	5160±80	–4000
Quercus wood	Molinia hollow	K–1421	5340±120	–4330
Quercus increase	Elsborg Bog	K–2421	7100±115	
Tilia increase	Fredskild 1975	K–2251	7970±130	
Tilia increase	Andersen et al. 1982	K–1509	>8030±100	
Tilia increase	Andersen et al. 1982	K–2174	8140±100	
Tilia increase	Nilsson 1964	St–1001	>7950±85	
Tilia increase	Nilsson 1964	St–1002	<8160±110	
Tilia increase	Berglund 1966	St–1333	8140±90	
Corylus expansion	Tauber 1966	K–1082	>8990±140	
Corylus expansion	Tauber 1966	K–852	<9550±140	
Corylus expansion	Krog 1973	K–926	9300±150	
Corylus expansion	Berglund 1966	St–1679	9380±120	
Corylus expansion	Fredskild 1975	K–2320	>9120±130	
Corylus expansion	Fredskild 1975	K–2250	<9480±130	

TABLE 60. Inferred ages for levels at the *Molinia* hollow and the *Glyceria* hollow.

	Age in years		Comment
	^{14}C	Calendar AD/BC	
Molinia hollow			
Picea increase		1850	Historical date
Fagus expansion	1500	450	See Table 59
Quercus wood	5400	–4300	See Table 59
Quercus increase	7000	–5800	See Table 59
Glyceria hollow			
Fagus continuous	3000	–1300	Inferred from *Molinia* hollow
Ulmus decline	5200	–4000	See Table 59
Quercus increase	7000	–5800	See Table 59
Tilia increase	8000		See Table 59
Corylus increase	9400		See Table 59

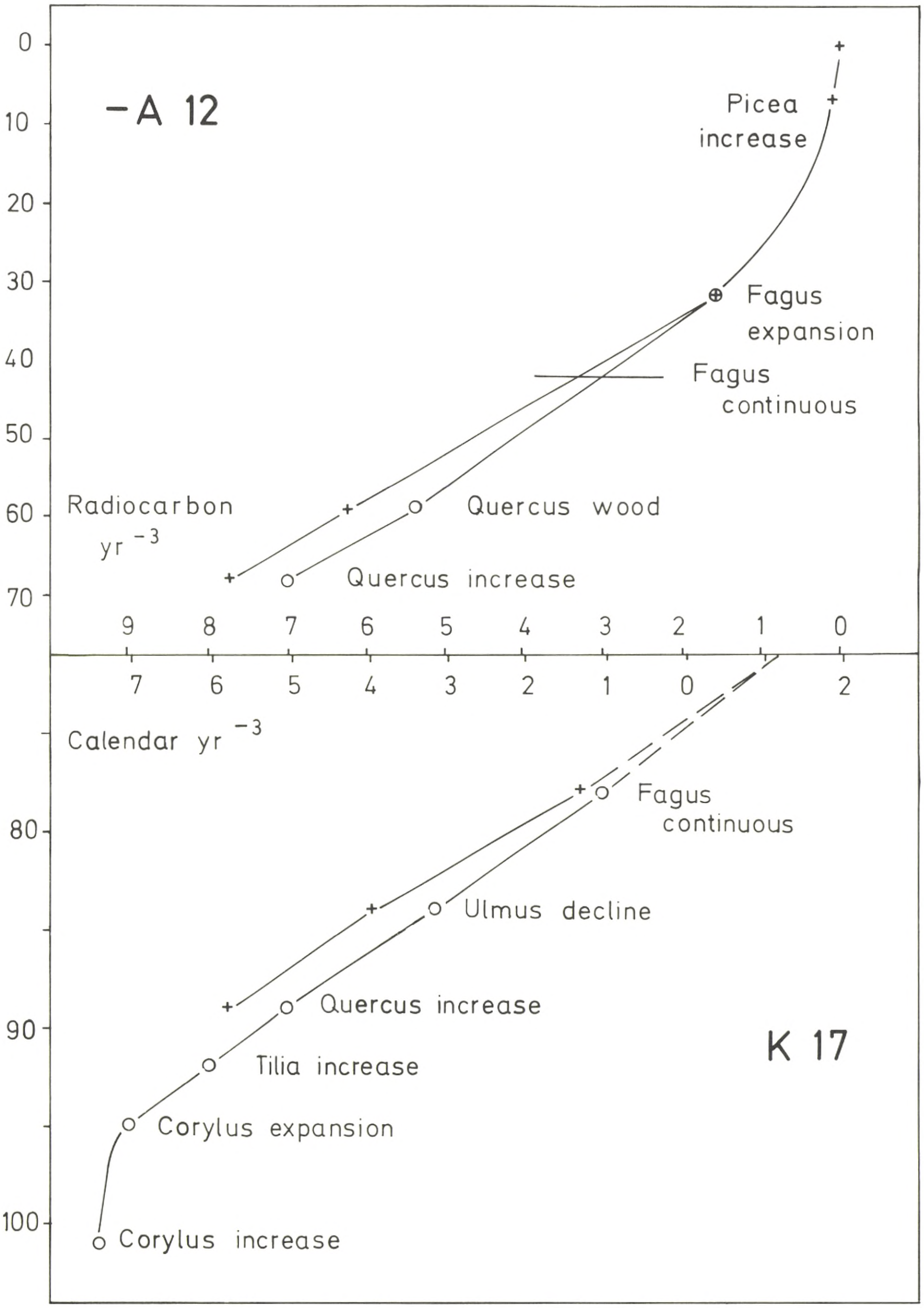


Fig. 67. Age of levels determined by pollen diagrams from the *Molinia* (-A 12) and *Glyceria* (K 17) hollows. Ages in radiocarbon years (○) and in calendar years (+) according to Table 60.

TABLE 61. Correlation of forest stages at the various sections. +, undisturbed deposit; –, disturbed deposit; F, *Fagus;* Q, *Quercus;* T, *Tilia;* B. *Betula;* C, *Corylus;* Pi, *Pinus;* Po, *Populus;* R, Recent; M, Medieval; S, Subboreal-early Subatlantic cultural influene.

Molinia hollow –A 12	Soil section –C 9	Soil section –A 13	*Glyceria* hollow K 17	Soil section H 16	Matrikel hollow Mah	Soil section Ma	General forest stages
+	+	+	–	+	+		
+ R	+ R	+ R	– (FQ)	+ FQ R	+ FQ(B) R	+ FQ(B) R	FQ
+	+	+	–	+	–	+	
+ FQ M	+ FQ(B) M	+ FQ M	–		+ QB M		
+ M	+ M	+ M	–		+ QTB M		
+	+	+	+		+	+	
+	+		+		+ QTC	+ QTC	
+ S			+				
+ S			+				
+ QTB S			+				
+ S			+ TQC				TQC
+ S	+ QTB		+				
+	+	+	+				
+ S	+ S	+ S	+				
+ TQC	+ TQC	+ TQC	+				
+			+				
+			+				
+ TC–			+				
+ PiB			+ CPi–				CPi–
			+ BPo				BPo
			+				
			+				
			+				
			+				
			+ B				B
			+				

Molinia hollow were assumed to be synchronous with these events at the *Molinia* hollow at about AD 500 and 800-1400. At the Matrikel hollow (Mah), the rise in *Betula* was assumed to be synchronous with the *Betula* increase at the *Molinia* hollow and section -C 9 at AD 800, and the *Fagus* increases at that site and at section Ma were assumed to be synchronous with the *Fagus* increase at the *Molinia* hollow at 1400.

The datings of these diagrams are thus based on assumptions rather than on factual datings. Synchronized curves for non-tree plants are shown on plate XXVIII.

Three periods with assumed human influence are indicated on the pollen diagrams on Plates XXVI-XXVIII: a Subboreal-early Subatlantic phase (S) with intermittant influence from about 4300 BC, and continuous influence from about 3000 BC to about AD 500; a medieval phase (M) from about AD 800 to about 1400; and a Recent phase (R) at about 1550 to 1800.

The forest stages at the various sites, and possible synchronizations, are shown on Table 61. Generally, the vegetational development in Eldrup Forest was divided into four stages: *Betula* stage, *Corylus- Pinus- Betula- Populus* stage, *Tilia- Quercus- Corylus* stage and *Fagus- Quercus* stage. The transition from the *Tilia- Quercus- Corylus* to the *Fagus- Quercus* stage was asynchronous.

NATURAL FOREST COMMUNITIES IN ELDRUP FOREST IN THE HOLOCENE

The pollen diagrams from the small hollows and soil sections in the research area in Eldrup Forest reflect natural forest communities, as well as forest influenced by human utilization. The natural forest communities can be assumed to be typical for the forests which prevailed in Denmark at various times in the Holocene on soils similar to those which occur in Eldrup Forest: sandy tills and sands with low silt and clay content and poor in lime. The results from Eldrup Forest thus provide insight into the composition of dry-land forest communities from the Holocene. They were compared with tree pollen spectra from similar sites at Grib Skov and Næsbyholm on Zealand (Iversen 1960, Andersen 1980b) and at Draved in southern Jutland (Iversen 1957, 1964, 1969, Aaby 1983). Comparisons with tree pollen spectra from large lakes and bogs, which reflect a broader spectrum of forest types, make it possible to distinguish tree communities on other soils. Regional pollen spectra from Elsborg Bog (Plate X), from elsewhere in Djursland (Iversen 1937, 1941, Troels-Smith 1942), and from southern Denmark (Mikkelsen 1949, A. Andersen 1954, Jørgensen 1963, Krog 1973, Fredskild 1975) were used.

Betula forest

The oldest Holocene forest type that was recorded in Eldrup Forest is the *Betula* forest which prevailed in Preboreal time from about 9600 to about 9000 ^{14}C-years ago (*Glyceria* hollow, Plates XII, XIII and XXVI). The Preboreal *Betula* forest resembles the *Betula* forest recorded from Allerød time shortly prior to 11,000 ^{14}C-years ago.

A transition from Late Weichselian open vegetation to forest is not recorded. *Betula* was at first present alone; *Betula pendula* as well as *B.pubescens* probably occurred. *Corylus avellana* and *Pinus sylvestris* invaded the forest later, but did not expand. The tree cover was initially fairly dense, but became discontinuous in the late part of the *Betula* stage.

Juniperus communis was present in a shrub layer in the late part of the *Betula* stage, whereas *Salix* probably was mainly restricted to wet ground. Heliophilous herbs such as *Artemisia*, *Rumex acetosella*, *Botrychium*, *Polygonum aviculare*, *Saxifraga oppositifolia*, *Campanula*, *Sedum* and *Plantago maritima* occurred in the field vegetation near or at a distance from the site, and grasses and herbs such as *Epilobium*, *Thalictrum*, *Potentilla*, *Geum* and *Filipendula* were probably frequent. Hence, there was a rich field vegetation. Acidophilous plants such as *Empetrum nigrum*, *Gymnocarpium dryopteris* and *Lycopodium annotium* were present. It can thus be assumed that the soils, although mainly brown earths, had become somewhat acid. The drecrease of *Pinus* and *Corylus*, and the disruption of the tree canopy, were probably due to soil disturbances of a local nature (the melting of buried ice?).

Whereas *Pinus* was initially scarce in the Preboreal *Betula* forest in Eldrup Forest, *Pinus* pollen is more common (25%) in early Preboreal pollen spectra from the small hollow on Zealand and in the regional pollen spectra from Elsborg Bog (20%) and southern Denmark (10-30%). The scarcity of *Pinus* in the early Preboreal in Eldrup Forest therefore seems to be a local feature. A similar situation seems to exist with respect to *Populus*, as *Populus* pollen may be frequent in early Preboreal pollen spectra.

As mentioned on p. 139, the failure of *Corylus* to spread in the late Preboreal in Eldrup Forest was of local significance, as the *Corylus* curve increases steeply in the regional pollen diagrams.

Herb pollen is scarce in the early Preboreal in the regional pollen diagrams of Mikkelsen (1949) and Jørgensen (1963), whereas Fredskild (1975) recorded herbaceous vegetation similar to that found in Eldrup Forest.

Corylus- Pinus- Betula- Populus forest

The *Corylus- Pinus- Betula- Populus* forest prevailed in Boreal and early Atlantic time from about 9000 to about 7000 ^{14}C-years ago. (*Glyceria* hollow and, for the latest part, *Molinia* hollow, Plates XII, XIII, XV, XVI and XXVI).

Corylus avellana expanded and constituted about 50% of the tree cover. (This percentage may be slightly too low, due to differential destruction of *Corylus* pollen). *Betula* had become scarce, *Pinus sylvestris* initially expanded to about 30% and was then suppressed, and *Populus tremula* constituted up to 10% of the tree cover. *Tilia cordata* began to expand, but its expansion was slow and hampered by set-backs. Hence, the forest was unstable and underwent changes in composition.

Corylus, *Pinus* and *Populus* thus expanded at the cost of *Betula*, but *Pinus* and *Populus* were later checked, presumably due to increased density of the *Corylus* canopy. *Pinus*, *Populus* and *Betula* rejuvenated with difficulty because of insufficient illumination. *Corylus*, however, did not attain full dominance, and specimens of *Pinus*, *Populus* and *Betula* were able to penetrate the *Corylus* canopy. The set-backs of *Tilia* were utilized by *Pinus*, *Betula* and *Corylus*, and the ground vegetation.

Sorbus aucuparia was present in the tree layer. *Viburnum opulus* and *Frangula alnus*, though scarce, occurred in a shrub layer, whereas *Salix* presumably mainly occurred around the hollows. Hence, there was no well developed shrub layer beneath *Corylus*.

Empetrum, *Calluna*, *Gymnocarpium*, *Pteridium*, *Melampyrum* and *Anemone* occurred scarcely in the field layer, and there were a few open-ground herbs such as *Artemisia*, *Rumex*, *Plantago lanceolata*, *Jasione* and *Sedum*, and probably some grasses near the site or at some distance. *Gymnocarpium* and *Pteridium* were most important in the field layer, but spots with open-ground vegetation also occurred. The soils were acid brown earths, and a thin humus layer may have developed.

The soils were apparently too poor for the full development of *Corylus*. Soil disturbance seems to have delayed the expansion of *Tilia*.

Up to 70% *Corylus* was recorded in the small hollow at Næsbyholm on Zealand; the upland soils at this site were distinctively more fertile than the soils in Eldrup Forest. The highest percentages for *Corylus* in the Boreal *Corylus* maximum vary 50-80% in the regional pollen diagrams from southern Denmark.

Pollen from shrubs and herbaceous plants is usually very scarce in the regional pollen diagrams.

Tilia- Quercus- Corylus forest

Natural *Tilia- Quercus- Corylus* forest occurred in Eldrup Forest from about 7000 ^{14}C-years ago. The *Tilia- Quercus- Corylus* forest was increasingly influenced by Man from about 5400 ^{14}C-years (4300 BC) at the *Molinia* hollow, and from about AD 800 at the Matrikel hollow. The natural *Tilia- Quercus- Corylus* forest is recorded at the *Glyceria* hollow, the *Molinia* hollow, the Matrikel hollow, and in soil sections -C 9, -A 13 and Ma (Plates XII, XIII, XV, XVI, XVIII, XIX, XX, XXI, XXV, XXVI and XXVII).

Tilia was dominant in Atlantic time (about 60% of the crown cover) but became gradually scarcer, as seen at the *Glyceria* hollow. In Subatlantic time, *Tilia* had decreased to about 30-40% at the *Glyceria* and Matrikel hollows. *Tilia cordata* prevailed as only a few *T. platyphyllos* pollen grains occurred. *Quercus* was initially scarce and expanded somewhat later than *Tilia*, at about 7000 ^{14}C-years. The *Quercus* frequencies later increased gradually from about 20% to 30-50% at the cost of *Tilia*. The species identity of *Quercus* is unknown.

The frequency of *Corylus avellana* was about 10% in Atlantic time. (This percentage may be slightly too low due to differential pollen destruction). The *Corylus* percentages increase slightly in Subboreal and Subatlantic time at the *Glyceria* hollow.

Fagus pollen was continuously present in the late part of the *Tilia- Quercus- Corylus* stage at the Glyceria and Matrikel hollows. The *Fagus* pollen is so scarce there, that it can be assumed that *Fagus* occurred only scarcely, or not at all, near these sites. Pollen of other trees such as *Ulmus*, *Alnus*, *Acer*, *Fraxinus*, *Carpinus* and *Pinus* is also so scarce that it can be assumed to have derived from more or less distant sources. The find of a fruit of *Alnus glutinosa* at the *Molinia* hollow shows that single specimens of these trees may have occurred despite their low pollen frequencies.

Sorbus aucuparia pollen generally is scarce, but increases slightly in the late part of the *Tilia- Quercus- Corylus* stage at the *Glyceria* and Matrikel hollows. As its pollen frequencies are uncorrected, this tree is probably underrepresented; scattered specimens thus are likely to have occurred at that time.

Viscum album and *Hedera helix* occurred frequently in the *Tilia- Quercus- Corylus* forest. *Viscum*, no doubt, occurred as a parasite in the tree tops of *Tilia*- one of its preferred host plants - where light was plentiful. As a climber, *Hedera* probably occurred mainly around openings in the tree canopy, and flowered profusely in the tree tops. A few pollen grains of *Ilex aquifolium* were recorded. If present near the sites, this shrub was scarce.

Atlantic time

The average percentages in Atlantic time were 60% for *Tilia*, 19% for *Quercus* and 9% for *Corylus* (Table 62). *Betula*, *Pinus* and *Populus* were suppressed at the expansion of first *Tilia* and, slightly later, *Quercus* ; they could not rejuvenate due to shade and disappeared from the forest. The presence of *Quercus* indicates gaps in the tree canopy, where *Quercus* saplings survived. *Corylus* probably also utilized disruptions in the tree canopy and occurred, presumably, also in a scarce understorey below the trees. *Hedera* probably also utilized openings in the tree canopy to climb to the tree tops.

The best picture of the ground vegetation of the natural *Tilia- Quercus- Corylus* forest in late Atlantic and early Subboreal time may be obtained from the pollen diagrams from the mineral soils at the soil sections -C 9 and -A 13 (*Tilia- Quercus- Corylus* stage, Plates XX and XXI), because pollen and spores present there derived directly from the ground vegetation, and the spectra were not influenced by pollen derived from vegetation on wet ground, as is the case at the hollow sites. The pollen and spores present in these sections were buried during a former brown earth stage. Pollen corrosion was moderate at -C 9, and somewhat stronger at -A 13; the pollen spectra differ only slightly, however, and are, accordingly, not strongly influenced by differential destruction of pollen.

Shrubs were very scarce at the two sites. *Calluna* and herbaceous plants were also very scarce, except for fern spores. Hence, only *Gymocarpium dryopteris* and other ferns, possibly *Dryopteris carthusiana* and related species, were frequent in the local field layer. The *Anemone* pollen present at -A 13 and a few grains of *Oxalis* probably derived from field vegetation of *Anemone nemorosa* and *Oxalis acetosella*. Pollen and spores from other non-tree plants are so scarce that they can be assumed not to have been present at the sites.

The herbaceous flora recorded at the hollow sites was somewhat richer than at the soil sections. Hence, a wider range of plant communities is reflected there; it appears that small open areas and a few sunny spots occurred occcasionally in the *Tilia- Quercus- Corylus* forest.

The soils of the *Tilia- Quercus- Corylus* forest from Atlantic time were acid brown earths.

Iversen (1960) found by ecological reasoning that *Tilia cordata* must have been dominant on high ground in Denmark in Atlantic time. He explained the comparatively low *Tilia* percentages found in regional pollen diagrams by poor pollen dispersal, and he predicted that a clear picture of the forest development on high ground could rather be obtained from small kettleholes. This supposition was confirmed by two pollen analyses from a kettlehole on Zealand, where *Tilia* had higher percentages than in a regional pollen diagram from that area. From this evidence, Iversen concluded that *Tilia* was dominant in forest on high ground; whereas a

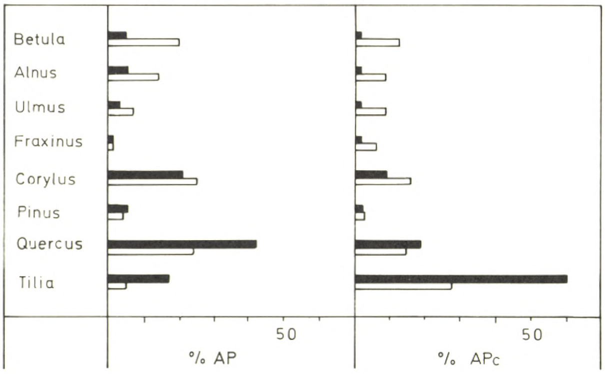


Fig. 68. Average tree pollen percentages in Atlantic time at Elsborg Bog (white bars, levels 188-194 cm, n = 4) and in Eldrup Forest (black bars, *Glyceria* hollow, levels 84-88 cm, n = 5). Uncorrected (% AP) and corrected (% APc) pollen frequencies.

mixed forest of *Quercus robur*, *Fraxinus excelsior*, *Tilia* and *Alnus glutinosa* occurred on damp fertile soils where the competitive power of *Tilia* was reduced; and *Alnus* prevailed on soils with a high ground water level. Iversen also concluded that *Quercus* expanded in Atlantic time on thin peaty soils and probably also on well-drained poor sandy soils. Based on pollen analyses of a sample from a former podzoloid soil and a superposed humus layer from Draved Forest, southwest Jutland, Iversen (1960) found that *Tilia* also occurred on low-lying sandy soils, here mixed with *Quercus*, *Corylus*, *Betula* and *Alnus*. These results were subsequently confirmed (Iversen 1964, 1969).

There exist, as yet, only few pollen analyses which show the composition of the *Tilia*-dominated forests in Denmark in Atlantic time. The reults from Eldrup Forest are compared with the two sites from Zealand mentioned above and with samples from Draved Forest in Table 62. *Quercus* is higher and *Corylus* lower in Eldrup Forest than at the other sites, and *Alnus* and *Betula* are significant in Draved. *Quercus* thus replaced *Corylus* in the *Tilia* forests on the well-drained sandy soils in Eldrup Forest. *Tilia* and *Quercus* are more frequent on sandy soils with low pH (less than 5) than *Corylus* (Rackham 1980); hence, *Corylus* was apparently restricted in Eldrup Forest by poor soils, to the advantage of *Quercus*.

TABLE 62. Corrected tree pollen spectra (%APc) from hollows and soils (Draved Forest) from Atlantic time.

	Eldrup Forest (averages) (%)	Hertugdalen Zealand (2 samples) Iversen 1960 (%)	Næsbyholm Zealand (averages) Andersen 1980b (%)	Draved Forest (3 samples) Iversen 1969 (%)
Tilia	60	68–82	49	33-54
Quercus	19	2– 5	10	7– 8
Corylus	9	4–20	19	15–34
Alnus	2	4– 5	6	8-15
Betula	2	1	3	6–14
Ulmus	2	3	6	0– 2
Fraxinus	2	–	1	0– 1
Pinus	2	1– 2	7	1

The pollen spectra in Table 62 confirm Iversen's conclusion (1960), that *Ulmus*, *Fraxinus* and *Alnus* were restricted to low-lying fertile soils, and that *Quercus* also occurred on such soils in Atlantic time. *Corylus* was apparently also frequent on fertile soils, both well-drained and low-lying (Andersen 1978a). Average pollen spectra from Eldrup Forest and from the regional pollen diagram at Elsborg Bog (and c), are compared in Fig. 68. *Betula*, *Alnus*, *Ulmus*, *Fraxinus* and *Corylus* have higher, and *Quercus* and *Tilia* lower, percentages in the regional than in the local pollen spectrum, whereas *Pinus* has low percentages in both. Hence, *Betula*, *Alnus*, *Ulmus* and *Fraxinus* occurred mainly on low-lying soils; *Corylus* and *Quercus* on high ground as well; *Tilia* mainly on high ground; and *Pinus* was absent in this area.

Iversen (1960) argued for ecological reasons that *Quercus robur* prevailed on low-lying soils and thin peats, and that *Quercus petraea* occurred on sandy hills in Central Jutland in Atlantic time. For the same reasons, it can be proposed that *Quercus petraea* prevailed in Eldrup Forest, as it does today.

Tilia cordata today occurs on a wide variety of soils, ranging from 3.2 to about 7 in pH (Rackham 1980). *Quercus* (*robur*) does not regenerate in *Tilia* forest on fertile soil (Pigott 1975). Rackham in contrast, noticed stands of *Tilia cordata* and *Quercus petraea* on "unusually" acid soils in eastern England, and Passarge (1953) and Matuszkiewicz & Matuszkiewicz (1956) described woodlands with *Quercus petraea* and *Tilia cordata* on well-drained, sandy brown earths in Central Germany and Poland (*Querceto petraeae- Betuletum tilietosum cordatae*, *Querceto- Carpinetum*, *Vaccinium myrtillus Variante*). There was a sparse understorey of *Corylus avellana* in these woodlands, and several acidophilous species occurred in the field vegetation. A somewhat similar plant community occurred apparently on sandy soils in Denmark in Atlantic time.

Subboreal and Subatlantic time

At the *Glyceria* hollow, the decrease in *Tilia* and increase in *Quercus* began in late Atlantic time, and continued in Subboreal and Subatlantic time. *Corylus* and *Betula* increased slightly, but somewhat later than *Quercus*, in early Subboreal time. These changes coincide with the earliest *Quercus* peaks and the increases of *Quercus*, *Betula* and *Corylus* caused by human activity at the *Molinia* hollow. It might be assumed, therefore, that the increases in *Quercus*, *Betula* and *Corylus* at the *Glyceria* hollow were due to pollen transported from the vicinity of the *Molinia* hollow. Transects from present-day forests (Andersen 1970) show, however, that the corrected pollen percentages decrease to nearly zero immediately outside stands of a tree species. The distance between the two sites is about 100m. Hence, it is unlikely that noticeable amounts of pollen were transferred to the *Glyceria* hollow from the clearings at the other site. Neither was the *Fagus* expansion at the *Molinia* hollow reflected at the *Glyceria* hollow, where the *Fagus* frequencies remain low in late Subboreal and early Subatlantic time. The increase in *Quercus*, at least, can, therefore, be supposed to reflect a local change in tree composition; *Corylus* probably also increased slightly, whereas *Betula*, in contrast, remains so scarce that one may assume that the tree was not present, and that this pollen originated elsewhere.

There is no evidence of human activity at the *Glyceria* hollow in Subboreal and early Subatlantic time. *Betula* thus remained insignificant, and the herbs from open ground were scarce. The decrease of *Tilia* and the increase of *Quercus* must, accordingly, reflect a natural development. The slight increase for *Corylus* and a slight increase for *Salix* and aquatic plants indicate a more open tree canopy around and over the hollow. Decreased vitality of *Tilia*, therefore, is indicated. *Tilia* today is less frequent than *Quercus* on strongly acid soils (pH less than 4, Rackham 1980); its growth is subdued in *Quercus petraea- Tilia cordata* forests (Passarge 1953, cp. p. 123). Hence, the slow decrease of *Tilia* and increase of *Quercus* in Eldrup Forest may be ascribed to slow impoverishment of the soils. There is, however, no other distinctive evidence of poorer soils, as acid-humus herbs are rather unchanged at the *Glyceria* hollow, and a few plants from neutral forest soil are recorded (*Anemone*, *Mercurialis* and *Stellaria holostea*).

The latest part of the *Tilia- Quercus* stage is recorded at the Matrikel hollow (Mah, *Quercus- Tilia- Corylus* stage, Plates XVIII, XIX and XXVI). These pollen spectra are very similar to the latest pollen spectra from the *Glyceria* hollow.

The flora of the late *Tilia- Quercus- Corylus* stage is recorded in the mineral soil at the Matrikel bank (section Ma, Plate XXV). *Sorbus aucuparia* was scarce. Pollen from *Calluna* and open-ground herbs is nearly lacking, and these plants obviously did not occur near the site. Plants from acid humus were scarce; the frequencies of *Dryopteris*-type spores thus are very low, and *Gymnocarpium* is nearly absent, in contrast to the mineral soils from Atlantic time. Hence, the ground flora had become extremely poor, perhaps an indication of increased acidity; the soils, on the other hand, remained acid brown earths at this stage. Iversen (1969) found a similar poor ground flora in *Quercus- Tilia* forest on acid humus in Draved Forest.

Shrubs, Ericales and herbaceous plants were slightly more common at the *Glyceria* and Matrikel hollows than they were in the soil section at the Matrikel bank. Some of this pollen derived from field and pasture areas, and from vegetation around the hollow; strangely enough, however, a forest field plant such as *Gymnocarpium* was also more frequently recorded in the hollows than in the soil.

The tree pollen curves in regional pollen diagrams from Djursland and elsewhere reflect human disturbance in Subboreal and Subatlantic time (p. 116). *Tilia*-dominated forest which was unaffected by human influence in Subboreal time was recorded by Iversen (1958) and Aaby (1983). A pollen spectrum from the latest *Tilia- Quercus- Corylus* forest at Eldrup is compared with spectra from Draved Forest in Table 63 which derive from a humus layer near to clayey soils (gley, Iversen 1958) and former acid brown earths on sand and sandy till (Aaby 1983). The forest on clayey soil had high *Corylus* frequency and occurred, accordingly, on soil which had not been leached; the forest on the sandy soils in Draved was rich in *Tilia* and poor in *Corylus* and occurred, therefore, on somewhat impoverished soil, whereas the forest on well-drained sandy soils in Eldrup Forest had low *Tilia* and high *Quercus* frequencies, and thus occurred on soils, which had become very poor. *Quercus* replaced *Tilia* and *Corylus* in Draved Forest at the onset of humus accumulation (Iversen 1960, 1964, 1969).

Fagus- Quercus forest

Fagus sylvatica expanded about AD 500 in the vicinity of the *Molinia* hollow and became dominant there (70-80% of the crown cover), mixed with some *Quercus* (*Molinia* hollow and the soil sections -C 9 and -A 13, Plates XV, XVI, XX, XXI). The *Fagus- Quercus* forest succeeded a stage with cultural disturbance around the *Molinia* hollow, but did not expand to the areas around the *Glyceria* and the Matrikel hollow further northwest in the research area. *Fagus* thus expanded only in areas where the *Tilia- Quercus* forest had been previously disturbed.

TABLE 63. Corrected tree pollen spectra (% APc) from the late *Tilia–Quercus–Corylus* stage in Eldrup Forest compared with pollen spectra from moist sandy soils (Aaby 1983) and gley-soils (Iversen 1958) in Draved Forest from Subboreal or early Subatlantic time. The pollen spectra from Iversen (1958) were recalculated by Aaby (1983).

	Eldrup Forest (averages) (%)	Draved Forest (averages) Aaby 1983 (%)	Draved Forest (averages) Iversen 1958 (%)
Tilia	29	70–80	40
Quercus	48	5–10	20
Corylus	12	5–10	20
Alnus	2	5	20
Betula	4	–	2
Ulmus	–	1	1
Fraxinus	1	–	1
Fagus	1	1	1
Pinus	2	–	–

The *Fagus- Quercus* forest was, on the other hand, originally unaffected by cultural influence once established.

Cultural influence occurred intermittantly from about AD 800; comparatively natural *Fagus- Quercus* forest prevailed in the vicinity of the *Molinia* hollow from about 1400 to 1550, and from about 1850 till today.

Fagus- Quercus forest initially was established in the vicinity of the *Glyceria* and Matrikel hollows about 1400 after a period of human activity (Matrikel hollow and soil sections H 16, C 19, E 13 and Ma, Plates XVIII, XIX, XXII-XXV and XXVII). *Fagus* constituted 60-90% of the crown cover at these sites. The *Fagus- Quercus* forest in this area was influenced by human activity from 1550 till about 1800.

The *Fagus- Quercus* forest survived the period with cattle grazing from 1550 till 1800 in continuous stands on the slopes in the southeastern part of the research area and in clumps interspersed with open glades in the northwestern part. The old trees were felled in the early 19th century, and the forest rejuvenated by sprouts from the stumps of the felled trees or by seed plants (p. 136, Plates III-IV). Humus layers were at that time limited, and brown earths predominant; hence *Fagus* seedlings presumably met with less difficulty in their establishment than today. The present forest has been thinned by foresters, a practice which has not affected tree distribution (p. 37), and was, otherwize, left undisturbed.

Undisturbed *Fagus*- *Quercus* forest thus occurred in the research area in Eldrup Forest from AD 500 to about 800, from about 1400 to 1550, and from about 1850 until present.

Humus accumulated around the *Molinia* hollow during the expansion of *Fagus* at AD 500 and onwards (soil section -C 9 and -A 13, Plates XX and XXI). The accumulation of humus thus accelerated at the time when human activity ceased. A similar development was noticed at the Matrikel bank section (Ma, Plate XXV and p. 139), at about 1400 (Plate XXVII). The humus accumulation also began during the *Fagus* forest stage at section H 16 (Plate XXII), which is situated in a small depression. The level soils near this site were still brown earths at that time; humus accumulation began there about 1850 when the forest had regenerated after the previous grazing stage (sections C 19 and E 13, Plate XXIII, XXIV p. 138). Accumulation of humus - and podzolization of the mineral soils - accelerated thus at varying times but, in all cases, during the regeneration of *Fagus*-*Quercus* forest following upon a period of disturbance. All humus layers which are less than 20cm deep probably derive from after 1850 (p. 19). Brown earth thus prevailed in the research area till about 1850; only a few patches remain today.

Quercus formerly occurred with 10-20% of the crown cover on soils covered by a humus layer (-C 9, -A 13, Ma, Plates XX, XXI, XXV) and on sorted sand (E 13, Plate XXIV) and was nearly absent on sandy till (around H 16 and at C 19, Plates XXII and XXIII). *Quercus petraea* almost certainly was present alone. It appears, acordingly, that the *Fagus* forest was less dense on the poorest soils than on the more fertile soils.

Rejuvenation of *Fagus* today is absent on sites under *Fagus* trees, whereas it regenerates abundantly under *Quercus*, due to reduced competition from root mats. The present *Fagus*-dominated forest can therefore regenerate only under scattered specimens of *Quercus* ; in openings created by storm fall; and, in the future, possibly when the *Fagus* root systems become weakened due to senescence (p. 55).

Viscum has, together with *Tilia*, disappeared from Eldrup Forest. There are a few finds of *Hedera*, but this vine was very scarce in the *Fagus*- *Quercus* forest, if present at all. *Hedera* is scarce on acid soils today (Rackham 1980); hence, its disappearance from Eldrup Forest may have been due to the increased acidification of the soils.

The pollen diagrams from the humus layers in the soil sections (-C 9, -A 13, H 16 and Ma, Plates XX-XXV) show that *Sorbus aucuparia* was very scarce or absent in the natural *Fagus*- *Quercus* forest. No mature *Sorbus aucuparia* ocur today; the species regenerates mainly under *Quercus* trees.

Pollen from *Calluna* and the open-ground herbs is scarce in the humus layers and was transported from pastures and fields outside the forest. Ferns with *Dryopteris*-type spores and a few wet-ground plants (*Carex*-type, *Sphagnum*) were at first present at section -C 9, but decreased later presumably due to initially moist conditions, followed by decreased moisture. Ferns with *Dryopteris*-type spores were present at the other sites but became increasingly scarce. *Gymnocarpium* was scarce, and other herbs were scarce as well. Hence, the field vegetation of the natural *Fagus*- *Quercus* forest was poor on sites with a humus layer, except for moist sites which formerly fostered field vegetation of ferns and wet-ground plants. In the enclosure today, sites in *Fagus* forest with thin litter and humus layers accomodate a *Deschampsia flexuosa* community with species such as *Luzula pilosa*, *Carex pilulifera*, *Melampyrum pratense*, *Maianthenum bifolium*, and *Oxalis acetosella* (p. 75). *Ilex aquifolium* occurs occasionally on deep humus and has apparently survived from former times. Sites with deep litter and humus layers under *Fagus* trees have, otherwize, no field vegetation. *Molinia caerulea* and *Dryopteris carthusiana* occur on some moist sites on deep humus (p. 80).

It is somewhat difficult to evaluate the ground flora of the former brown earth sites both because of vertical mixing of the pollen assemblages and because of the presence of fern spores which have survived from former vegetation stages (sections C 19 and E 13, Plates XXIII and XXIV). The field layer obviously was poor, but it is not possible to say whether ferns were present or not. Today, species such as *Gymnocarpium dryopteris*, *Viola riviniana*, *Lapsana communis* and *Anemone nemorosa* are confined to the few remaining patches of brown earth (p. 78) and are, thus, relics from a formerly more widespread plant community.

The *Fagus* pollen frequencies at Elsborg Bog increased to about 40% about AD 450 and, from that time onwards, *Fagus* dominated the regional woodlands (Plate X).

VEGETATION IN ELDRUP FOREST INFLUENCED BY HUMAN ACTIVITY IN THE PAST

The vegetation in the research area in Eldrup forest was influenced by Man in Subboreal-early Subatlantic time (4300 BC to AD 500), Medieval time (AD 800 to 1400) and Recent time (1550 to 1800). The last of these human interventions still influences the vegetation in the area today.

Subboreal and early Subatlantic time (4300 BC to AD 500)

Vegetation influenced by Man in Subboreal and early Subatlantic time was traced in the pollen diagrams from the *Molinia* hollow and soil sections -C 9 and -A 13 (Plates XV, XVI, XX, XXI and XXVI).

Minima for *Tilia* and peaks for *Quercus* at the *Molinia* hollow signify the first possible traces of human influence. Slight peaks for aquatics indicate more open tree cover over the hollow at the same time. At section -C 9 there is a slight *Betula* maximum within the *Tilia- Quercus- Corylus* stage, which was smoothed out by soil-mixing, and there is a *Quercus* maximum at section -A 13, which correlates with the first *Quercus* peak at the *Molinia* hollow. Ferns (*Dryopteris*-type and *Gymnocarpium dryopteris*) remained frequent at the two soil sections, and *Anemone* increased distinctively at -A 13. Hence, the field vegetation of ferns was not disturbed and *Anemone* increased, presumably due to improved illumination. Other herbs were scarce, or absent. There are accordingly indications that some *Tilia* trees were felled, favouring *Quercus*, but there is no evidence of other exploitation such as grazing by cattle.

The first traces of human intervention in Eldrup Forest were contemporaneous with the regional *Ulmus* decline at Elsborg Bog (at 4000 BC, Plate X). The first neolithic cultures in Djursland occur at about the same time (Troels-Smith 1982), and a landnam was traced at Elsborg Bog at between 3500 and 3200 BC (p. 116). Hence, it appears that early Neolithic people may occasionally have been active in Eldrup Forest.

Tilia decreased distinctively at the *Molinia* hollow at about 3000 BC and persisted at low frequencies (10-20%) until about AD 500, whereas *Quercus* and *Betula* increased. *Quercus* remained frequent (about 50%) with one minimum, and *Betula* had several minor, and one major peak (about 50%), at the cost of *Quercus* (*Quercus- Tilia- Betula* stage). *Corylus* also increased slightly and reached a few minor peaks. The first increases of *Quercus* and *Betula* were also recorded at soil section -C 9, but no organic material was preserved from that time until *Fagus* expanded at the end of the *Quercus- Tilia- Betula* stage. The entire *Quercus- Tilia- Betula* stage is absent from soil section -A 13. The mentioned changes in tree composition were interpreted as indications that *Tilia* trees were felled favouring *Quercus*, that *Betula* expanded intermittantly due to felling of trees, and that *Corylus* was slightly favoured due to improved illumination (p. 127). *Fagus* invaded the area later, at about 1300 BC, but was checked intermittantly by felling. The simultaneous occurrences of *Sorbus aucuparia* and *Frangula*, as well as *Salix* scrub and herbaceous vegetation, around and within the *Molinia* hollow, indicate openings in the tree canopy. The frequencies for *Juniperus*, *Calluna*, open-ground herbs and Poaceae increase slightly, but they do not exceed the values found in the contemporaneous pollen spectra from the undisturbed vegetation at the *Glyceria* hollow (Plate XII). Hence, these plants occurred on distant field and pasture areas. *Anemone* was slightly more frequent than before, probably due to improved light conditions, and acid-humus plants were unchanged. There are thus no indication that the forest was grazed.

Sorbus aucuparia and *Dryopteris*-type spores were frequent at soil section -C 9, whereas other non-tree plants were scarce. Hence, the tree cover was rather open, but the field vegetation was scarce, except for the ferns.

The decrease of *Tilia* and increase for *Quercus* and *Betula* coincided with a change from oligotrophic brown earth to podzoloid and subsequently accumulation of humus at section -C 9, presumably because of impoverishment of the soil fauna due to the change in the composition of the leaf litter (p. 133). The absence of organic debris from extended periods at the two soil sites is somewhat mysterious. Organic litter, including pollen grains, apparently disintegrated completely on the soil surface, probably as a result of the human activity.

It was mentioned on p. 127 that the most likely purpose of human intervention - the felling of *Tilia* in favour of *Quercus*- was to provide mast for browsing by pigs. Unlike cattle, pigs do not require clearings with a rich herbaceous vegetation, provided that mast is plentiful.

The human activity around the *Molinia* hollow persisted for more than three millenia, from the middle Neolithic throughout the Bronze Age, and the Pre-Roman and Roman Iron Age. The increase of the pollen from field and pasture areas at Elsborg Bog (p. 116) cannot be dated due to disturbance of the deposit. Extensive pastures belonging to the Beaker-Culture occurred at Dyrholmen 10km west of Eldrup Forest (Troels-Smith 1942, 1982), and there are indications of intensive agriculture at Fuglsø Bog 8km east of Eldrup Forest at about 2800 BC and between 800 BC and AD 220 (Bahnson 1973). Prehistoric barrows, furthermore, are numerous around the Løvenholm forests (Fig. 5, p. 7). Hence, there were dense settlements around the forests, which thus formed a marginal area. Nevertheless, these forests were exploited locally, at least, by peasants living in the settlements.

Mikkelsen (1949) noticed a decrease in agricultural indicator plants at middle Subatlantic time in a regional pollen diagram from southeast Denmark (Lake Even, near Præstø). Based on archaeological evidence, he dated this event to the transition from the Roman Iron Age to the Germanic Iron Age (about AD 400), a dating which was later confirmed by Andersen (1978a). Iversen (1973) ascribed the same date to similar events in a pollen diagram from Bundsø, southeast Jutland (In A. Andersen 1954), and discussed various reasons for a general depopulation at that time. There is no evidence for such a depopulation in Djursland; however, it is striking that the cessation of human activity in Eldrup Forest was contemporaneous with the evidence of depopulation from southern Denmark.

Medieval time (AD 800-1400)

Human influence on the vegetation in the research area in Medieval time (including the Viking period) was traced in nearly all of the pollen diagrams. Survey diagrams are shown on plates XXVII and XXVIII.

Molinia hollow

Fagus- Quercus forest had prevailed in the vicinity of the *Molinia* hollow since the cessation of human activity at about AD 500. Traces of human influence appear at soil section -C 9 (Plate XX) as an increase in *Betula*, which culminates in a maximum at 50%, at the cost of *Fagus*, and is reflected slightly at the *Molinia* hollow (Plate XXVII). At this site the and section -A 13 (Plate XXI), there is an increase in *Quercus*, which reaches a peak at 30-40%. These features indicate felling of *Fagus* trees. At section -C 9 there is a distinctive maximum for open-ground plants (Poaceae, *Rumex acetosella*, *Plantago lanceolata*) simultaneously with the *Betula* maximum, and a decrease in *Dryopteris*-type spores. The percentages for the open-ground plants exceed the frequencies found during the earlier period of human influence and may, together with the decrease of fern spores, indicate grazed patches near the site. If grazed, the herbaceous plants can be assumed to have produced less pollen; they may, accordingly, have been more common than indicated by their pollen frequencies. The open-ground herbs remain scarce at the *Molinia* hollow and section -A 13, low peaks for *Salix* and aquatics indicate a more open tree cover at the *Molinia* hollow at that time.

Matrikel hollow

At the Matrikel hollow there is a distinctive increase for *Betula* at the cost of *Quercus* (*Quercus- Tilia- Betula* stage, Plate XVIII). These changes appeared in a *Quercus- Tilia- Corylus* forest, which resembled the *Quercus- Tilia- Corylus* forest found in the advanced stage of the *Tilia- Quercus* forest at the *Glyceria* hollow (Plate XXVII). Poaceae and open-ground herbs were scarce, and *Gymnocarpium* frequent, hence there is no indication of grazing, rather it appears that some *Quercus* trees were felled, presumably for timber.

Tilia decreased, somewhat later, and there were consecutive maxima for *Betula* (25%) and *Quercus* (50%, *Quercus- Betula* stage). *Tilia* thus was felled by Man, and was at first replaced by *Betula* and, slightly later, by *Quercus*. There is some evidence that *Tilia* was exploited extensively for leaf-fodder in Medieval time; *Tilia* trees used for leaf-fodder have proved to occur very frequently in fresco-paintings in Danish parish churches. These trees are not pollard trees such as those which can still be seen in Northern Europe, but resemble shredded trees, as described by Rackham (1976, 1980). Unlike pollards, the entire trunk and the top branches of shredded trees are preserved, whereas adventitious side sprouts along the trunk are lopped repeatedly. Shredding is used for producing leaf-fodder in a wide area, ranging from Spain to India, but the common employment of shredding in Denmark in Medieval time was formerly unnoticed. There is, however, no decisive evidence that *Tilia* was shredded for leaf-fodder in Eldrup Forest. If that was the case, it is unlikely that *Betula* replaced *Tilia* as this tree should have been removed. Hence, it is more likely that *Tilia* was removed with the purpose of increasing the illumination of the ground flora. Open-ground plants thus increased at this time, giving some evidence of grazed patches.

Tilia and *Corylus* nearly vanished, and *Quercus* and *Betula* decreased due to a strong expansion of *Fagus*. The expansion of *Fagus* was thus a death blow to *Tilia* and *Corylus*, whereas *Quercus* survived as a subordinate member of the *Fagus* forest. These changes mark a cessation of human intervention.

At soil section Ma (Plate XXV) organic debris from the *Quercus- Tilia- Betula* and *Quercus- Betula* stages is lacking and was apparently destroyed totally, as was the case at other soil sections during periods of human intervention.

Soil sections C 19 and E 13

Comparatively high frequencies of *Calluna*, Poaceae, *Rumex acetosella*-type and *Hordeum*-type pollen were noticed at the base of the pollen diagrams from soil sections C 19 and E 13 (Plates XXIII, XXIV). The *Hordeum*-type pollen was particularly frequent (5-10%). The *Hordeum*-type pollen (including *Hordeum vulgare* and *Elymus repens*) was taken as an indication that fields, probably with Poaceae, *Rumex acetosella*, *Spergula* and *Centaurea cyanus* as weeds, occurred in the vicinity whereas the pollen of *Fagopyrum* probably derived from more distant fields. The pollen spectra were assumed to have become homogenized during burial; it could, therefore, not be determined whether the *Fagus* and *Calluna* pollen were contemporaneous with the fields or derived from later successional stages. *Fagus*- *Quercus* forest succeded the cultivation phase.

Conclusions

There are indications of human activity in Medieval time - beginning in the centuries before AD 1000 and lasting till about 1400 - in nearly all the pollen diagrams from the research area in Eldrup Forest.

Fagus trees were felled around the *Molinia* hollow in the southeast part of the research area, favouring *Betula* or *Quercus*, and there are traces of grazing by cattle; *Quercus* and, somewhat later, *Tilia* were felled around the Matrikel hollow in the north, giving way to *Betula*, and the forest was probably grazed for some time, and cultivated fields appear to have occurred in the central part of the research area. Apart from the cultivation of cereal crops, which probably was of limited extent, the general scope of the activity in Eldrup Forest seems to have been limited to cutting of timber and illuminating of the forest to varying degrees.

Pollen of *Centaurea cyanus* and *Fagopyrum* was noticed repeatedly (*Molinia* hollow, Matrikel hollow and soil sections -A 13, C 19 and E 13). Common occurrence of *Centaurea cyanus* pollen is a striking feature for the youngest part of Danish pollen diagrams (Mikkelsen 1949, 1952, 1954, A. Andersen 1954). The age is estimated variously, but seems to fall mostly within Medieval time. Macrofossils have been reported from early Medieval time and later (Jessen & Lind 1922-23, Jensen 1979 and unpublished). Historical records of *Fagopyrum esculentum* date back to around 1400 (Jessen & Lind 1922-23). Iversen (1964) found pollen of *Fagopyrum* in Draved Forest from shortly after AD 740; other finds from Denmark date from Medieval time (Sørensen 1973) or probably Medieval time (Jørgensen 1956). *Fagopyrum* pollen is frequent in cultivated soils ("Plaggenesche") from northwest Germany which date from the early Medieval and later (Behre 1976), and occurs in Poland back to about AD 900 (Szczepanek 1982). The finds of *Centaurea cyanus* and *Fagopyrum* in Eldrup Forest confirm thus the dating of this cultural phase to Viking and Medieval time. *Fagopyrum* and *Centaurea cyanus* pollen occur up to near-surface-levels in Eldrup Forest; *Fagopyrum* was still cultivated in Denmark in the early 20th century (Brøndegaard 1979).

There is accordingly, evidence of increased human activity in Eldrup Forest from around AD 800, but no settlements were established. The forest was apparently exploited marginally to denser settlements. Some of the villages around the Løvenholm-Fjeld forests (Figs. 2 and 3) have names with the suffix "-ing" from the Early or Middle Iron Age (Auning, Gesing, Hald 1965), but there are several villages with names derived from the "-torp" suffix, which dates from the Viking and early Middle Ages (Tøjstrup, Torup, Pindstrup, Klemstrup, Bøjstrup). One of them is Eldrup itself, which was first mentioned 1271 (p. 8). The local names ending in "-borg" (Hummelborg, Krusborg, Elsborg) probably were applied to single farms from the same time. Hence, several settlements were founded around and in the immediate vicinity of Eldrup Forest at the time when human activity was resumed in the forest.

At Præstø, southeastern Denmark, an expansion of agricultural indicator plants occurred about AD 1000 in the present author's interpretation (Mikkelsen 1949, Andersen 1978a). This expansion continued till 1300-1400. At Bundsø, southeast Jutland (A. Andersen 1954), there are slight indications of a similar expansion (the herb maximum may have been lost between two pollen spectra). The early Medieval agricultural expansion on Djursland thus coincided with a similar expansion in southern Denmark (cp. Andersen, 1978a).

Fagus expanded again at about 1400 in Eldrup Forest, an indication of decreased human activity. This decrease coincides with a general economic crisis in Denmark, during which many villages were abandoned (Gissel *et al.* 1981), and the Eldrup village may well have been among them. A decrease of the agricultural indicator plants at Præstø was ascribed to the same event by Mikkelsen (1949).

Recent time (1550-1800)

A decrease of *Fagus* in the research area in Eldrup Forest about AD 1550 was accompanied by increases for *Quercus* and *Betula* ; *Calluna* and open-ground herbs increased simultaneously in several pollen diagrams (Plates XXVII and XXVIII).

Quercus and *Betula* increased slightly at the *Molinia* hollow and soil section -A 13 (Plates XV and XXI); *Calluna* and the open-ground herbs increased only indististinctly at these sites. *Quercus* increased distinctively at section -C 9; *Calluna* and the herbs from open ground became common and *Dryopteris*-type spores decreased (Plate XX). Hence, grazed glades probably occurred near this site.

Fagus was unchanged in the tree layer at soil section H 16 (Plate XXII), *Calluna* increased slightly, and open-ground herbs increased distinctively. Similar features can be seen at C 19 and E 13 (Plates XXIII and XXIV), but here were masked by mixing of the pollen assemblages. *Quercus* increased slightly at E 13. At the Matrikel bank (Ma, Plate XXV), there is a distinctive maximum for *Betula* ; pollen from open-ground plants was rather common, and *Dryopteris*-type spores decreased. Hence, grazed glades occurred near the site.

Pollen of cultivated plants (*Hordeum*-type, *Avena*, *Secale*, *Fagopyrum*) occurs only occassionally and was, accordingly, transported from fields outside the present forest.

Fagus thus was replaced by *Quercus* and *Betula* at some of the sites, and there are indications that grazed glades occurred occasionally. It can be assumed that the grazing subdued the representation of the open-ground vegetation in the pollen spectra. *Fagus* trees thus were felled, giving way in some places to *Quercus* and *Betula*, and to open glades, whereas *Fagus* forest still prevailed on the slopes near the *Molinia* hollow. Cutting of wood for timber or fuel was probably one of the purposes of the human activity. The favouring of *Quercus* may have been due to a wish to produce mast for pigs; these animals prefer *Quercus* to *Fagus* mast (Bjerke 1959). A general effect of the activity of Man was lightening of the forest, promoting *Betula*, and appearance of glades which were utilized for grazing.

The humus layers at sections -C 19, -A 13, H 16 and Ma were apparently undisturbed by trampling of cattle. Pollen of *Ilex aquifolium* was recorded at the Matrikel bank section (Ma, Plate XXV). This species was also recorded from the *Tilia- Quercus-Corylus* forest (p. 123). *Ilex* was thus probably indigenous to the forest and survived the browsing by cattle. *Calluna*, Poaceae and *Rumex acetosella* ocurred in the ground flora; the flora of the glades was thus poor and acidophilous. *Calluna* was scarcer than the herbaceous plants. *Calluna vulgaris* is strongly reduced even by light grazing, *Deschampsia flexousa* is slightly reduced, whereas *Holcus mollis*, *Agrotis tenius* and *Rumex acetosella* expand at grazing on similar soils (Bülow-Olsen 1980, 1982).

The Danish forests were increasingly exploited during the 17th and 18th centuries. In common practice, the trees belonged to the land owners, mostly the large estates, whereas peasants owned the rights to grazing. This lead to devastation of the forest: Trees were felled increasingly for the production of timber for building and for firewood, and increased grazing prevented regeneration of the trees.

The Løvenholm-Fjeld forests had been strongly affected by 1800 (p. 8 and Estrup 1943); however, Eldrup Forest which had belonged to the Stenalt Estate (p. 8) since 1683, does not seem to have been devastated to as great an extent, according to the pollen diagrams. The appearance of the forest by 1800 may be surmised from that of a small woodland, Hummelborg, just northwest of Eldrup Farm (Fig. 7, Plate IV), which is still being grazed. Here clumps of old *Fagus* trees are interspersed with glades, whereas continuous *Fagus* forest prevails on an ajoining slope (Plate IV). The soil at Hummelborg is, however, more fertile than were the soils in Eldrup Forest; the present ground vegetation of the glades at Hummelborg, therefore, differs from that found in the glades in Eldrup Forest at around 1800.

The Recent period of Man's intervention in Eldrup Forest was preceded by a period of practically no activity. In pollen diagrams from southern Denmark, the curves for agricultural indicator plants increase strongly at about 1600 (A. Andersen 1954, Andersen 1978a). The expanding human activity in Eldrup Forest thus coincided with increased human activity elsewhere in Denmark.

In the Forest Protection Law of 1805, cattle grazing in the Danish forests was forbidden. The law also proscribed the erection of fences or earth banks around the forests. The earth bank which delimits Eldrup Forest to the north and east was not built until some time after 1820 (p. 89) The tree-ring countings from the research area indicate, however, that cattle browsing was not intensive 1808-1822 and ceased entirely in the early 1820's (p. 41). Hence, forest protection clearly had already become effective in Eldrup Forest shortly after the enactment of the law in 1805, and caused a vigorous regeneration of trees there. Whereas *Fagus* regenerated within the former tree stands, *Quercus petraea* sowed itself in the glades giving rise to the present stands of nearly pure *Quercus*. This vigorous regeneration of *Quercus* shows that deer browsing was not as intensive at that time as it was when the present deer fence was erected 1969. The young *Quercus* trees were about 6m tall and began flowering vigorously by 1850 as evidenced by the tree-ring counts and the pollen diagrams, whereas *Fagus* did not begin to flower until later, probably at around 1900. *Betula* also invaded the glades giving rise to small maxima in the pollen diagrams; the *Betula* trees were, however, soon removed by felling. *Calluna* and the herbs began to flower vigorously at the cessation of the grazing, and their pollen frequencies increased strongly. One may also notice occasional occurrence of *Vaccinium*-type (probably *Vaccinium myrtillus*), *Jasione*, *Melampyrum* and *Pteridium*. *Juniperus* invaded the glades and began flowering slightly later than *Calluna*. These features are reflected with varying strength in the pollen diagrams (Plate XXVIII). The Matrikel earth bank was erected at a time when *Calluna* and *Juniperus* flowered vigorously and before planted *Picea* began flowering, that is, some time after the cattle grazing ceased. *Juniperus*, *Calluna* and the herbs were suppressed as the young *Quercus* trees began to form a closed canopy at about 1850.

The fauna of the brown earths found in the glades became increasingly poor during the grazing; the burrowing earthworms disappeared and were replaced by an arthropod fauna in a podzoloid stage, which followed the cessation of grazing (p. 138). Accumulation of humus and podzolization of the mineral soils began about 1850. At that time, the *Quercus* trees had reached a substantial size. The arthropod fauna could, apparently, no longer consume the increasingly large amounts of leaf-litter produced by the trees.

Fagus sylvatica and *Quercus petraea* today regenerate vigorously under the *Quercus* trees; openings in the tree canopy are necessary, however, for growth of the *Quercus* saplings (p. 57). The present *Quercus* stands are, therefore, ephemeral and will give way, in future, to *Fagus* dominated forest similar to that which occurred before cattle-grazing produced the glades.

The *Quercus* stands in the enclosure today house field vegetation characterized by *Pteridium aquilinum* and *Vaccinium myrtillus*. Other common species are *Deschampsia flexuosa* and *Melampyrum pratense*. These sites have a deep litter layer and moderately deep humus (p. 78).

THE DECLINE OF *TILIA*, *CORYLUS*, *HEDERA* AND *VISCUM*

Tilia cordata, once a dominant tree, has vanished from the Løvenholm forests, as have its associates *Corylus avellana*, *Viscum album* and *Hedera helix*.

Tilia cordata

At the *Molinia* hollow in the research area in Eldrup Forest, *Tilia* decreased strongly at about 3000 BC due to human attack but did not disappear till about AD 500, at which time it was replaced by *Fagus sylvatica*. *Tilia* survived thus the anthropogenic influence. Prior to that time, *Tilia* had been dominant, mixed with *Quercus* and *Corylus*, and grew on rather poor brown earth. *Corylus* was favoured slightly by the felling of *Tilia*, but *Corylus*, *Viscum* and *Hedera* nearly vanished together with *Tilia*.

Tilia, *Corylus* and *Hedera* pollen occurs occasionally in the *Fagus*- *Quercus* forest stage at the *Molinia* hollow and soil section -C 9 (Plates XV, XX and XXVI). Some of this pollen was probably redeposited. There are, however, small maxima for *Tilia*, *Corylus* and *Hedera*, which coincide with the felling of *Fagus* in Medieval time. Hene, a few plants possibly survived at these sites and were favoured by the increased illumination.

Impoverished *Tilia* forest - with increasing dominance of *Quercus*- persisted around the *Glyceria* and Matrikel hollows in the central and northwestern parts of the research area and was not invaded by *Fagus* until nearly a millenium later than at the *Molinia* hollow. The final stage of the *Tilia* forest was seen in the pollen diagram from the Matrikel hollow (Plate XXVII). Initially, shortly before AD 1000, *Quercus* trees were felled and were replaced by *Betula* ; somewhat later, at about 1200-1300, *Tilia* trees were felled and were replaced by *Betula*, and then *Quercus*, and grazing by cattle occurred. However, the final disappearance of *Tilia* was not seen until *Fagus* expanded vigorously at the cessation of human activity, at about 1400. Near the *Glyceria* hollow are traces of fields from Medieval time; *Fagus* expanded there after cessation of cultivation; the last traces of *Tilia* are found at the bottom of the pollen diagram from section H 16 (Plate XXVII).

Corylus, *Viscum* and *Hedera* still occurred at the Matrikel hollow in Medieval time, and disappeared with *Tilia*.

Fagus thus did not invade the *Tilia*- *Quercus* forest in Eldrup forest until a stage, where previous human disturbance had ceased. According to Aaby (1983), *Tilia* persisted as a dominant tree locally on sandy soil in Draved Forest a long time after the immigration of *Fagus*, and was not replaced by *Fagus* and *Quercus* till about 1600, after a period of human disturbance.

The inability of *Fagus* to invade natural *Tilia* or *Tilia*- *Quercus* forest, although the tree was present in the vicinity, is very remarkable, and difficult to explain. It appears indeed that a natural ecosystem can be very conservative and resistant to invasion by new immigrants.

The failure of *Tilia* to re-expand after being cheked by human activity is equally difficult to explain. Aaby (1983) found that the replacement of *Tilia* by *Fagus* and *Quercus* coincided with the onset of humus accumulation. *Tilia* is scarce on acid humus in Draved Forest (Iversen 1958, 1969); the failure of *Tilia* to re-expand after the cessation of human activity is thus explained by the contemporaneous formation of a humus layer in these instances. Humus accumulation also began at the *Fagus* expansion in Eldrup Forest in several cases. There is, however, evidence that brown earths persisted elsewhere for a long time after the invasion by *Fagus*. *Fagus* for example occurred on brown earth near sections C 19 and E 13 till around 1850. Today, *Tilia* and *Fagus* thrive together in mixed forest on rich brown earth on moist, clayey soil in Draved Forest (Iversen 1958), and in a stand on fertile clayey till in Jonstrup Vang, north of Copenhagen (Østergaard 1957). *Tilia* reproduces successfully in both places. *Tilia* occurs today on acid soils with pH down to 3.6 (Rackham 1980), without competition from *Fagus*, however. It thus appears that *Tilia* was expelled from Eldrup Forest partly because of the spreading of humus layers when *Fagus* expanded, and partly because it could not compete successfully with *Fagus* on the acid brown earths, once the natural equilibrium had been disturbed by human intervention.

If undisturbed by Man, the *Tilia- Quercus* forest in Eldrup would presumably have become increasingly richer in *Quercus* and poorer in *Tilia*. Iversen (1960, 1964, 1969) demonstrated in Draved that replacement of *Tilia- Quercus* forest by *Quercus* forest without preceding human intervention coincided with onset of humus accumulation A similar development might have taken place in Eldrup Forest. If man had not intervened, such a *Quercus*-dominated forest with a raw humus layer would presumably have been open to invasion by *Fagus*, and might thus have turned into *Fagus*-dominated forest in the course of time.

Tilia-dominated forests on sandy soils in Denmark thus became increasingly richer in *Quercus*, but were replaced by *Fagus* after human intervention. They would probably have become invaded by *Fagus*, ultimately, if left undisturbed. *Tilia* forest might have persevered on richer soils. *Tilia*, however, was attacked by Man in many ways (cp. Iversen 1960), and disapeeared in regional pollen diagrams in the course of Subboreal and Subatlantic time. Relic *Tilia*-dominated forests have survived in a few cases on moist gley-soils (Draved Forest, Vindeholme Forest), on fertile morainic soils, mixed with *Fagus* (Jonstrup Vang), and in a small stand on similar soils on Ormø, at Holsteinborg. The last-mentioned *Tilia* woodland is, however, threatened by a new factor: invasion by cormorant (*Phalacrocorax carbo*). A stand of *Tilia cordata* and *T.platyphyllos* on a small island in Brændegaard Sø, Brahetrolleborg, Funen, was recently exterminated by cormorants.

Corylus avellana

Corylus survived periods with human activity in Eldrup Forest and disappeared, practically speaking, with *Tilia* at the expansion of *Fagus*. *Corylus avellana* today is scarce in *Fagus* forest on various soils, probably due mainly to shade. The species might have persisted in Eldrup Forest as a pioneer tree in openings of the *Fagus* forest together with *Quercus*. As *Corylus* is scarcer than *Tilia* on acid soils today (Rackham 1980), its near disappearance at the expansion of *Fagus* indicates increased impoverishment of the soil.

Hedera helix

Hedera was common in Eldrup Forest in Atlantic and early Subboreal time; hence gaps in the canopy alowed *Hedera* to climb to the tree tops. *Hedera* decreased somewhat in the late part of the *Tilia- Quercus- Corylus* stage at the *Glyceria* hollow and in the *Quercus- Tilia- Betula* stage at the *Molinia* hollow, in both cases in middle Subboreal time (at about 2000 BC). *Hedera* was formerly exploited by Man for leaf-fodder, according to Troels-Smith (1960). As there were no other traces of local human activity at the *Glyceria* hollow, it is unlikely that the derease of *Hedera* in middle Subboreal time in Eldrup Forest was due to human influence; it was rather more likely due to impoverishment of the soil. *Hedera*, like *Corylus*, is scarcer than *Tilia* on acid soils today (Rackham 1980).

The *Hedera* pollen frequencies in Eldrup Forest were 0.5-1% in Atlantic time (calculated as percentages of the uncorrected tree pollen sum, Plates XI and XIV). *Hedera* pollen was scarce at Elsborg Bog in zone VII (0.1%); the *Hedera* pollen was, accordingly, not well dispersed to that site. Higher frequencies (0.5-1%) occur at Lake Korup and Dyrholmen in Djursland (Iversen 1941, Troels-Smith 1942).

The decline of *Hedera* in regional pollen diagrams from Denmark has been discussed intensively, and alternative explanations have been proposed (see Iversen 1960, Troels-Smith 1960). The species declined at the Atlantic/Subboreal transition, about 4000 BC, and nearly disappeared in the course of Subboreal time. *Hedera*, however, did not decrease at the Atlantic/Subboreal transition in Eldrup Forest, which shows that the decline seen in regional pollen diagrams was not conditioned by a change in climate, but was due, rather, to human influence, as suggested by Troels-Smith (1960).

Like *Tilia* and *Corylus*, *Hedera* nearly disappeared in Eldrup Forest at the expansion of *Fagus* (about AD 500 at the *Molinia* hollow and about 1400 at the Matrikel hollow, Plate XVII). A few occurrences from Medieval time were noticed at the *Molinia* hollow. *Hedera* today is scarce in *Fagus* forest as a tree climber, probably due to shade, and is scarce on acid soils. Hence it is likely that *Hedera* disappeared at the expansion of *Fagus* because of both shade and soil impoverishment.

Viscum album

Viscum pollen occurs rather frequently in deposits from Atlantic and early Subboreal time in Eldrup Forest. The pollen frequencies decrease slightly in middle Subboreal time at the *Molinia* hollow (Plate XV, about 2500 BC) and in late Subboreal time at the *Glyceria* hollow (Plate XII about 1300 BC), in both cases coinciding with decreasing *Tilia* frequencies.

It has been surmised that *Tilia* was the most important host tree of *Viscum* in Atlantic and Subboreal time (Iversen 1960, Walldén 1961, Aaby 1983). *Viscum album* ssp. *album* today occurs on dicotyledonous trees in Central and North Europe, whereas ssp. *abietis* and ssp. *austriacum* occur on coniferous trees (*Abies*, *Pinus* and *Larix*, respectively), and are confined to central and southern Europe (Tubeuf 1923, Ball 1964). The *album* subspecies is therefore more likely to have occurred in Denmark than the other two subspecies. This subspecies occurs on a wide range of trees today. It occurs very rarely on *Quercus robur* and *Q. petraea* (Tubeuf 1923) and extensively on *Betula* species in eastern Europe and North and Central Germany but is very rare on *Betula* at its northern and western distribution boundaries (Scandinavia, the British Isles, The Netherlands, Belgium, Tubeuf 1923, Hanssen 1933, Wallden 1961, Kloss 1960, Adolphi & Dickoré 1980). The fact that *Viscum* did not increase together with *Betula* at the *Molinia* hollow in middle Subboreal time indicates that *Viscum* did not occur on that tree. Today *Tilia* is by far the most common host tree of *Viscum* in Norway and Sweden, - it occurs only on five *Betula* trees in the whole of Norway and on seven *Betula* trees in Sweden, in contrast to northern Germany (Hanssen 1933, Walldén 1961, Ødum 1968). Walldén (1961) concluded, that an ecotype of *Viscum* preferring *Betula* is absent in Sweden today. There is, accordingly, reason to believe that *Viscum* grew mainly on *Tilia* in Denmark, and that an ecotype preferring *Betula* was - and is - absent for climatic reasons, since it does occur considerably south of Denmark today. The decrease of *Viscum* in Eldrup Forest can, therefore, be ascribed to the decrease of *Tilia*- in one case (*Glyceria* hollow) because of soil deterioration, and in the other case (*Molinia* hollow), because of attack by Man.

Viscum pollen occurs regularly with frequencies at 0.1-0.4% in Eldrup Forest in Atlantic and early Subboreal time (as percentages of the uncorrected tree pollen sum); the pollen is only sporadic in zone VII at Elsborg Bog, Dyrholmen (Troels-Smith 1942) and Lake Korup (Iversen 1941). Hence, *Viscum* pollen was apparently poorly dispersed in the regional pollen rain.

Like *Hedera*, *Viscum* did not decrease in Eldrup Forest at the Atlantic/Subboreal transition as they do in regional pollen diagrams. Hence, the supposition of Troels-Smith (1960) that the decrease of *Viscum*, like *Hedera*, was due to human influence, seems to be correct.

The persistence of *Viscum* together with *Tilia* and its subsequent disappearance with *Tilia* from Eldrup Forest is explained by the asumption that *Tilia* was the main host plant of *Viscum*, as also supposed by Aaby (1983) for Draved Forest. This event occurred about 500 BC at the *Molinia* hollow and about 1400 at the *Glyceria* hollow. *Viscum* persisted with *Tilia* till around 1600 in the pollen diagrams of Aaby (1983) and till near-surface-levels in Iversen's diagram from a site near the present *Tilia* stand (Aaby 1983). Aaby (1983) concluded that the extinction of *Viscum* in Denmark was not due to changes in climate but to the decrease of *Tilia*. It remains to be explained why *Viscum* has disappeared from the present *Tilia* stands in Denmark. These stands have been cut down and rejuvenated by sprouting - for example, the stand in Draved in 1862. *Viscum* obviously could not survive such treatment. The last *Viscum* on *Tilia* in Denmark were reported by Vaupell (1863) by the middle of the last century.

THE HISTORY OF *QUERCUS PETRAEA* IN ELDRUP FOREST

It was mentioned on p. 9 that the Løvenholm-Fjeld forests are distinguished by the common occurrence of *Quercus petraea* and the absence of *Q. robur*. *Quercus robur*, in contrast, is found on low-lying alluvial soils in the area.

Quercus petraea and *Q. robur* are thus ecologically separated: *Quercus petraea* occurring on well-drained, poor and sandy soils, and *Q. robur* on damp and fertile soils. Such a distribution pattern is characteristic of the two species and is often mentioned in the literature; it is, however, difficult to explain ecologically (Rackham 1980). *Quercus robur* has been favoured by culture and has frequently spread to secondary habitats - either on its own or with the help of Man (Iversen 1960, Rackham 1980); the species is thus common in *Quercus* copses in central and western Jutland, more or less mixed with *Q. petraea*. The purity of *Quercus petraea* in the Løvenholm-Fjeld forests can therefore be taken as evidence of their long standing as original woodlands, a conclusion also drawn for similar woodlands in Britain by Rackham (1980).

The pollen diagrams from Eldrup Forest have given no direct evidence as to the history of *Quercus petraea* there, as pollen grains of *Q. robur* and *Q. petraea* could not be distinguished. The diagrams have, however, shown that the forest has never been cleared extensively and that the present tree populations originated far back in time. Since its first expansion in middle Atlantic time (about 7000 ^{14}C years ago), *Quercus* has been a constant in Eldrup Forest - first associated with *Tilia* and later with *Fagus*- on poor, sandy soils which became increasingly impoverished. Based on these findings and on the present ecology of the *Quercus* species, it was surmised that *Quercus petraea* was the dominant, and probably the only, *Quercus* species present.

THE FORMER AQUATIC AND WET-GROUND PLANT COMMUNITIES IN ELDRUP FOREST

Local aquatic and wet-ground communities occurred within and around the three wet hollows in the research area (*Glyceria* hollow, Plate XIII, *Molinia* hollow, Plate XVI, Matrikel hollow, Plate XIX, for recent communities, see Oberdorfer 1957, Runge 1980, Pott 1980).

Aquatic plant communities

Ranunculus community

The earliest aquatic plant community, found in the *Betula*-stage at the *Glyceria* hollow, was rather poor, there are only occasional finds of pollen of *Ranun-*

culus trichophyllus-type, *Callitriche*, *Myriophyllum spicatum* and *Potamogeton*. Colonies of *Pediastrum*, however, were frequent. A similar flora was recorded from the Late Weichselian Allerød Chronozone (Table 57).

The aquatic *Ranunculus* species represented by the *R. trichophyllus*-type pollen (*R. aquatilis*, *R. circinatus*, *R. fluitans*, *R. peltatus* and *R. trichophyllus*, Andersen 1961) - and the other aquatics mentioned above, characterize plant communities belonging to *Potametea* (*Nymphaeion*) which consist of rooted aquatics with or without floating leaves in calcareous or moderately acid and shallow fresh-water. The scarcity of their pollen points toward a poorly developed community; the abundance of *Pediastrum* colonies indicates rather eutrophic conditions.

Callitriche- Lemna-(Glyceria) community

An aquatic community characterized by *Callitriche* and *Lemna* succeded the *Ranunculus* community in the *Corylus- Pinus- Betula- Populus* stage at the *Glyceria* hollow; a similar community occurred continuosly till near-surface-levels at the *Molinia* and the Matrikel hollows. *Potamogeton* pollen occurs occasionally, and there are a few finds of *Ranunculus trichophyllus*-type, *Hottonia*, *Nymphaea* and *Myriophyllum alterniflorum*.

The *Lemna* species (including *Spirodela polyrhiza*) form floating communities (*Lemnetea*) in ponds and in sheltered locations of larger lakes. The species range from mesotrophic (*L. minor*) to eutrophic sites (*L. gibba*) with slightly acid to alkaline water and are less or more dependent on nitrogen (Køie & Køie 1939, Oberdorfer 1962, Pott 1980). The appearance of *Lemna* in the *Corylus- Pinus- Betula- Populus* stage may therefore indicate increased influx of nitrogen perhaps due to the admixture of *Corylus* leaves. The species can tolerate periodic desiccation, as long as small wet pools are preserved. The *Callitriche* species occur mostly in stagnant water ranging from acid and oligotrophic (*C. hamulata*) to eutrophic sites poor in lime (*C. palustris*, Pedersen 1966, Oberdorfer 1962). They tolerate desiccation and, today, often occur in *Potametea* communities - particularly in associations belonging to the *Nymphaeion* and *Ranunculion fluitantis*. *Myriophyllum alterniflorum* occurs at oligotrophic sites. *Glyceria* pollen occurs frequently together with *Callitriche* and *Lemna* in the hollows in Eldrup Forest. The species *G. fluitans*, *G. plicata* and *G. declinata* are rather alike ecologically occurring around and within mesotrohic (*G. fluitans*) or eutrophic (*G. plicata*) pools or in slowly moving water. These amphiphytes tolerate submergence but flower more vigorously, when desiccated. *Glyceria fluitans* is characteristic of ponds in woodlands (Pedersen 1974), and a few specimens still occur in the *Glyceria* hollow. *Glyceria*, probably *G. fluitans*, thus also characterized the vegetation within and around the small, periodically desiccated ponds in Eldrup Forest.

The small hollows in Eldrup Forest have thus contained a characteritic community of *Callitriche*, *Lemna* and *Glyceria*-species, associated with a few other aquatic plants. This community seems nearly related to the present-day *Hottonietum palustris* (with *Hottonia*, *Callitriche palustris* and *Lemna minor*), and *Ranunculetum aquatilis* (with *Ranunculus aquatilis*, *Callitriche palustris*, *Lemna minor* and *Glyceria fluitans*), which are characteristic of shallow ponds with fluctuating water level. The community was thus conditioned by periodic desiccation of the ponds, which probably were mesotophic and slightly acid, with some admixture of nitrogen.

The ponds in the *Molinia* and Matrikel hollows were overgrown by peat and subsequently dried out, whereas the pond in the *Glyceria* hollow still exists. Even so, only *Glyceria fluitans* has survived there. The impoverishment of the flora in the *Glyceria* hollow was probably due to oligotrophication at the time when acid humus layers developed on the surrounding soils.

Wet-ground plant communities

Carex community

Traces of a *Carex* community are recorded from the *Betula* stage at the *Glyceria* hollow. It is somewhat uncertain how much of the *Carex* pollen derived from a wet-ground community and how much of it was transported from the field layer of the *Betula* forest. *Glyceria*, *Caltha* and *Menyanthes* pollen is rather frequent, pollen from Poaceae and other plants in the uncertain category may also have derived from a wet-ground community.

It is difficult to charaterize this community, because the species identity of the *Carex* and Poaceae pollen is unknown. The *Glyceria* species are meso-eutrophic, *Caltha palustris* and *Menyanthes trifoliata* occur on wide ranges of soils and in several plant communites. Due to the scarcity of *Sphagnum*, the *Carex*-community probably was meso- or eutrophic and only slightly acid. Hence, it was related to present-day *Phragmitetalia*.

Carex- Thelypteris (- Sphagnum) community

A wet-ground community with *Carex* and *Dryopteris*-type spores (presumably *Thelypteris palustris*) developed during the *Corylus- Pinus- Betula- Populus* stage at the *Glyceria* hollow, and in the *Tilia- Quercus- Corylus* and *Quercus- Tilia- Betula* stages at the *Molinia* hollow. *Sphagnum* spores were more common at the *Molinia* than at the *Glyceria* hollow. A similar community was present at the Matrikel hollow and *Glyceria* was present at all three sites. *Typha latifolia*, *Sparganium*-type, *Alisma*, *Osmunda*, *Schoenoplectus* and *Hydrocotyle* are recorded occasionally. Macrofossils of *Carex rostrata*, *C. caespitosa* and *Ranunculus flammula* occurred at the *Molinia* hollow.

These communities are related to various present-day wet-ground communities (*Phragmition*, *Magnocaricion*, *Caricion nigrae*, *Alnion glutinosae*). The sites were probably meso- to oligotrophic and somewhat acid.

The *Carex- Thelypteris* (- *Sphagnum*) community is not present at the *Glyceria* hollow today, presumably because the peat was destroyed by the wallowing of the red deer (p. 88). The community disappeared at the *Molinia* and the Matrikel hollows due to desiccation; communities dominated by *Molinia caerulea* occur on the peat today (*Quercus petraea- Molinia caerulea- Dryopteris carthusiana* community, p. 80).

Salix community

Scrub *Salix*, probably *Salix cinerea*, occurred periodically around the *Glyceria* and *Molinia* hollows, especially at times when the tree cover was discontinuous. The *Salix* scrub has vanished today.

General conclusions

THE LØVENHOLM AND FJELD FORESTS IN DJURSLAND

The Løvenholm and Fjeld forests to-day form the largest woodland area on Djursland, East Jutland. They consisted in the late 18th century of smaller woodlands, which to-day are united by *Picea* plantations. The northern part of the Djursland peninsula is glacigenous landscape which, except for the Løvenholm area, was densely inhabited in prehistoric and historic time. The Løvenholm forests thus formed a marginal area surrounded by settlements.

Fagus sylvatica predominates in the natural woodlands in northern Djursland, which are noticeable because of the common occurrence of *Quercus petraea*, in Denmark otherwise confined to western Jutland. 1969 a research area was established in Eldrup Forest with the special purpose of studying the history and ecology of *Quercus petraea*. Soils, present vegetation and vegetational history of the research area were examined.

GEOLOGICAL SUBSTRATE AND SOILS IN THE RESEARCH AREA IN ELDRUP FOREST

Eldrup Forest occupies the northeast slope of a glacigenous ridge. The research area contains several kettle-holes, which are partly filled by gyttja and peat. Sandy till and sorted sand occur near the surface. The sorted sand is superposed on the till and is irregularly distributed.

The depth of the leaf litter is mainly determined by exposure to the wind. Humus layers mostly cover the mineral soil outside the wet hollows; layers less than 20cm deep predominate and are less than 130 years old. The depth of the humus depends strongly on the depth of the leaf litter and slightly on the content of clay and silt in the topmost soil. Still deeper humus layers occur in a few places.

Podzols predominate within the research area. The depth of the leached horizon depends strongly on the silt and clay content of the topmost mineral soil and slightly on the depth of the humus layer. Brown earth occurs in a few patches, and hydromorphic soils in depressions.

THE PRESENT VEGETATION IN THE RESEARCH AREA IN ELDRUP FOREST AND ITS ENVIRONMENT

There are no traces of former tilling within the research area. Former grazing by cattle ceased shortly after 1805; thereafter, the forest was subjected to forest management (tree thinning, felling of single mature trees). Deer browsing occurred until 1969. At that time, tree reproduction consisted of *Fagus sylvatica* and *Picea abies*, and no young *Quercus petraea* were present. The reproductive tree layer was removed and a deer fence was erected 1969. Since that time, new tree reproduction has appeared. An artificial clearing was established by the felling of four trees.

Trees and tree stumps within the enclosure were mapped and tree heights and diameters measured. Tree saplings were counted in lm^2 circular plots at the main points of a coordinate system. Tree seedlings and other field vegetation were recorded for the same plots by Iversen's modification of the point method of Levy and Madden. The ground vegetation data were analyzed by two numerical methods, Principal-Component-Analysis (PCA) and Two-Way-Species-Indicator-Analysis (TWINSPAN). The TWINSPAN analysis is described by H.J.B. Birks.

Ecological variables

Surface gradients vary 0-16°; gradients less than 4° predominate in the northwestern part of the enclosure, which forms a rather high plateau, and gradients larger than 4° in the southeastern part, where rather large slopes occur. Variations in litter and humus depth, and in pH and water content of the topsoil, are shown in Fig. 22. The highest pH measured was 5.5. As root competition in the topmost soil is strong near *Fagus* trees, plots with *Fagus* as the nearest tree were also recorded; they constitute 49% of all plots. Plots without tree cover and ajacent plots were recorded; the frequency of the "light"-plots is 18%.

Organic and mineral content, and pH, in topsoil samples were compared with eleven geochemical elements. Samples with high mineral content were particularly rich in soluble Fe, P, Na, Mn and Al, and the samples with the highest pH in Fe, P and Mn (Table 6). Of six ecological variables (litter depth, humus depth, water content, pH, exposure to light and *Fagus*-nearest-tree), litter depth and water content were strongly positively, and pH strongly negatively, correlated with humus depth (Table 9). In comparisons of the density data (frequency or coverage) for tree saplings and seedlings, and field plants, with the six ecological variables, averages, density percentages, normalized density distributions and correlations were calculated.

The canopy trees

Three species are present in the tree canopy: *Fagus sylvatica*, *Quercus petraea* and *Betula pendula*. Measurements of the petiole length of leaves of *Quercus petraea* compared with *Q. robur* show that *Quercus petraea* in Eldrup Forest is well separated from the other species. *Fagus* predominates on slopes in the southeastern part of the enclosure and occurs in clumps interspaced with *Quercus* stands in the northwestern part (Fig. 27). *Betula pendula* is very scarce.

The tree diameters were normally distributed indicating nearly equal age of the trees. *Fagus* is taller than *Quercus* in the southeastern part of the enclosure, and both trees are taller in southeast than in northwest (Fig. 30). The *Fagus* trees in southeast are thicker, and *Quercus* slightly thicker, than in northwest.

The four *Quercus petraea* felled in 1968 derived from sometime before 1808-1828. They increased vigorously 1820-1850. Former cattle grazing, which was forbidden by the Forest Protection Law of 1805, thus had ceased entirely not later than 1820. The whole tree generation in the research area probably derives from the early 19th century, and trees from before that time have been removed. It is assumed that the present *Quercus* stands originated in glades formerly grazed by cattle.

The frequency of *Fagus* increases with the surface gradient in the southeastern part of the enclosure (Fig. 33). Otherwize, tree distribution shows no relationship to ecological variables.

The *Fagus* trees found on the large east-facing slopes in the southeastern part are tallest; there the canopy reaches the same altitude as the trees growing at higher altitude to the west (Figs. 35 and 37). The *Fagus* trees on the slopes thus have utilized shelter from the predominating westerly and southwesterly winds, probably due to decreased evaporation in the tree tops.

The reproductive tree layer

Saplings of *Fagus sylvatica*, *Quercus petraea* and *Sorbus aucuparia* have appeared since the deer fence was erected, and formerly suppressed shrubs of *Ilex aquifolium* have grown in height.

The density of saplings and seedlings was compared with six ecological variables (Table 25, Fig. 41). The fruits of *Fagus* and *Quercus* need protection by leaf litter against predators and drought, and those of *Fagus* germinate somewhat better on shallow than on deep humus. The seedlings of *Fagus* and *Quercus* survive particularly well on shallow humus, but the *Quercus* seedlings need light to develop into saplings. Seedlings of *Fagus* and *Quercus* are absent on sites near *Fagus* trees, presumably due to water deficit.

As *Fagus* reproduces vigorously beneath *Quercus* trees the *Quercus* stands will tend to become dominated by *Fagus* in the future. The *Fagus* stands do not reproduce at present, but their root systems may become weakened at a greater age, allowing new reproduction, and *Fagus* and *Quercus* reproduction is likely to appear near stormfelled trees.

The clearing

Ground vegetation analyses from the artificial clearing were compared with plots from a strip around the clearing. *Fagus* saplings were least frequent in the open area, and there were very few seedlings. *Quercus* seedlings and saplings were frequent in the open area; specimens 1-4m tall occurred only there. The *Quercus* saplings thus need full illumination for a vigorous height growth.

Nearly all field layer plants were more common in the open than in the shaded area, and were thus favoured by better illumination. Only a few species not already present in the forest had appeared in the clearing.

The ground vegetation

Tree saplings and field vegetation were included in the analyses of the ground vegetation. No attempt was made to distinguish *a priori* plant communities; instead, an attempt was made to structure the ground vegetation by statistical analysis and to compare the units distinguished with ecological variables.

The PCA did not contribute very succesfully to the separation of units. Species loadings indicated a grouping of some of the species. Plot scores on the first principal component were strongly correlated with species numbers and plant densities, those on the second with humus depth and water content, and those on the third slightly with pH.

The TWINSPAN analysis arranged the 670 vegetation plots into eight plot groups and the 31 species into ten species groups. The eighth plot group comprises plots without ground vegetation (Table 34). Plot groups 2, 3, 5 and 8 were the most important.

The eight plot groups were compared with six ecological variables (Table 36 and Fig. 44). The main plot groups were distinctive ecologically. The plant combinations of plot group 2 avoid thick litter cover, are restricted to shallow-humus and dry sites with high pH, do not avoid *Fagus*-trees, and tolerate shade. Those in plot group 3 tolerate deep litter, prefer a moderately deep humus layer with moderate moisture and pH, avoid root competition from *Fagus* and require some illumination. Plot group 5 prefers deep humus and peat with high water content and low pH. The plot groups 1-7 reflect plant combinations with increasing soil moisture requirements; plot group 8 occurs at moderate litter cover, deep humus, mostly near *Fagus* trees, and in shade.

Normalized density scores in the eight plot groups were calculated for species. The ten species groups unite species with similar distributions over the plot groups (Fig. 45).

Normalized densities of the plant species were compared with the ecological variables (Table 39 and Figs. 46-51). Species concentrated in one plot group have ecological characteristics similar to those of that plot group, whereas species distributed over several plot groups have broader ecological requirements.

Plant communities in Eldrup Forest

Based on tree distribution and ground vegetation groups, four ecologically distinctive plant communities were distinguished: *Fagus sylvatica- Deschampsia flexuosa* community; *Quercus petraea- Fagus sylvatica* community; *Quercus petraea- Molinia caerulea- Dryopteris carthusiana* community; and *Fagus sylvatica* community.

The four plant communities show affinities to common phyto-sociological units.

THE VEGETATION AND THE SOILS OF ELDRUP FOREST IN THE PAST

Three small wet hollows and six soil sections were selected for a study of the local vegetational history and soil development throughout the Holocene. In addition, sections from the adjacent Elsborg Bog were studied in order to obtain a picture of vegetational development on a regional scale. The sections were studied by microfossil analysis (pollen and hypha fragments), macrofossil analysis, geochemical analysis, and radiocarbon dating.

Elsborg Bog is 900x500m wide. The sections studied derived from a small area, where the original peat is preserved (Fig. 7). The three small hollows studied in Eldrup Forest are located in the southeastern part of the research area (*Molinia* hollow), the central part (*Glyceria* hollow), and the northern part (Matrikel hollow, Fig. 8). They are less than 20m in minimum diameter and are covered by tree canopy. The uppermost deposit at the *Glyceria* hollow was disturbed by wallowing of red deer. The six soil sections (Fig. 8) are podzols with a humus layer. One section (Matrikel bank) was beneath an earth bank which was erected in the early 19th century and delimited Eldrup Forest towards the north.

Many problems exist as to the construction of the pollen diagrams, and several methods were employed. The tree pollen spectra from Eldrup Forest were corrected according to the method of Andersen (1970, 1978a). Non-tree plants are varyingly represented in the pollen spectra, but they could not be corrected for over- or underrepresentation.

Observations on pollen corrosion served two purposes: evaluation of possible modification of the pollen spectra and evaluation of the depositional environment. The frequency of pollen grains with corrosion marks varies in various taxa. Comparisons of contemporaneous pollen spectra, which contained varying frequencies of corroded grains, showed that the differences were small (Table 53, Fig. 62). Corroded pollen grains are frequent in sediments formed in the presence of oxygen at pH higher than 5. Corroded grains in limnic sediments and peats indicate periodic desiccation and pH higher than 5. Corrosion of pollen in terrestrial soils indicates pH higher than 5.

Former stages in the evolution of terrestrial soils were evaluated by changes in the length of fungal hypha fragments, content of organic matter, and pollen corrosion. Four stages were distinguished: a neutral brown earth stage, an oligotrophic brown earth stage, a podzoloid stage, and a humus accumulation stage (cp. Andersen 1984, Figs. 65-66).

Eighteen samples from Elsborg Bog were dated by the radiocarbon method. Only two samples from Eldrup Forest were dated, because the samples generally were unsuitable for radiocarbon dating. Ages are stated in conventional ^{14}C-years before 1950 or in calendar years (corrected according to Clark, 1975).

The vegetational sequence at Elsborg Bog

The pollen diagram from Elsborg Bog (Plate X) was divided into conventional pollen zones. The datings of the *Fagus*-increase at one section (1972) are considered unreliable due to mixing by human activity. The rise of *Fagus* was dated at an adjacent section (1974). Large amounts of *Cannabis / Humulus* pollen indicate that the site was used repeatedly for retting of *Cannabis* stems (from AD 450 to the 19th century).

The vegetational sequences in Eldrup Forest

Pollen diagrams from the sites in the research area in Eldrup Forest are shown in Plates XI-XXV. At the *Glyceria* hollow, a few pollen spectra from the Late Weichselian Allerød Chronozone were recorded. The entire Holocene up to to-day is represented in the pollen diagrams. As the tree pollen spectra exclusively reflect tree communities on dry ground, they cannot be referred to regional pollen assemblage zones; local forest stages were used instead. A survey of the Holocene forest stages represented at the various sites, and their correlation are shown in Table 61. Three periods with cultural influence were distinguished, Subboreal-early Subatlantic, Medieval and Recent (Table 61). The vegetational development at sites in the southeastern part of the research area differed from that in its central and northwestern part in Subboreal and early Subatlantic time.

The pollen diagrams from the *Glyceria* and *Molinia* hollows were synchronized on a common time scale using one radiocarbon date and ages for specific levels inferred from radiocarbon dates elsewhere or historical information (Fig. 67). The pollen diagrams from the other sites were dated using correlations with the *Molinia* hollow. Synchronized survey diagrams are shown on Plates XXVI-XXVIII. The periods with cultural influence appear at about 4300 BC to AD 500 (Subboreal-early Subatlantic), AD 800 to 1400 (Medieval), and 1550 to 1800 (Recent).

Natural forest communities in Eldrup Forest in the Holocene

The pollen diagrams from Eldrup Forest reflect natural forest communities and forest influenced by human utilization. The natural forest communities in Eldrup Forest can be assumed to be typical for the forests which prevailed in Denmark at various times in the Holocene on soils similar to those which occur in Eldrup Forest: sandy tills and sands with low silt and clay content poor in lime. The tree pollen spectra from Eldrup Forest were compared with local tree pollen spectra from elsewhere in Denmark. Comparisons with tree pollen spectra from large lakes and bogs, which reflect a broader spectrum of forest communities, make it possible to distinguish tree vegetation on other soils.

Betula forest

Betula-dominated forest prevailed in Preboreal time from 9600-9000 ^{14}C-years ago. *Pinus* and *Corylus* immigrated, but did not expand. *Juniperus* and heliophilous herbs occurred and there was a rich field vegetation with a few acidophilous species. The tree cover became fairly open in the late part of the *Betula*-stage, possibly due to local soil disturbance. The scarcity of *Pinus* and *Populus* was a local feature. The soils are likely to have been acid brown earths.

Corylus- Pinus- Betula- Populus forest

Corylus- Pinus- Betula- Populus forest prevailed in Preboreal and early Atlantic time from 9000 to 7000 ^{14}C-years ago. *Corylus* constituted about 50%, *Pinus* up to 30%, and *Betula* and *Populus* up to 10% of the tree cover. *Tilia* invaded but was hampered by setbacks. Shrubs and field vegetation were sparce. The soils were acid brown earths and were too poor for a full development of *Corylus*. *Corylus* was more common on fertile dry-land soils and damp soils than in Eldrup Forest.

Tilia- Quercus- Corylus forest

Tilia cordata became dominant at 7000 ^{14}C-years ago. The *Tilia- Quercus- Corylus* forest became increasingly influenced by Man from 4300 BC at the *Molinia* hollow and from AD 800 at the Matrikel hollow. The youngest part of the *Tilia- Quercus-Corylus* stage at the *Glyceria* hollow was disturbed by trampling by red deer.

Tilia constituted 60% of the tree crown cover in Atlantic time but became increasingly scarce in Subboreal and early Subatlantic time at the *Glyceria* and Matrikel hollows, where the forest was yet undisturbed by Man. *Quercus* expanded at 7000 ^{14}C-years ago and increased gradually from 20% to 30-50% at the cost of *Tilia*. *Corylus* was about 10%. *Viscum* and *Hedera* were frequent.

Shrubs and field plants were very scarce in Atlantic time except for *Gymnocarpium* and other ferns. The soils were acid brown earths. *Quercus* was more frequent and *Corylus* scarcer in Eldrup Forest than on more fertile dry-land soils in Denmark (Table 62). *Ulmus*, *Fraxinus*, *Alnus* and *Betula* were restricted to low-lying soils. The *Quercus* present in Eldrup Forest was probably *Q. petraea*. A few woodlands with *Tilia cordata* and *Quercus petraea* occur to-day on acid brown earths in England, Germany and Poland.

The gradual decrease of *Tilia* and increase of *Quercus* in Subboreal and early Subatlantic time was seen at the *Glyceria* hollow. At the same time, from about 3000 BC, *Tilia* was felled by Man around the *Molinia* hollow. The decrease of *Tilia* at the *Glyceria* hollow was probably due to slow impoverishment of the soils, as the vitality of *Tilia* is subdued on strongly acid soils to-day. The ferns became scarce, and the ground flora was thus very poor. Pollen spectra from forests undisturbed by Man from Subboreal time show *Tilia*-dominated forest with high *Corylus*-frequencies on fertile gley-soils and low *Corylus* on sandy soils (Table 63).

Fagus- Quercus forest

Fagus expanded around the *Molinia* hollow about AD 500 after a period with human disturbance, and became dominant there (70-80% of the crown cover), mixed with some *Quercus*. Cultural influence occurred intermittantly from about AD 800; comparatively natural *Fagus- Quercus* forest prevailed from about 1400 to 1550 and from about 1850 till to-day. *Fagus* did not expand in the central and northern part of the research area till about 1400.

Accumulation of humus and podzolization of the mineral soils accelerated at about AD 500 at the *Molinia* hollow, at about 1400 at the Matrikel hollow, and after 1850 in most of the research area except for a few patches, where brown earth still prevails.

Quercus, presumably *Q. petraea*, occupied 10-20% of the crown cover. Shrubs and field plants were scarce on sites with a humus layer, except for moist sites, where ferns with *Dryopteris*-type spores ocurred. Sites under *Fagus* with shallow litter and humus layers to-day accomodate a *Deschampsia flexuosa* community. *Ilex aquifolium* occurs occasionally to-day and has survived from former times. Sites with deep litter and humus layers have no ground vegetation. The former brown earths of the *Fagus-Quercus* forest presumably had scarce field vegetation.

Vegetation in Eldrup Forest influenced by human activity in the past

Subboreal and early Subatlantic time (4300 BC to AD 500)

Minima for *Tilia* and peaks for *Quercus* at the *Molinia* hollow signify the first possible traces of human influence. The field vegetation of ferns was not disturbed, and there are no indications of grazing by cattle.

Tilia decreased distinctively at the *Molinia* hollow at about 3000 BC and persisted at low frequencies until about AD 500, whereas *Quercus* and *Betula* increased. *Quercus* remained frequent (about 50%), and *Betula* had one major peak (about 50%). These changes indicate felling of *Tilia* trees favouring *Quercus*. *Fagus* invaded the area at about 1300 BC, but was checked by felling. There are no indications of open glades grazed by cattle in the vicinity. The purpose of the removal of *Tilia* was probably to encourage *Quercus* in order to produce mast for browsing by pigs. This activity persisted for more than three millenia; its abandonment at 500 BC coincided with indications of depopulation elsewhere in Denmark.

Medieval time (AD 800-1400)

In the vicinity of the *Molinia* hollow, there are distinctive minima for *Fagus* and maxima for *Betula* or *Quercus*, indicating tree-felling in Medieval time. At one section (-C 9), there is evidence for the existence of glades grazed by cattle.

At the Matrikel hollow, there is first evidence of felling of some *Quercus* trees. Somewhat later, *Tilia* decreased, and maxima for *Betula*, *Quercus* and open-ground plants indicate a more open forest with grazed glades. *Fagus* expanded at the cessation of this activity.

At soil sections from the central part of the research area (C 19 and E 13) there is evidence of the cultivation of small fields.

Eldrup Forest thus was exploited by Man in various ways from sometime before AD 1000 till about 1400. Several villages were founded around the Løvenholm area in the Viking and Early Middle Ages. Eldrup near the forest was one of them; this village was later deserted. The abandonment of human activity in Eldrup Forest coincides with a general economic crisis in Denmark.

Recent time (1550-1800)

Fagus decreased at about 1550 in the research area, and *Quercus*, *Betula*, *Calluna* and herbaceous plants increased indicating the existence of a more open forest and grazed glades. Eldrup Forest thus was again utilized for timber production and grazing, an exploitation also known from historical records. Upon the abandonment of the grazing in the early 19th century, the glades were invaded by *Calluna*, *Juniperus* and *Quercus petraea*, which grew up to form the present *Quercus* stands, whereas *Fagus* rejuvenated in the former clumps of *Fagus* trees. The former acid brown earths changed to podzoloids during the grazing. Accumulation of a humus layer and podzolization of the soils began at about 1850, at a time when the new tree generation had formed a closed canopy.

The decline of *Tilia*, *Corylus*, *Hedera* and *Viscum*

Tilia cordata persisted during the period of human exploitation in Subboreal and early Subatlantic time at the *Molinia* hollow, but disappeared there upon the expansion of *Fagus*. In the central and northern part of the research area (*Glyceria* and Matrikel hollows), *Tilia* decreased gradually due to impoverisment of the soils, and disappeared on the expansion of *Fagus* after the abandonment of human activity in Medieval time. The failure of *Tilia* to expand together with *Fagus* was probably due to inability to compete with *Fagus* on the impoverished soils. *Tilia*-dominated forests have survived in a few cases on fertile soils elsewhere in Denmark.

Corylus avellana suffered the same fate as *Tilia* in Eldrup Forest.

Hedera helix was common in Eldrup Forest in Atlantic time. The species decreased slightly in middle Subboreal time, probably due to soil impoverishment, and disappeared at the expansion of *Fagus*.

Viscum album was also common in Atlantic time. This species decreased slightly in late Subboreal time. It is surmised that *Viscum* was a parasite mainly on *Tilia* and that ecotypes preferring *Betula* did not occur in Denmark because of inadequate summer temperature. The decrease of *Viscum* in Eldrup Forest was therefore ascribed to the decrease of *Tilia*. The species persisted into Medieval time and then disappeared together with *Tilia*. The absence of *Viscum* in the present-day *Tilia* stands in Denmark is probably due to the fact that these stands have been cut down and rejuvenated by sprouting.

The history of *Quercus petraea* in Eldrup Forest

Quercus occurred in Eldrup Forest as a subordinate member of first *Tilia* forest, and later *Fagus* forest. Based on the ecology of *Quercus petraea*, it is surmised that this species was present in Eldrup Forest from early Atlantic time till to-day.

The former aquatic and wet-ground plant communities in Eldrup Forest

Two aquatic plant communities occurred in former ponds in the hollows in Eldrup Forest: a *Ranunculus* community and a *Callitriche- Lemna* (- *Glyceria*) community. Only *Glyceria fluitans* has survived.

Wet ground around the hollows formerly housed *Carex* and *Salix* communities, and a *Carex- Thelypteris* (- *Sphagnum*) community occurred on peat formed as the hollows were filled-in by sediments. A *Quercus petraea- Molinia caerulea- Dryopteris carthusiana* community occurs on artificially drained peat to-day.

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TABLE 64. *Glyceria* hollow, K 17, S2, E2. Number of samples with scarely represented taxa not shown in the pollen diagram. Forest stages as in Table 61. P: frequencies are shown in the pollen diagram.

Forest stage	B	CPi –BPo	TQC a	TQC b	FQ
No. of samples	9	5	5	13	2
Shrubs					
Crataegus	1	–	–	–	–
Myrica	–	–	–	–	1
Ericales					
Vaccinium-type	–	–	–	–	1
Herbaceous plants					
Open ground					
Armeria maritima	1	–	–	–	–
Dianthus	–	–	1	–	–
Plantago major	–	–	–	–	1
Plantago maritima	–	–	1	–	–
Plantago media	1	–	–	–	–
Rumex acetosa	–	–	2	–	–
Scleranthus perennis	–	–	–	–	1
Spergula arvensis	–	–	–	1	–
Trifolium cf. *T. pratense*	–	–	–	1	–
Trifolium cf. *T. repens*	–	–	–	1	–
Cultivated					
Secale cereale	–	–	–	–	1
Forest, brown earth					
Stellaria holostea	–	–	–	–	1
Acid humus					
Lycopodium clavatum	–	–	–	1	–
Uncertain					
Cerastium-type	–	–	–	1	–
Cirsium-type	3	–	–	–	–
Lotus	–	–	1	–	–
Mentha-type	–	3	–	–	–
Ophioglossum vulgatum	–	–	1	–	–
Rubus	–	1	–	2	–
Trollius europaeus	–	–	–	2	–

TABLE 65. *Molinia* hollow, –A 12, N4, E3. For explanation, see Table 64.

Forest stage	TC– PiB	TQC	QTB	FQ
No. of samples	10	17	18	21
Vines and ephiphytes				
Lonicera periclymenum	–	–	1	–
Shrubs				
Crataegus	–	–	–	2
Hippophaë rhamnoides	–	1	–	–
Ilex aquifolium	1	2	1	1
Myrica gale	–	–	1	6
Sambucus	–	–	–	4
Taxus baccata	1	–	–	–
Viburnum opulus	7	4	4	–
Herbaceous plants				
Open ground				
Campanula	3	1	1	2
Plantago maritima	–	–	–	1
Plantago media	–	–	1	–
Polygonum aviculare	–	–	2	3
Polygonum persicaria-type	–	–	1	–
Rumex acetosa	–	3	3	2
Forest, brown earth				
Mercurialis perennis	–	–	1	–
Acid humus				
Lycopodium alpinum-type	–	1	–	–
Lycopodium annotinum	5	1	2	1
Lycopodium clavatum	1	–	–	–
Oxalis acetosella	–	1	1	–
Uncertain				
Allium	3	2	2	–
Botrychium	4	–	–	–
Arctium cf. A. *tomentosum*	–	1	–	–
Caryophyllaceae undiff.	5	1	3	–
Cerastium type	–	1	1	–
Cirsium	–	–	–	1
Gentiana	–	–	–	1
Geum	2	–	6	4
Lamiaceae undiff.	–	–	2	1
Lathyrus-type	10	7	2	2
Liliaceae undiff.	1	1	–	1
Lotus	–	1	4	–
Mentha-type	–	1	–	–

Parnassia palustris	–	1	–	–
Rhinanthus-type	–	–	–	3
Rubus	2	–	–	–
Scrophulariaceae undiff.	–	–	–	2
Succissa pratensis	2	1	1	–
Thalictrum	1	1	4	2
Wet ground				
Alisma	1	–	–	–
Caltha palustris	–	–	1	2
Lysimachia	–	3	–	–
Typha latifolia	1	–	–	–
Aquatics				
Nymphaea	–	–	1	–

TABLE 66. Matrikel hollow (Mah). For explanation, see Table 64.

Forest stage	QTC	QTB	QB	FQ	FQB
No. of samples	2	5	4	9	5
Shrubs					
Ilex aquifolium	–	–	–	2	–
Myrica gale	–	–	1	1	2
Sambucus	–	–	–	–	1
Viburnum opulus	–	–	1	–	–
Herbaceous Plants					
Open ground					
Botrychium	–	–	1	–	–
Centaurea undiff.	–	1	–	–	1
Campanula	–	–	–	1	–
Hypericum	–	–	–	2	–
Plantago major	–	–	–	1	3
Polygonum aviculare	–	–	–	–	1
Uncertain					
Achillea-type	–	–	2	5	1
Allium	–	1	–	–	–
Caryophyllaceae undiff.	1	–	–	2	–
Lathyrus-type	–	–	–	1	1
Rubus	–	–	–	2	1
Succissa pratensis	–	–	–	2	–
Thalictrum	–	–	1	1	–
Wet ground					
Lysimachia	–	–	–	1	–
Menyanthes trifoliata	–	–	1	–	–
Typha latifolia	1	–	–	–	–
Sparganium-type	–	–	–	1	2

TABLE 67. Soil section –C 9. For explanation, see Table 64.

Forest stage	TQC	QTB	FQ(B)
No. of samples	20	5	22
Trees			
Acer	1	–	2
Fagus sylvatica	9	4	P
Shrubs			
Crataegus	–	–	1
Frangula alnus	1	1	3
Prunus	–	–	1
Sambucus	–	–	3
Herbaceous plants			
Hypericum	–	–	1
Plantago maritima	–	–	1
Rumex acetosa	–	–	1
Sagina cf. *S.procumbens*	–	–	1
Scleranthus perennis	–	–	1
Sedum	1	–	–
Forest, brown earth			
Anemone	–	3	3
Stellaria holostea	–	–	1
Acid humus			
Lycopodium annotium	–	–	2
Lycopodium clavatum	1	–	1
Oxalis acetosella	1	1	–
Uncertain			
Achillea-type	–	1	4
Apiaceae undiff.	–	–	4
Cerastium-type	–	–	1
Galium-type	–	1	3
Geum	–	1	2
Humulus-type	–	–	4
Rubus	–	–	1
Senecio-type	1	2	1
Thalictrum	–	2	1
Urtica dioica	–	–	2
Wet ground			
Alisma	–	–	1
Caltha palustris	–	–	1
Hydrocotyle vulgaris	–	–	1
Typha latifolia	–	–	1
Sparganium-type	1	–	2
Aquatics			
Littorella uniflora	–	–	1

TABLE 68. Soil section –A 13, N4, E2. For explanations, see Table 64.

Forest stage	TQC	FQ
No. of samples	14	18
Acer	7	–
Carpinus betulus	2	1
Fagus sylvatica	6	P
Shrubs		
Myrica gale	–	1
Salix	2	6
Sambucus	–	2
Sorbus aucuparia	3	1
Ericales		
Vaccinium-type	–	2
Herbaceous plants		
Open ground		
Ambrosia	–	1
Hypericum	–	1
Jasione montana	–	2
Plantago maritima	–	1
Polygonum aviculare	–	2
Polygonum persicaria-type	–	2
Spergula arvensis	–	1
Cultivated		
Avena	–	6
Triticum	–	1
Acid humus		
Lycopodium annotinum	1	1
Lycopodium clavatum	–	1
Melampyrum	2	4
Uncertain		
Achillea-type	4	5
Apiaceae undiff.	–	1
Asteraceae,, Liguliflorae	1	7
Filipendula	1	1
Galium-type	2	1
Geum	1	1
Humulus-type	–	4
Potentilla	–	1
Senecio-type	1	3
Succissa pratensis	–	1
Wet ground		
Caltha palustris	–	1

TABLE 69. Soil sections H 16, C 19 and E 13. For explanation, see Table 64.

Section	H 16	C 19	E 13
Forest stage	FQ	FQ	FQ
No. of samples	25	21	19
Trees			
Acer	2	1	–
Carpinus betulus	4	2	1
Fraxinus excelsior	6	–	3
Tilia	14	–	2
Ulmus	8	6	5
Vines and epipytes			
Hedera helix	1	–	–
Shrubs			
Frangula alnus	1	–	–
Hippophaë rhamnoides	–	–	1
Myrica gale	2	1	3
Prunus	–	–	1
Salix	10	4	3
Sambucus	–	4	4
Sorbus aucuparia	2	1	2
Viburnum opulus	1	–	–
Ericales			
Empetrum nigrum	–	1	–
Vaccinium-type	P	1	5
Herbaceous plants			
Open ground			
Botrychium	–	–	1
Centaurea undiff.	–	1	–
Hypericum	–	1	–
Jasione montana	P	3	P
Plantago major	2	3	3
Plantago maritima	1	2	–
Polygonum aviculare	2	1	P
Polygonum persicaria-type	–	1	–
Rumex acetosa	2	–	–
Scleranthus annuus	1	–	–
Scleranthus perennis	3	–	–
Trifolium cf. *T. medium*	–	–	1
Trifolium cf. *T. pratense*	2	1	P
Cultivated			
Triticum	1	1	–
Forest, brown earth			
Anemone	3	–	1
Mercurialis perennis	–	1	–
Acid humus			
Lycopodium clavatum	P	P	5
Melampyrum	P	4	P
Oxalis acetosella	–	–	2
Uncertain			
Achillea-type	P	6	P
Apiaceae undiff.	4	2	3
Caryophyllaceae undiff.	2	–	–
Cerastium-type	–	1	1
Cirsium	1	1	–
Epilobium undiff.	–	1	–
Filipendula	6	3	2
Galium-type	5	–	2
Humulus-type	6	1	–
Knautia arvensis	–	–	1
Lathyrus-type	–	1	–
Lotus	1	–	–
Ranunculus acer-type	12	7	3
Rubus	1	–	–
Senecio-type	4	4	–
Succissa pratensis	–	–	2
Thalictrum	1	–	–
Urtica dioica	1	2	2
Valeriana	1	–	–
Veronica	–	–	1
Wet ground			
Caltha palustris	1	1	–
Lysimachia	–	–	1
Menyanthes trifoliatta	1	–	–
Sparganium-type	2	–	–

TABLE 70. Soil section Matrikel bank (Ma). For explanation, see Table 64.

Forest stage	QTC	FQ
No. of samples	7	10
Trees		
Acer	1	–
Carpinus betulus	1	5
Fagus sylvatica	6	P
Picea abies	–	2
Populus tremula	–	1
Shrubs		
Frangula alnus	–	4
Myrica gale	–	3
Sambucus	–	1
Viburnum opulus	–	1
Herbaceous plants		
Open ground		
Botrychium	–	1
Campanula	–	2
Centaurea undiff.	–	1
Chenopodiaceae	–	3
Jasione montana	–	1
Polygonum aviculare	–	2
Rumex acetosa	–	1
Trifolium cf. *T. repens*	3	1
Cultivated		
Secale cereale	–	2
Acid humus		
Lycopodium clavatum	–	1
Polypodium vulgare	–	1
Uncertain		
Achillea-type	–	6
Apiaceae	4	3
Asteraceae, Liguliflorae	2	4
Filipendula	–	1
Galium-type	2	7
Humulus-type	–	2
Mentha-type	1	–
Rubus	3	–
Senecio-type	–	1
Succissa pratensis	–	1
Trollius europaeus	1	–
Urtica dioica	–	1
Wet ground		
Caltha palustris	–	1
Sparganium-type	1	1

PLATES

PLATE I. Section C 19. Podzol on sandy till. Dried samples from 3–110 cm below the surface. A_1: 0–5 cm; A_1: 5–7 cm; A_2: 7–14 cm; B_1: 14–19 cm; B_2: 19–46 cm; C: 46–110 cm (cp. Table 2 and Fig. 12). Depth of the samples (arranged in vertical columns, cemtimeters below the surface):

3–4
4–5
5–6
6–7
7–8
8–9
9–10
10–1i
11–12
12–13
13–14
14–15
15–16
16–17
17–18
18–19
19–20
20–21
21–22
22–23
23–24
24–25
25–26
26–27
27–28
28–29
29–30
30–32
32–34
34–36
36–38
38–40
40–42
42–44
44–46
46–48
48–50
50–52
52–54
54–56
56–58
58–60
60–62
62–64
64–66
66–68
68–70
70–90
100–110

PLATE II. Section W 14. Brown earth on sandy till. Dried samples from 0–40 cm below the surface. A: 0–10 cm; B: 10–35 cm: C: 35–40 cm (cp. Table 3 and Fig. 12). Depth of samples (arranged in vertical columns, cm below the surface):

0–2
2–3
3–4
4–5
5–6
6–7
7–8
8–9
9–10
10–11
11–12
12–13
13–14
14–15
15–16
16–17
17–18
18–19
19–20
20–21
21–22
22–23
23–24
24–25
25–26
26–27
27–28
28–29
29–30
30–31
31–32
32–33
33–34
34–34
35–35
36–37
37–38
38–39
39–40
–

PLATE I


C 19 3 - 4
C 19 13 - 14
C 19 23 - 24
C 19 36 - 38
C 19 56 - 58
C 19 4 - 5
C 19 14 - 15
C 19 24 - 25
C 19 38 - 40
C 19 58 - 60
C 19 5 - 6
C 19 15 - 16
C 19 25 - 26
C 19 40 - 42
C 19 60 - 62
C 19 6 - 7
C 19 16 - 17
C 19 26 - 27
C 19 42 - 44
C 19 62 - 64
C 19 7 - 8
C 19 17 - 18
C 19 27 - 28
C 19 44 - 46
C 19 64 - 66
C 19 8 - 9
C 19 18 - 19
C 19 28 - 29
C 19 46 - 48
C 19 66 - 68
C 19 9 - 10
C 19 19 - 20
C 19 29 - 30
C 19 48 - 50
C 19 68 - 70
C 19 10 - 11
C 19 20 - 21
C 19 30 - 32
C 19 50 - 52
C 19 70 -90
C 19 11 - 12
C 19 21 - 22
C 19 32 - 34
C 19 52 - 54
C 19 100 -110
C 19 12 - 13
C 19 22 - 23
C 19 34 - 36
C 19 54 - 56

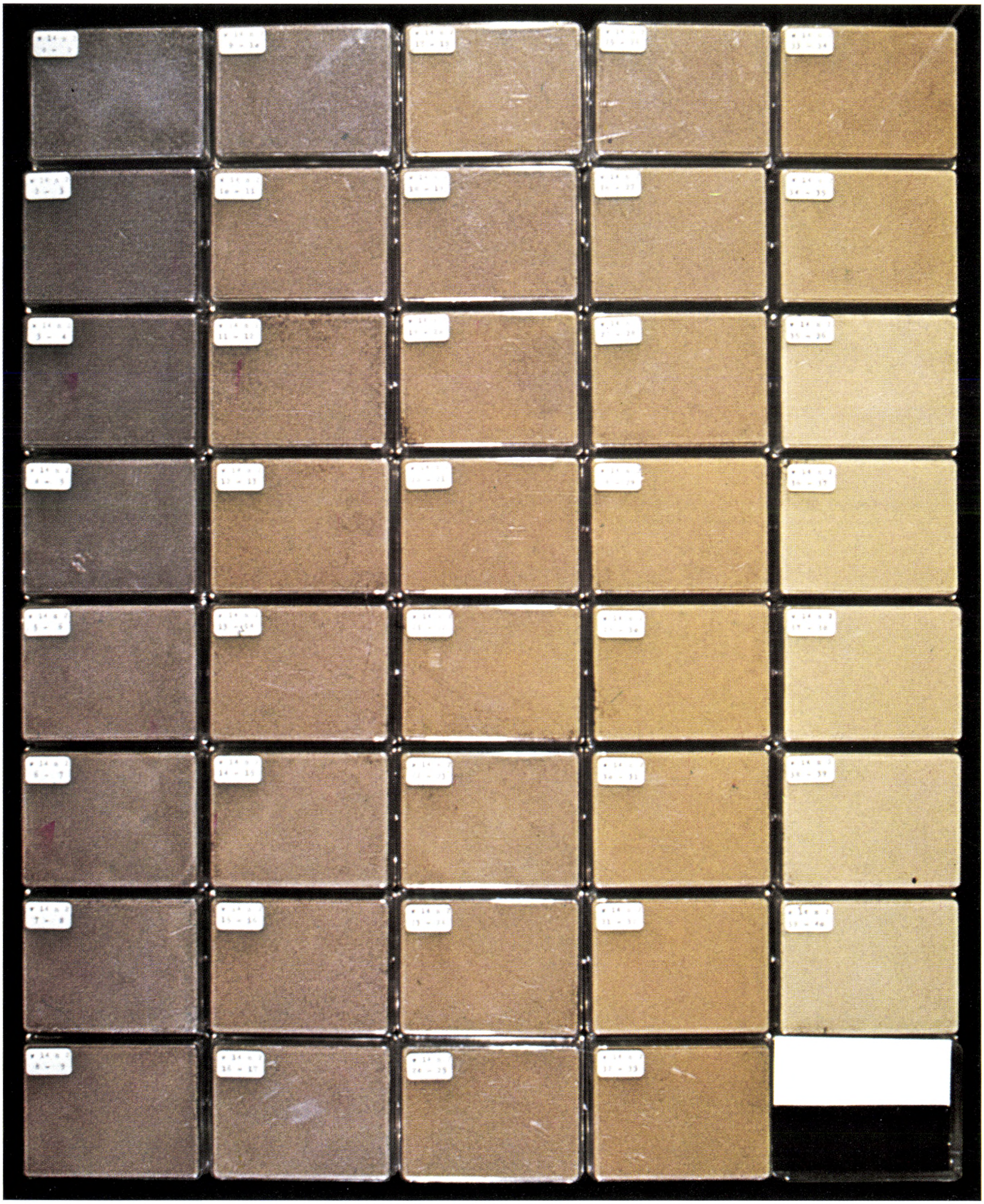


PLATE III. Above: *Fagus sylvatica* on the north slope in the southeastern part of the enclosure; the field vegetation is scarce. Below: *Fagus sylvatica* on the east slope in the central part of the enclosure (*Molinia* hollow to the right); field vegetation of *Deschampsia flexuosa*. July 1982.

PLATE IV. Above: Groups with grazed glades and dense forest of *Fagus sylvatica* at Hummelborg (east of Eldrup Forest, see Fig. 7). Below: *Fagus sylvatica;* trees derived as sprouts from the stumps of felled trees. July 1982.

PLATE V. Above: Stand of *Quercus petraea* with dense saplings of *Fagus sylvatica*. Below: Small saplings of *Quercus petraea* (with *Vaccinium myrtillus*) and scattered saplings of *Fagus sylvatica;* in shade beneath *Quercus petraea*. July 1982.

PLATE VI. Above: Tall saplings (about 1 m) of *Quercus petraea* in an area without crown cover. Below: Peat area in the southeastern part of the enclosure covered by *Vaccinium myrtillus*. Three *Quercus petraea* with shallow root systems were felled by a storm November 1981. Scattered saplings of *Fagus sylvatica* were killed due to a high ground water level 1981 and 1982. July 1982.

PLATE VII. The clearing. Above: Shortly after the felling of four *Quercus peatraea*. August 1969. Below: Tall saplings of *Sorbus aucuparia*, scattered saplings of *Fagus sylvatica*, and dense *Pteridium aquilinum*. July 1982.

PLATE VIII. Above: The *Molinia* hollow, seen from the south. *Molinia caerulea* dominated the field vegetation. August 1969. Below: The *Glyceria* hollow, seen from southeast; the water had not dried out yet. Juli 1982.

PLATE IX. The earth bank, which originally delimited the Eldrup Farm and the Løvenholm properties (Matrikel bank), erected in the early 19th century. The bank is traversed by a recent road. July 1982.

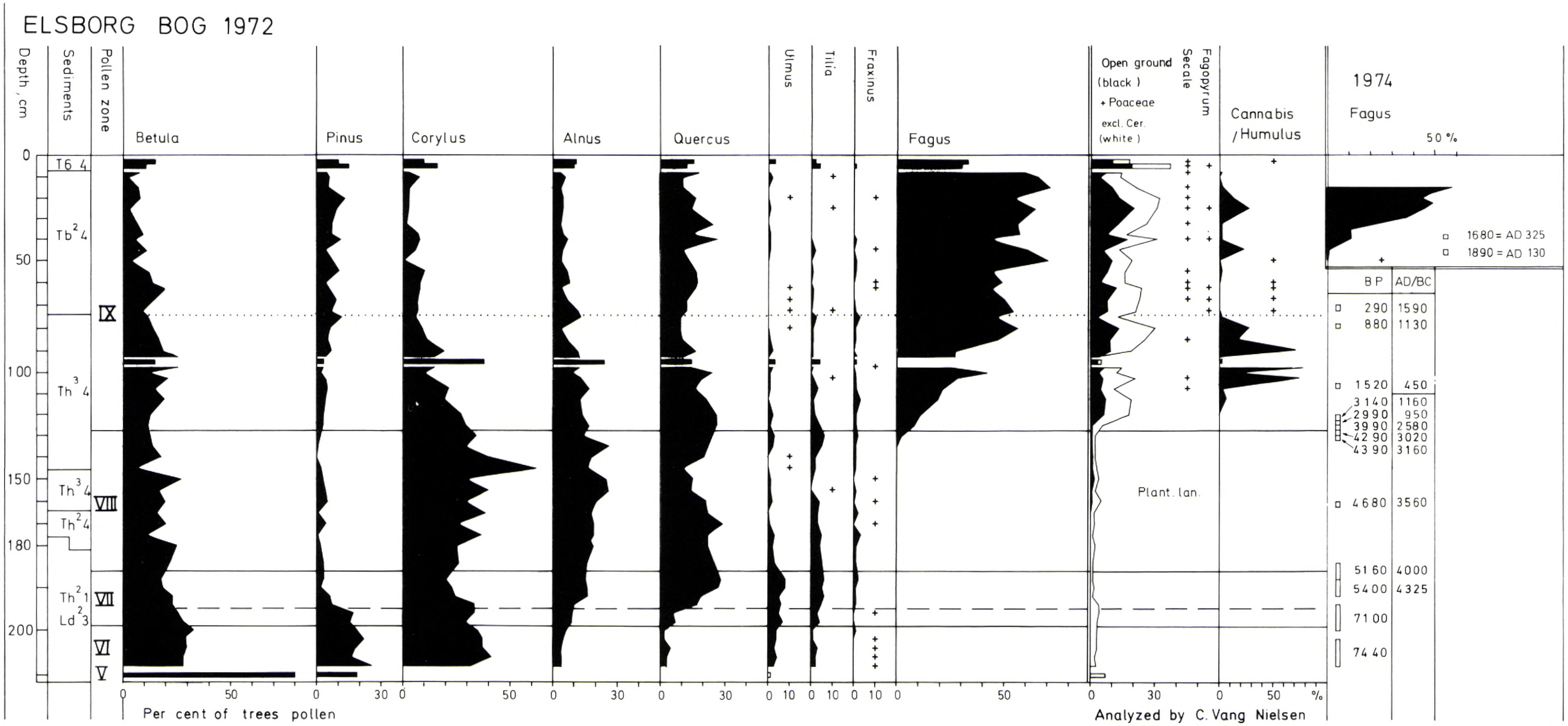


PLATE X. Pollen diagram from Elsborg Bog, section 1972. Percentages of tree pollen (AP), and dates in radiocarbon years before present (BP) and in calendar years (AD/BC, calibrated according to Clark, 1975). Inserted: *Fagus* curve and dates from section 1974. Symbols for sediments according to Troels-Smith (1955).

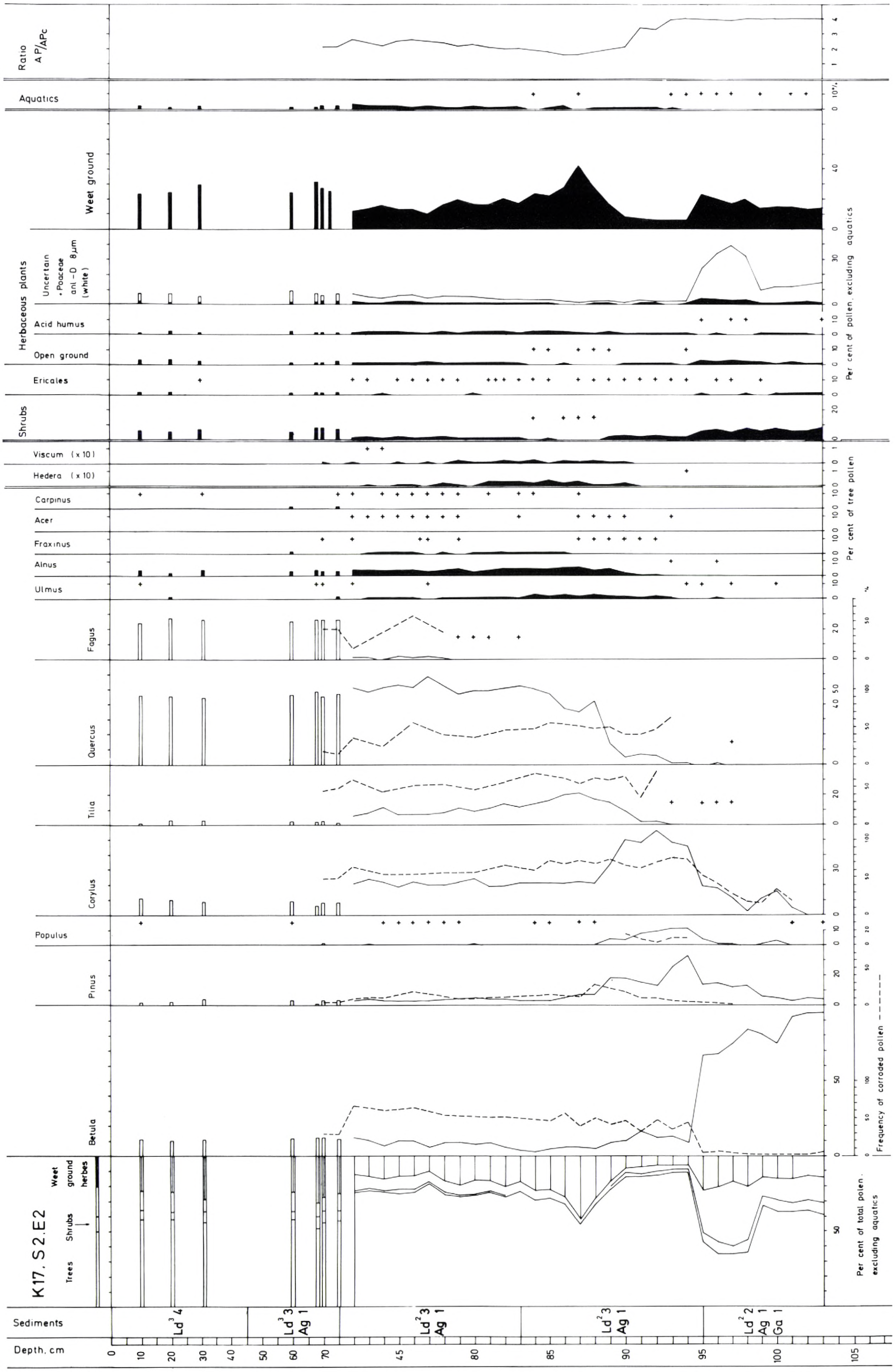


PLATE XI. Pollen diagram from the *Glyceria hollow*. Frequencies in percentage of total pollen and spores, tree pollen (trees), and total pollen and spores (non-tree categories); and frequencies of corroded pollen (trees). Pollen spectra from the disturbed deposit are indicated by bars. Symbols for sediments according to Troels-Smith (1955).

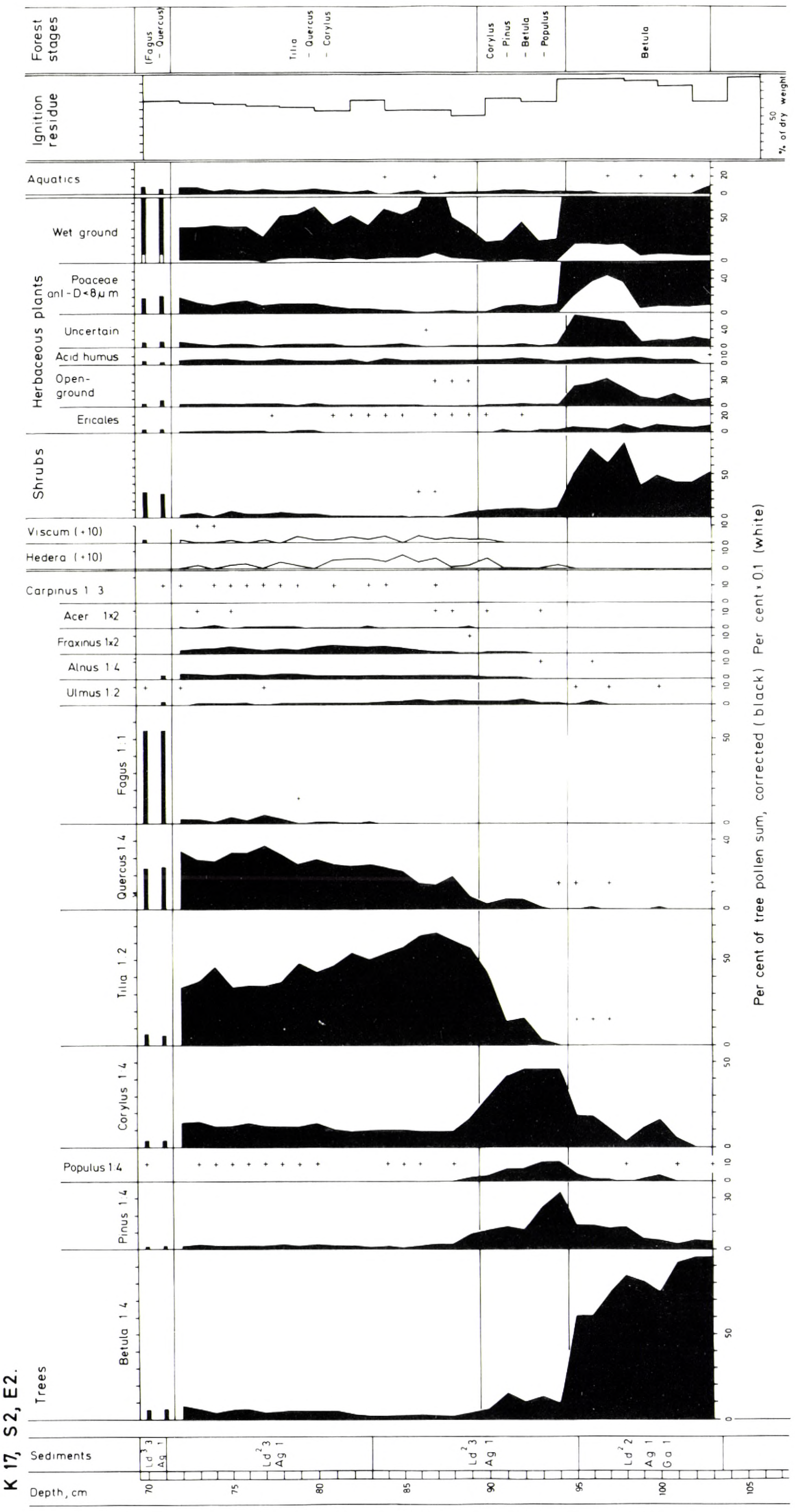


PLATE XII. *Glyceria* hollow. Corrected tree pollen frequencies and categories of non-tree pollen and spores, in percentage of corrected tree pollen (APc, two samples from the disturbed deposit are indicated by bars); and ignition residue. Symbols for sediments according to Troels-Smith (1955).

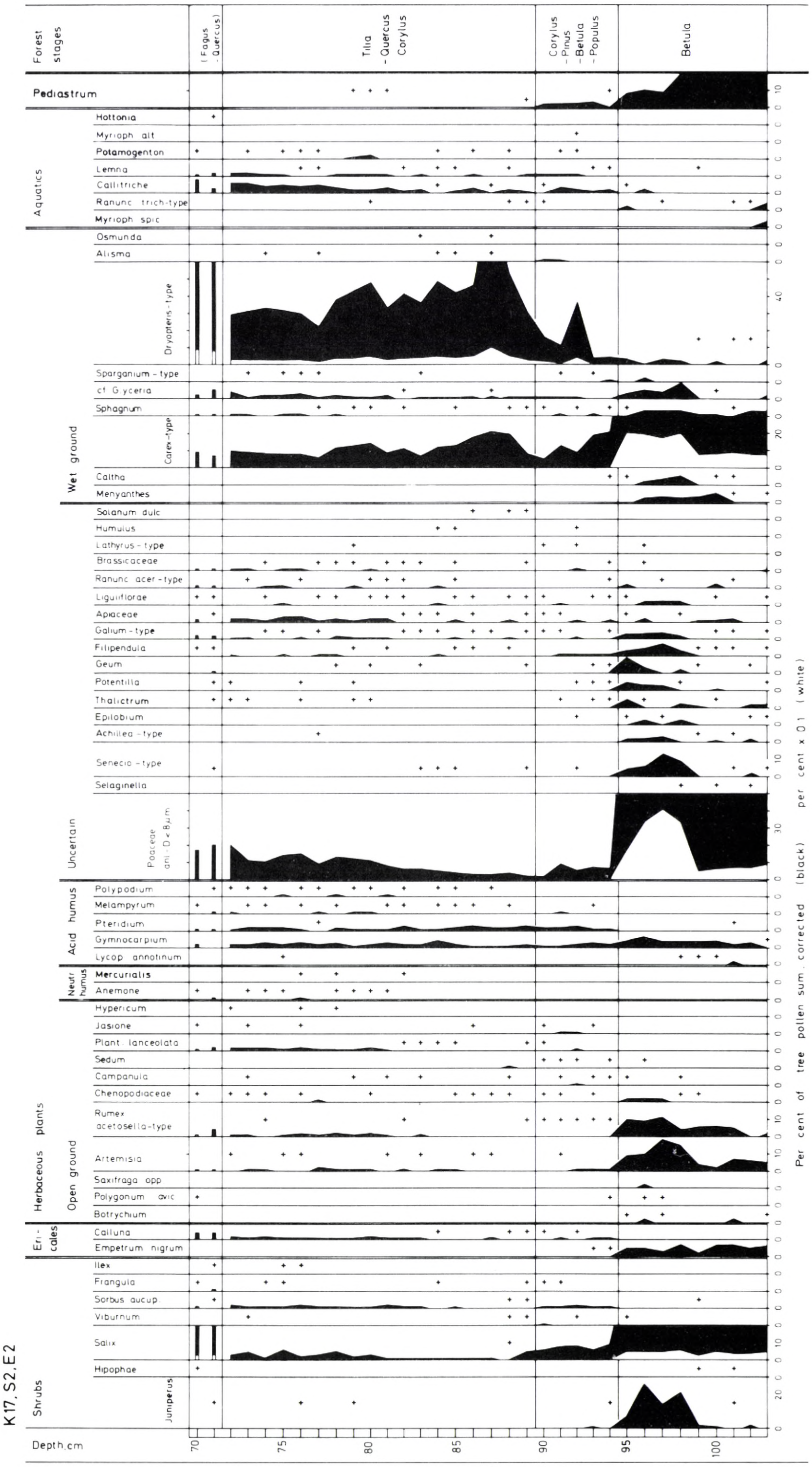


PLATE XIII. *Glyceria* hollow. Frequencies of non-tree pollen and spores, in percentage of corrected tree pollen (APc).

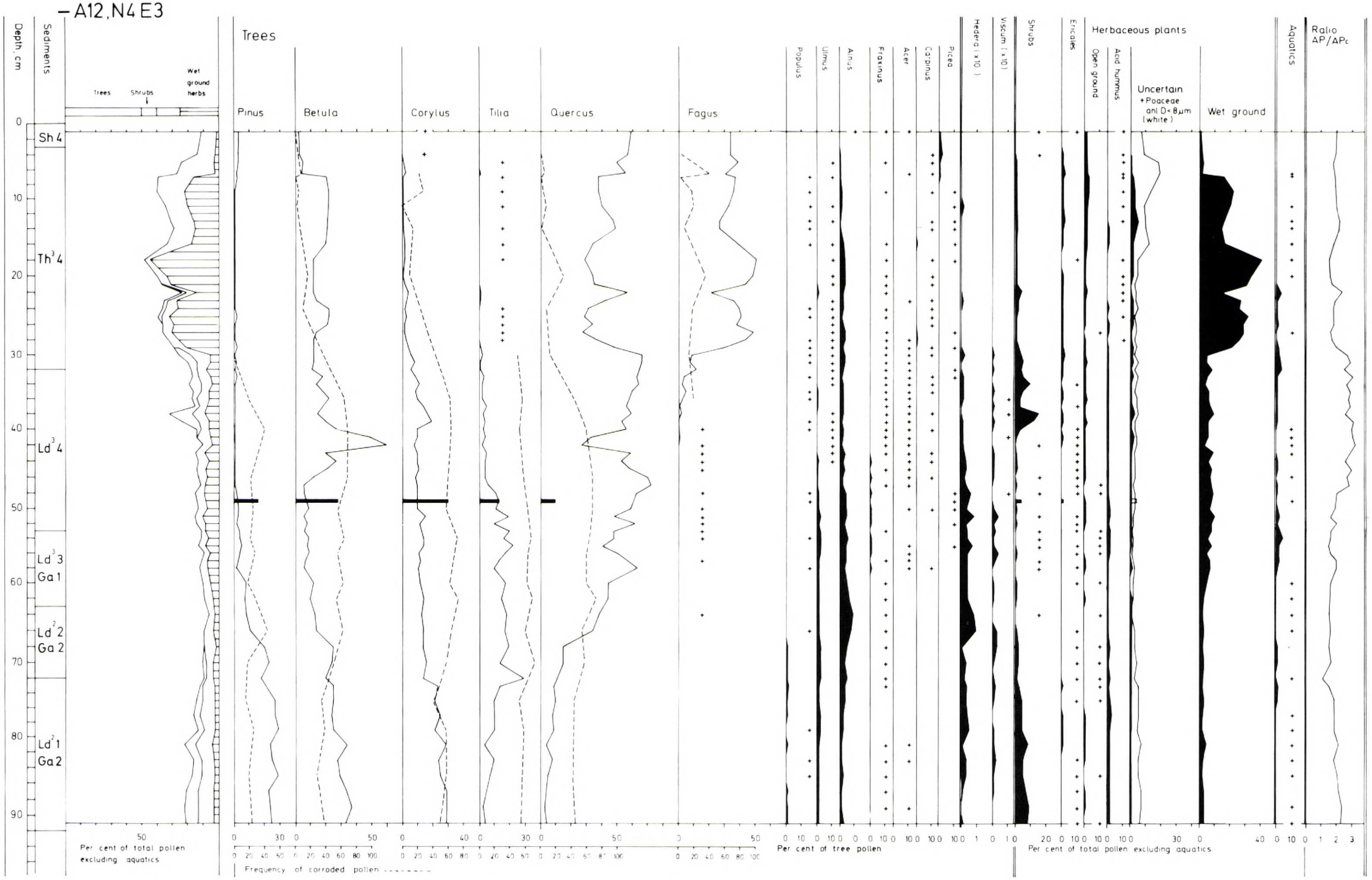


PLATE XIV. *Molinia* hollow. Frequencies in percentage of total pollen and spores, tree pollen (trees), and total pollen and spores (non-tree categories); and frequencies of corroded pollen (trees). Symbols for sediments according to Troels-Smith (1955).

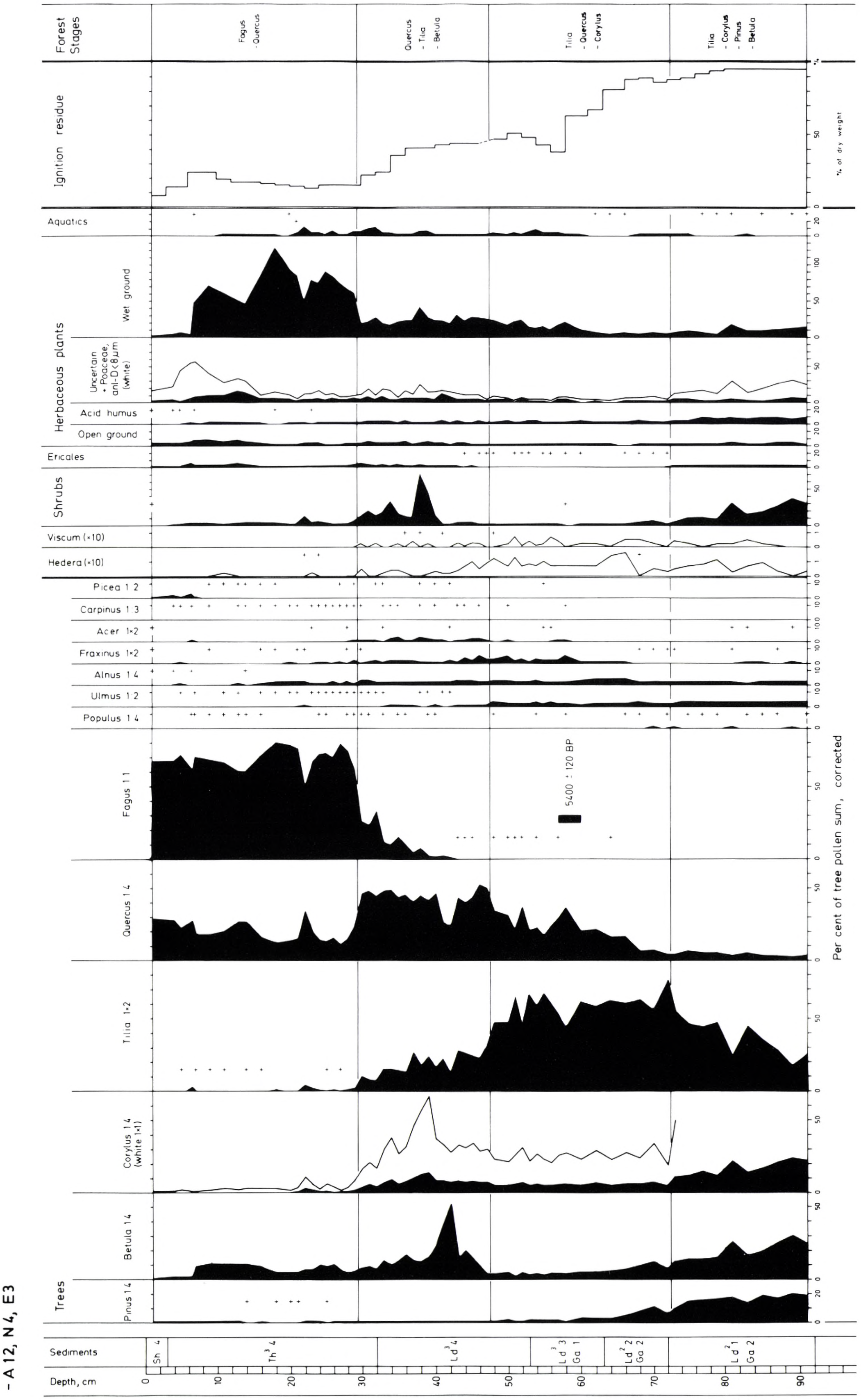


PLATE XV. *Molinia* hollow. Corrected tree pollen frequencies and categories of non-tree pollen and spores, in percentage of corrected tree pollen (APc, the white silhouette indicates *Corylus* uncorrected and calculated outside the tree pollen sum); and ignition residue. Symbols for sediments according to Troels-Smith (1955).

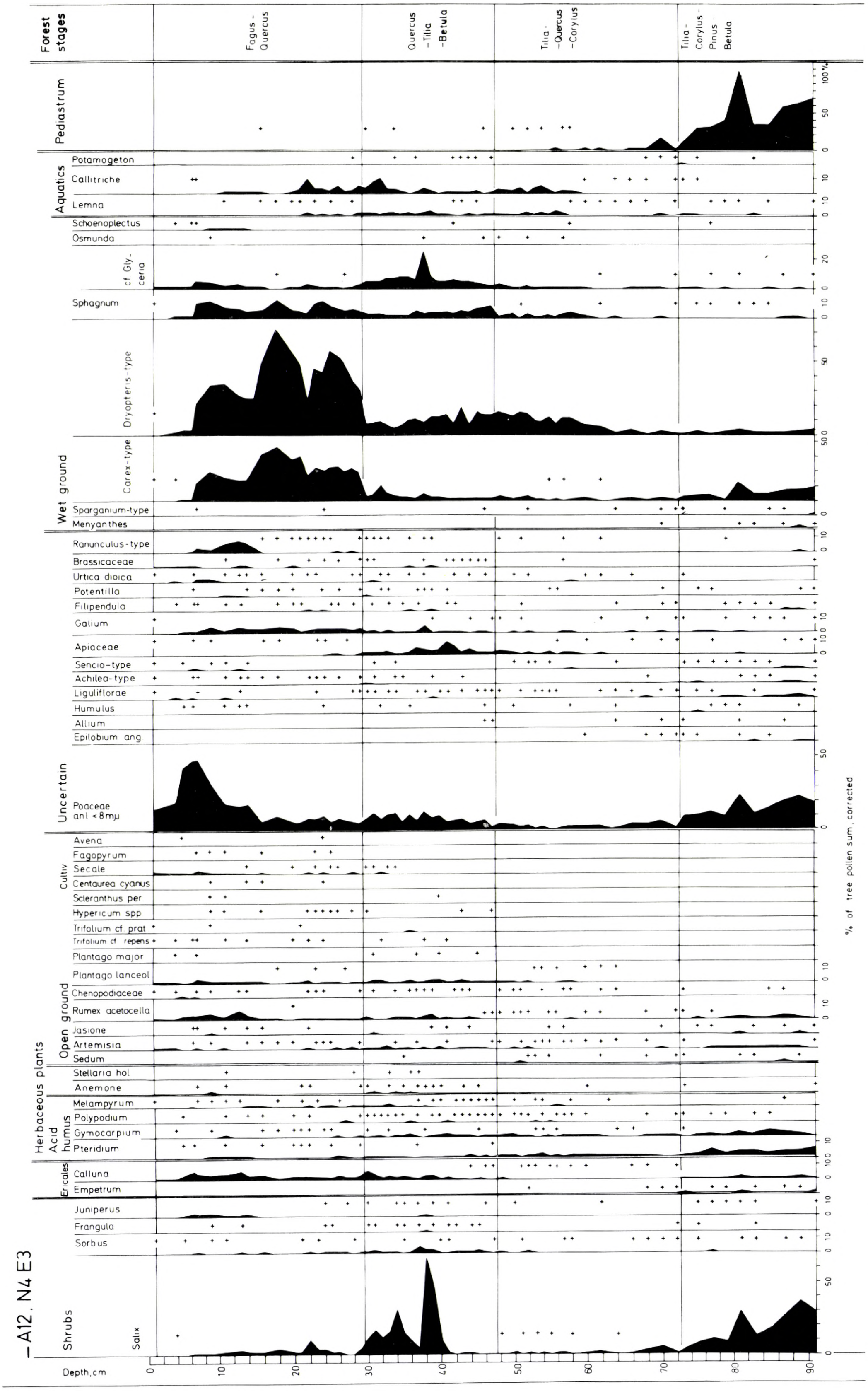


PLATE XVI. *Molinia* hollow. Frequencies of non-tree pollen and spores, in percentage of corrected tree pollen (APc).

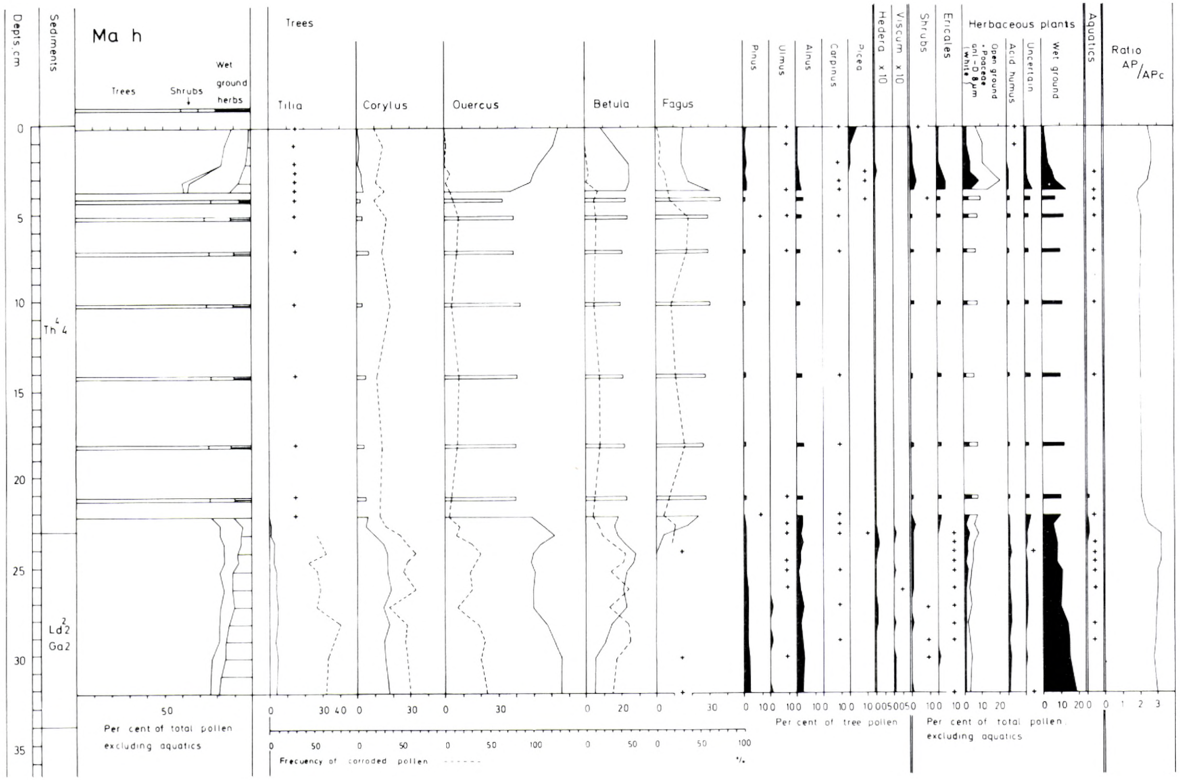


PLATE XVII. Matrikel hollow. Frequencies in percentage of total pollen and spores, tree pollen (trees), and total pollen and spores (non-tree categories); and frequencies of corroded pollen (trees). Pollen spectra from the disturbed deposit are indicated by bars. Symbols for sediments according to Troels-Smith (1955).

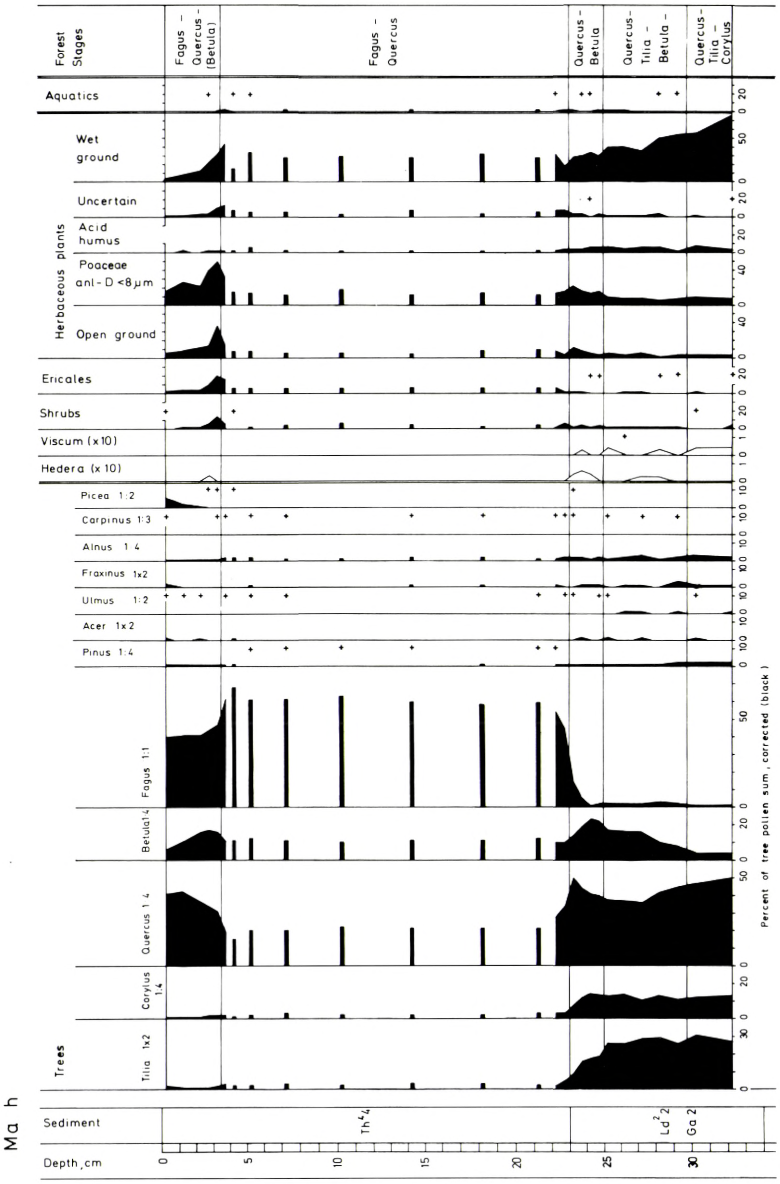


PLATE XVIII. Matrikel hollow. Corrected tree pollen frequencies and categories of non-tree pollen and spores, in percentage of corrected tree pollen (APc); and ignition residue. Symbols for sediments according to Troels-Smith (1955).

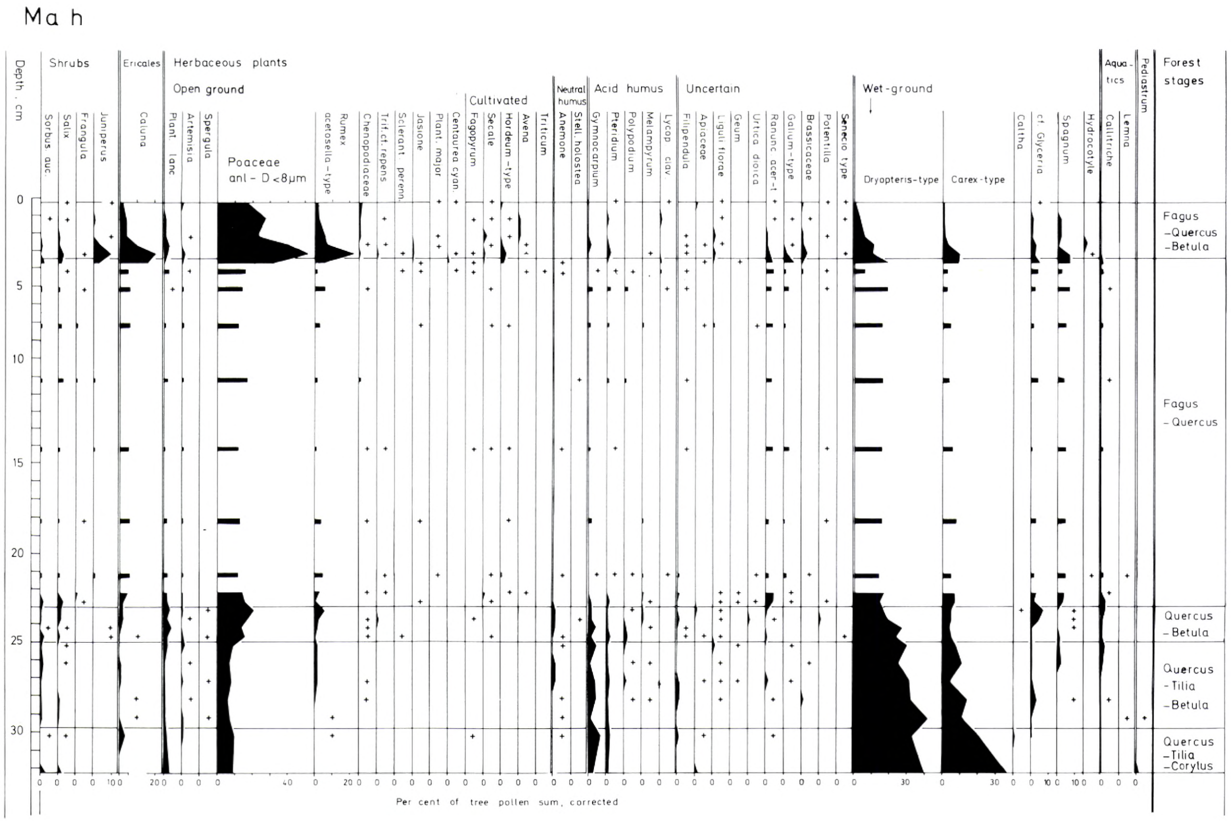


PLATE XIX. Matrikel hollow. Frequencies of non-tree pollen and spores, in percentage of corrected tree pollen (APc).

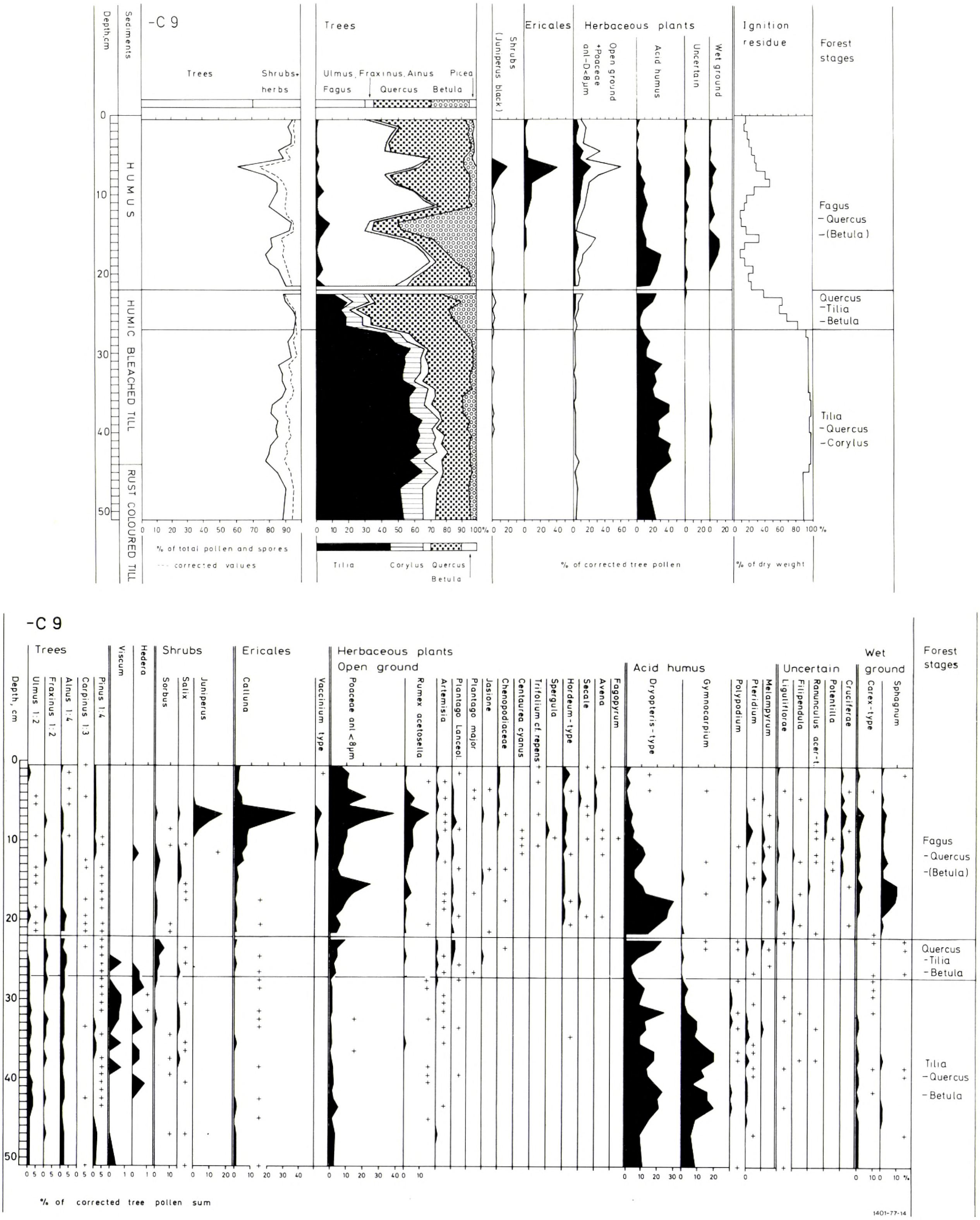
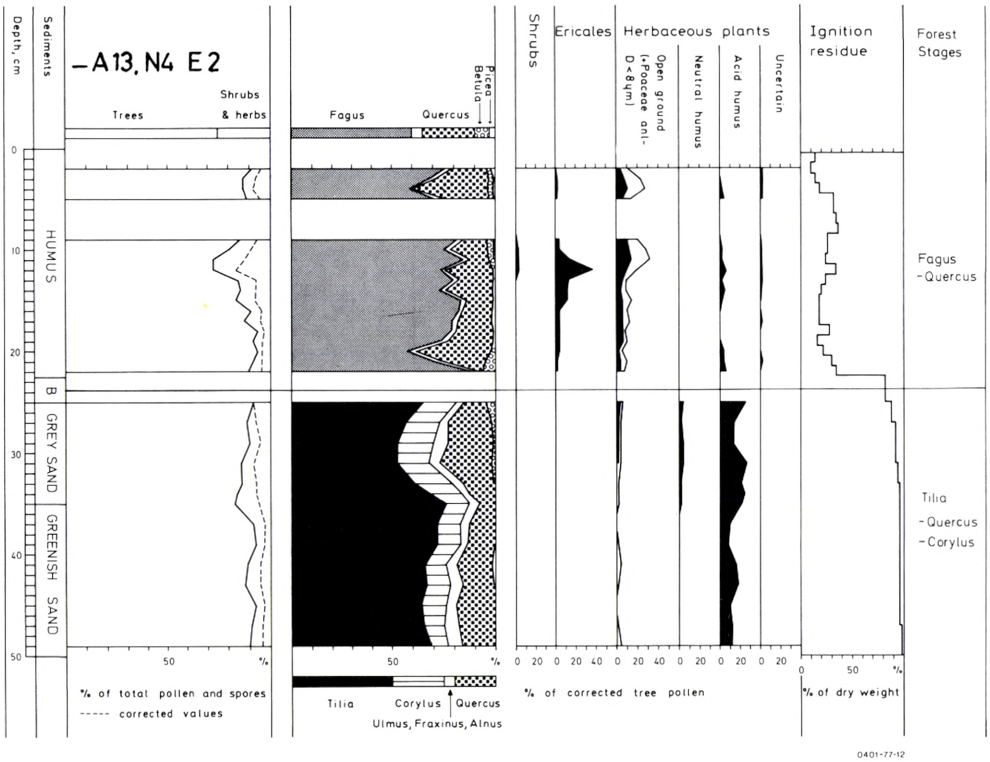


PLATE XX. Soil section -C9. Above: Frequencies in percentage of total pollen and spores (uncorrected and corrected values, cp. p. 99); corrected tree pollen frequencies and categories of non-tree pollen and spores, in percentage of corrected tree pollen (APc); and ignition residue. Below: Corrected tree pollen frequencies and non-tree pollen and spores, in percentage of corrected tree pollen (APc).



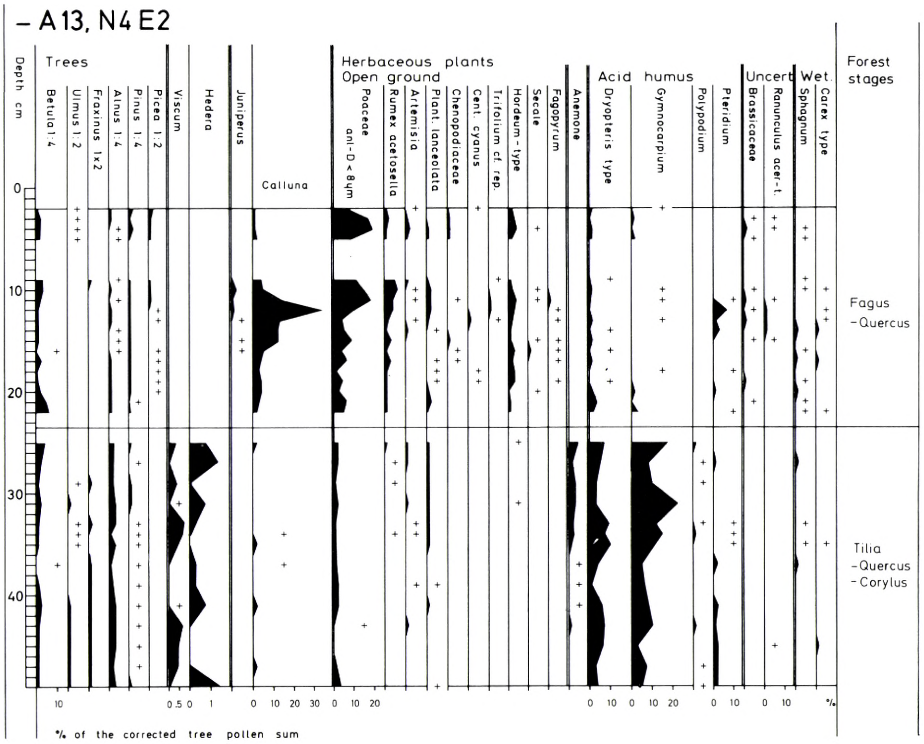


PLATE XXI. Soil section -A 13, N4, E2. As Plate XX.

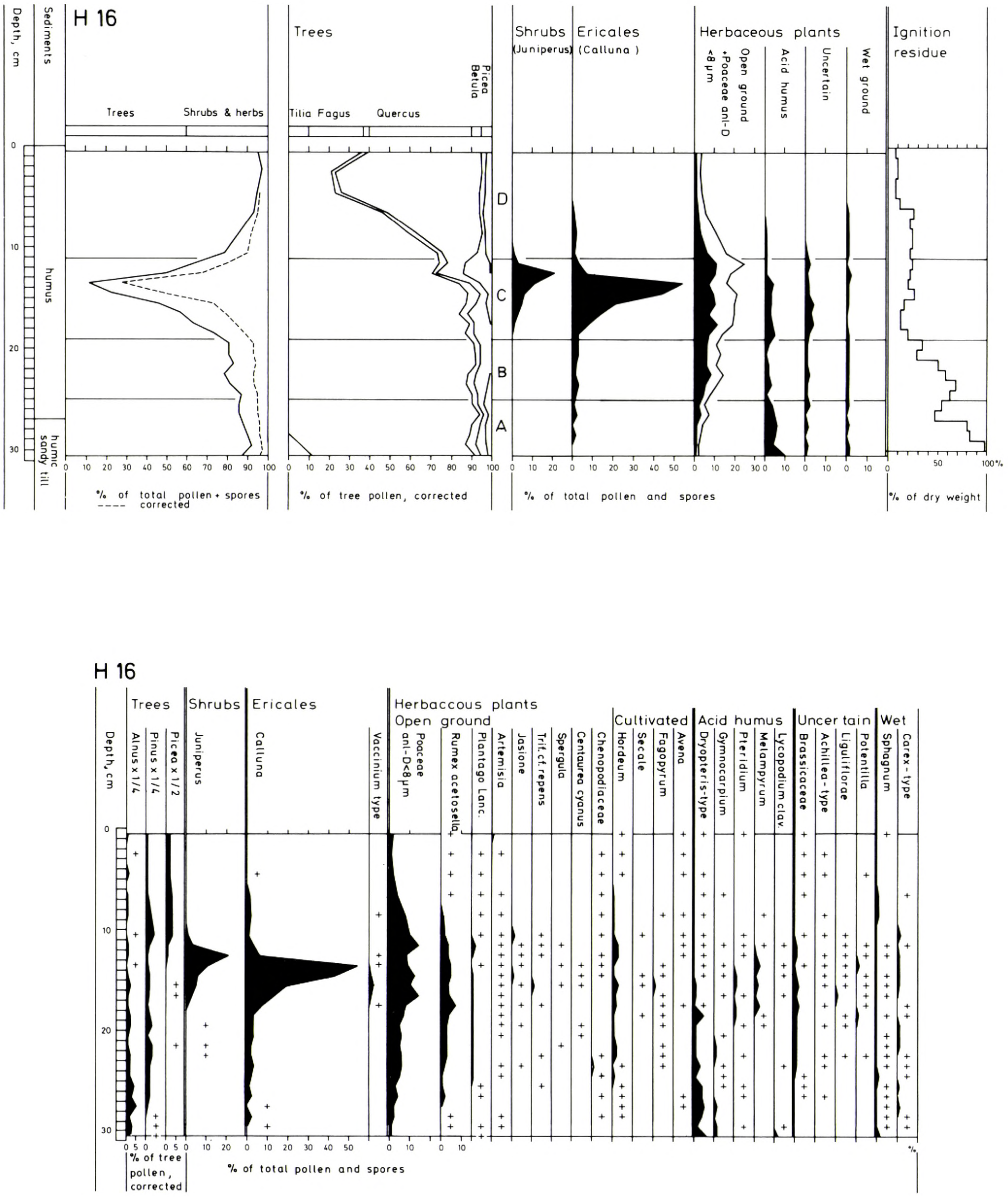


PLATE XXII. Soil section H 16. Above: Frequencies in percentage of total pollen and spores (uncorrected and corrected values, cp. p. 99); corrected tree pollen frequencies in percentage of corrected tree pollen (APc); categories of non-tree pollen and spores, in peercentage of total pollen and spores; and ignition residue. Below: Corrected tree pollen frequencies, in percentage of corrected trees (APc); and non-tree pollen and spores, in percentage of total pollen and spores. *Fagus-Quercus* stage.

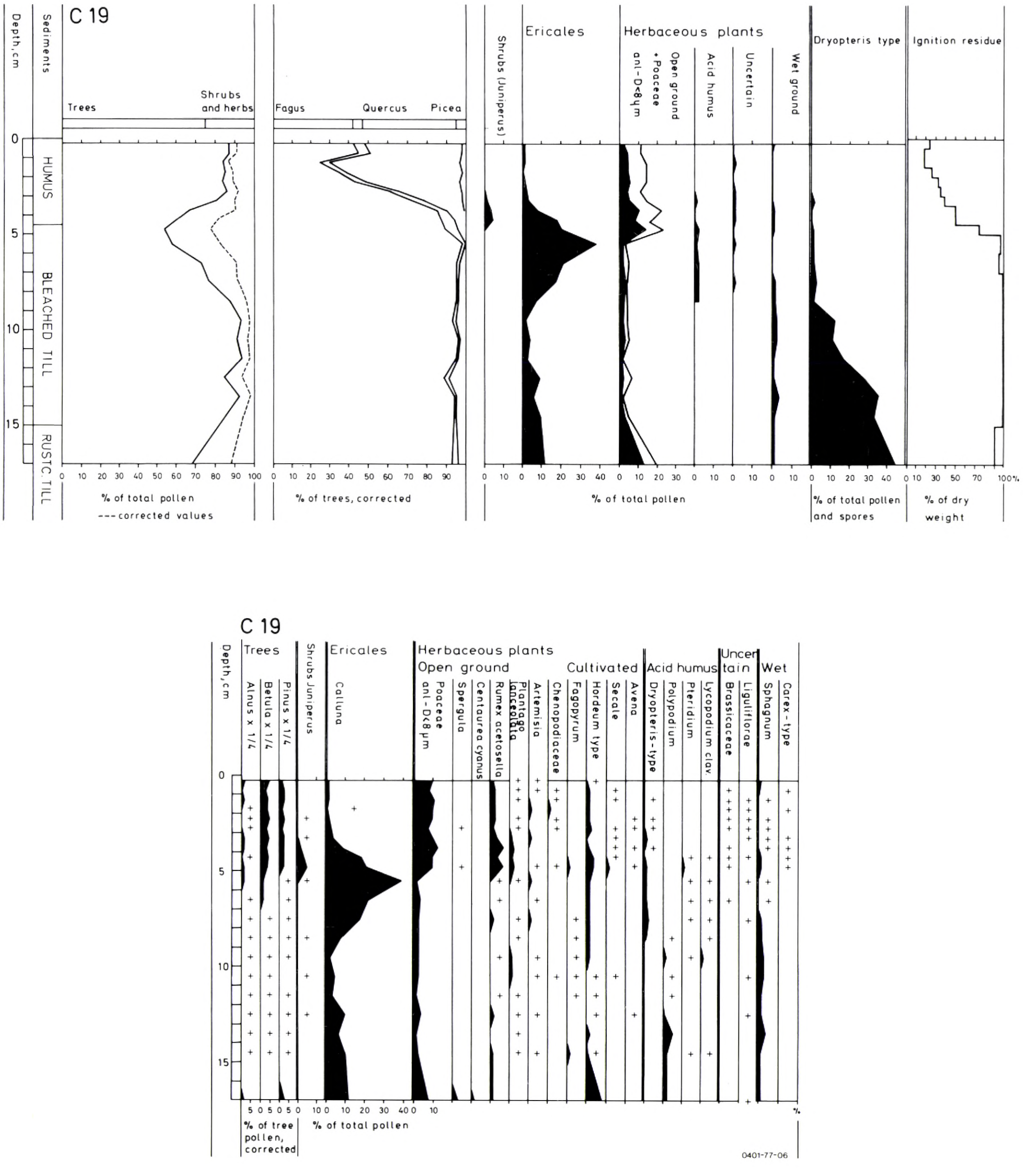
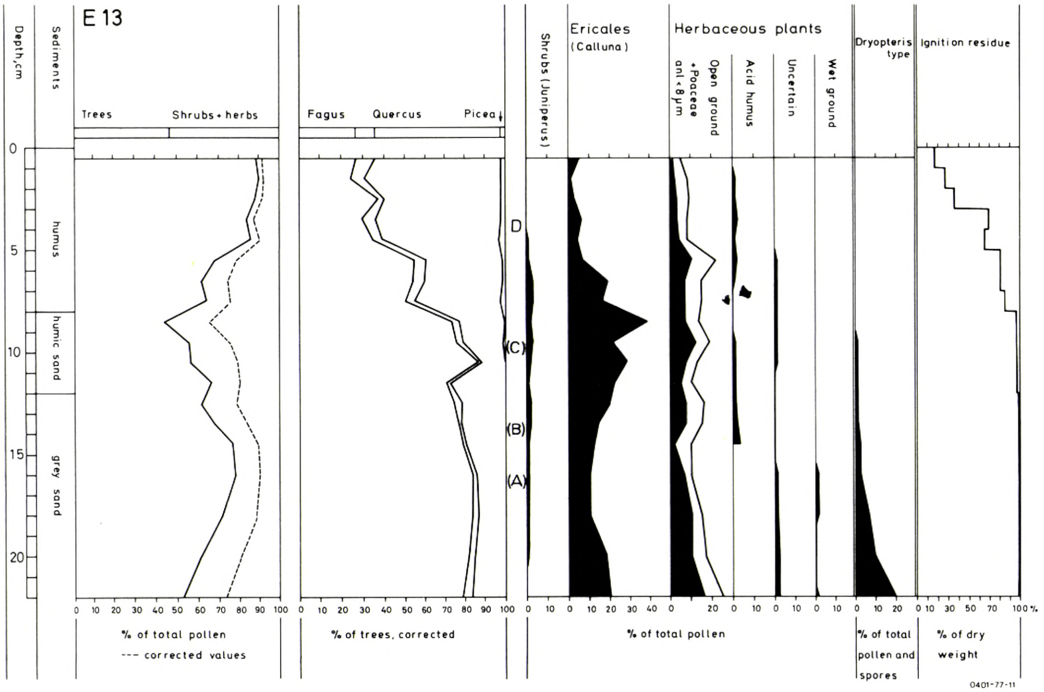


PLATE XXIII. Soil section C 19. As Plate XXII, but excluding spores from the total. *Fagus-Quercus* stage.



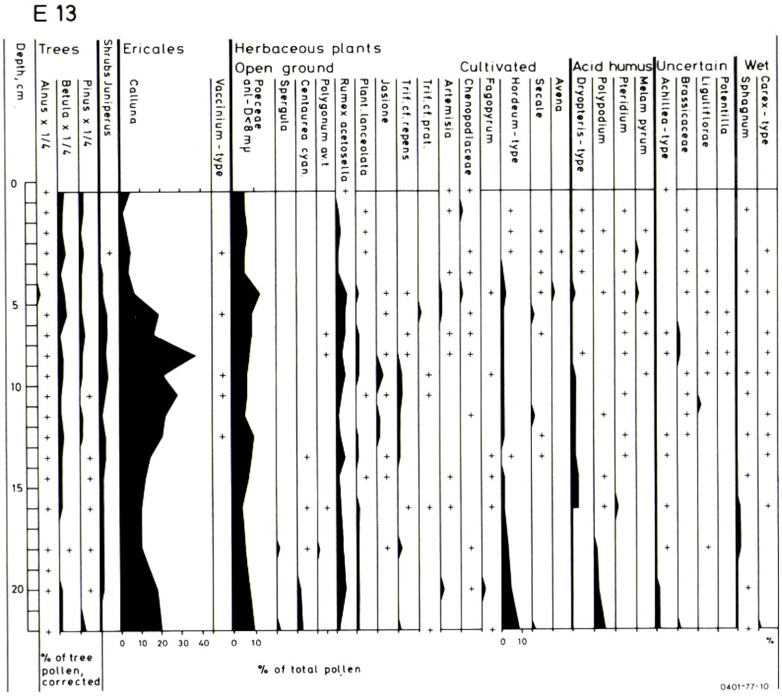


PLATE XXIV. Soil section E 13. As Plate XXIII. *Fagus-Quercus* stage.

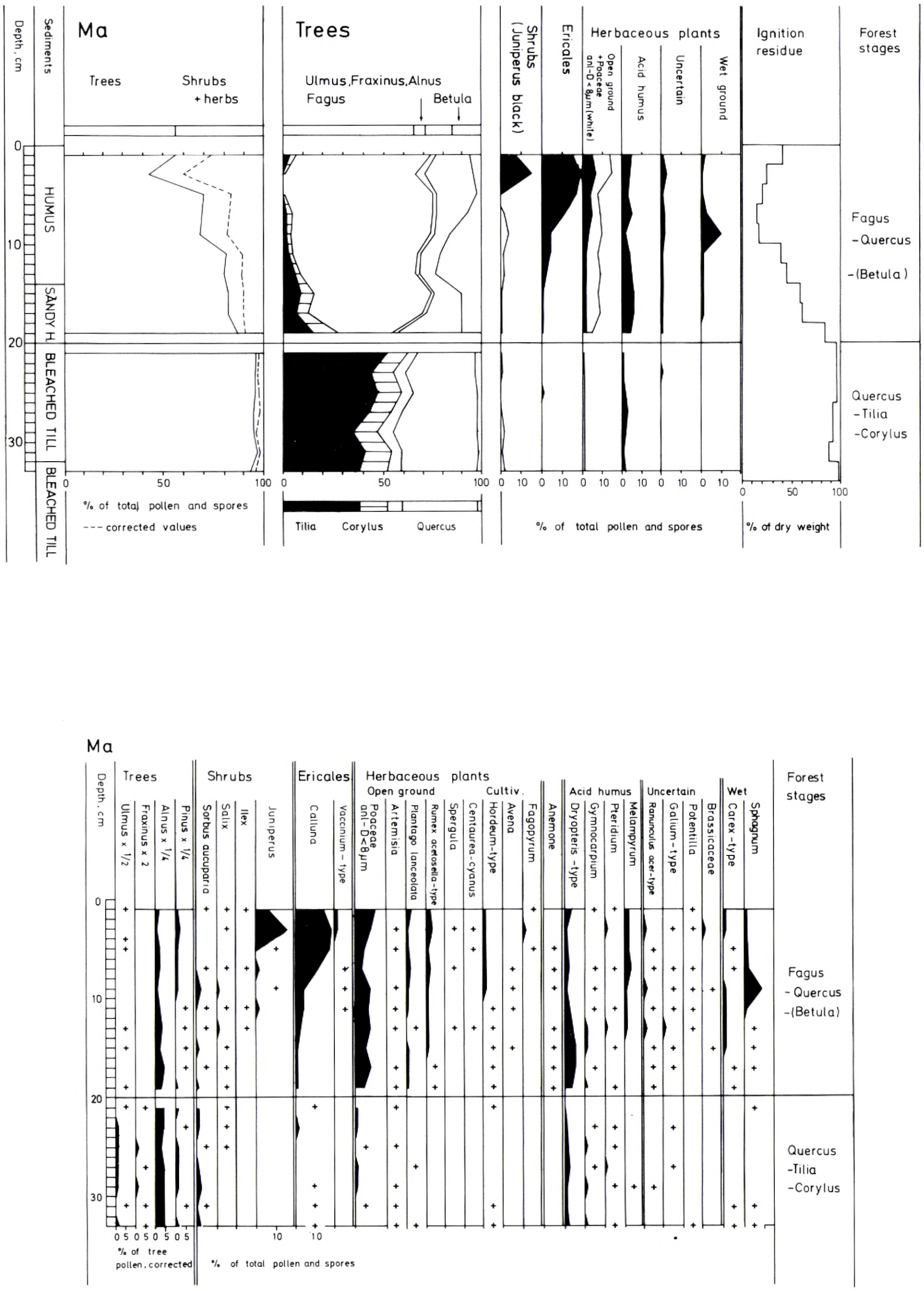


PLATE XXV. Soil section at the Matrikel bank (Ma). As Plate XXIII.

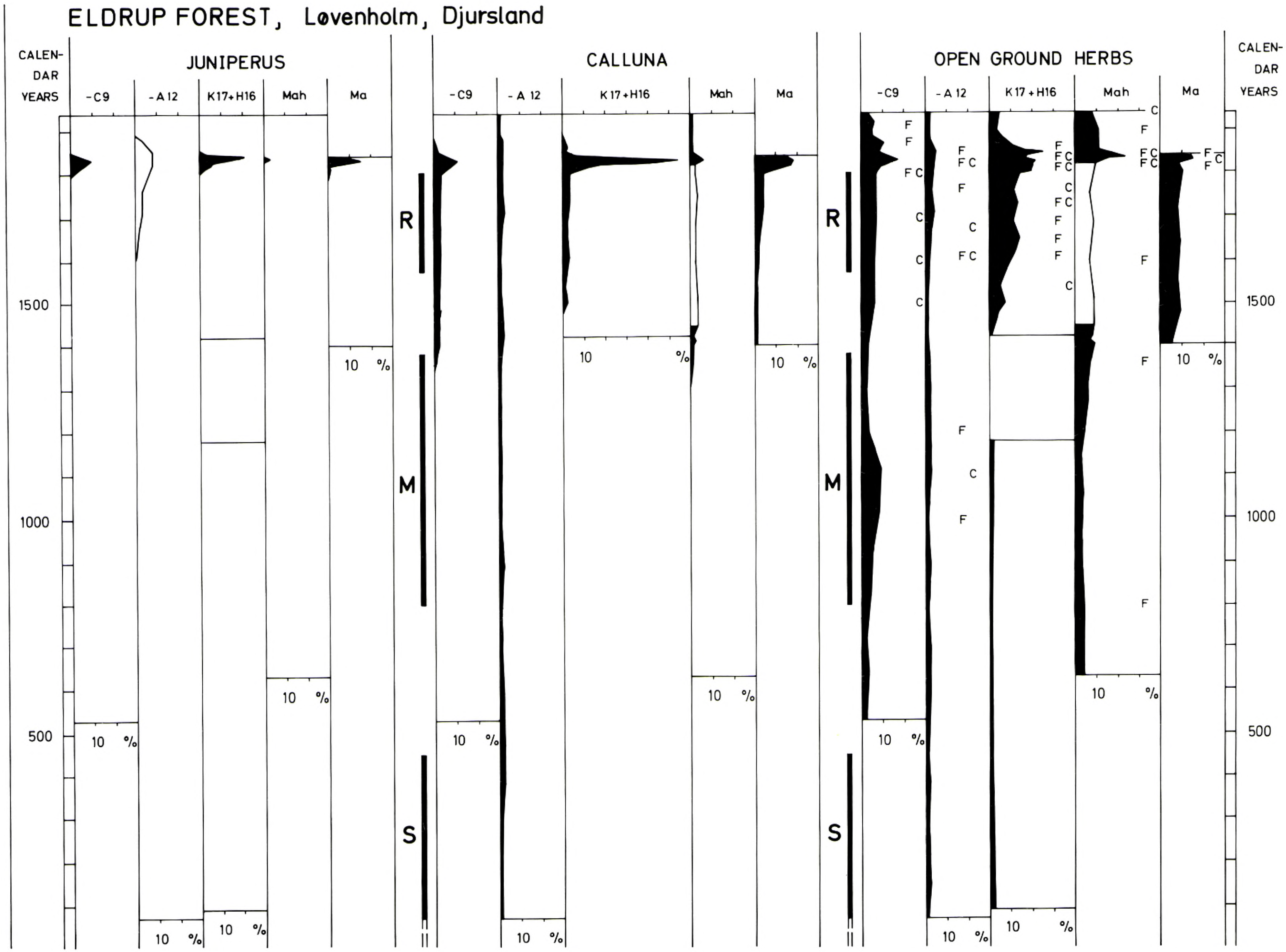


PLATE XXVIII. Synchronized curves for non-tree plants for the sites shown in Plate XXVII. Percentages of tree pollen (AP, -C 9, -A 12, K 17, Mah) or total pollen and spores (H 16, Ma). Poaceae were included in open-ground herbs, except for -A 12 and K 17. *Juniperus* in -A 12 is x10 (white). F, *Fagopyrum;* C, *Centaurea cyanus*.

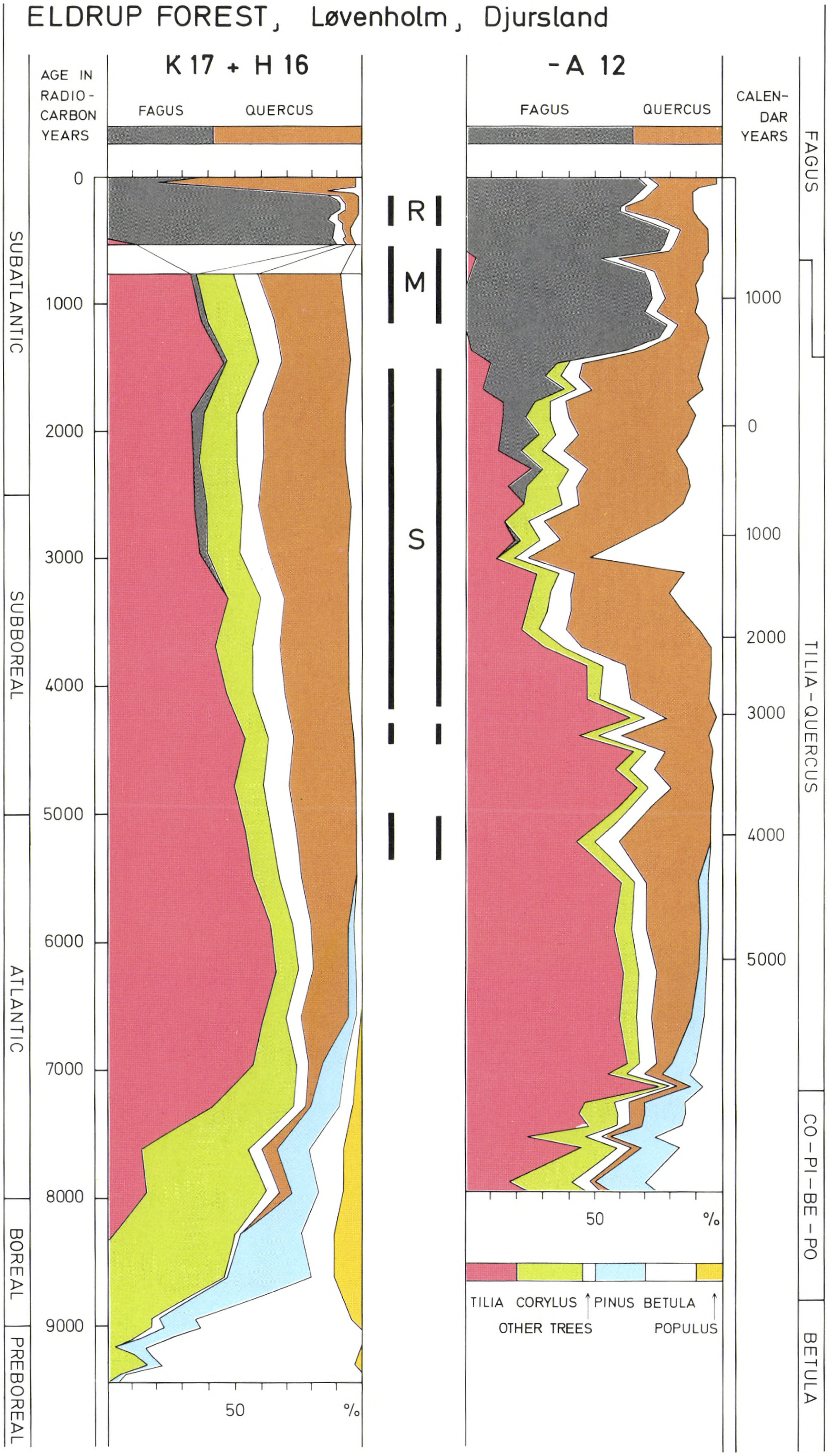


PLATE XXVI. Synchronized tree pollen diagrams from the Glyceria hollow and soil section H 16 (left-hand column), and the *Molinia* hollow (right hand column). Chronozones are in accordance with Mangerud *et al.* (1974); dates in calendar years are calibrated according to Clark (1975). Cultural stages: S, Subboreal and early Subatlantic; M, Medieval; R, Recent.

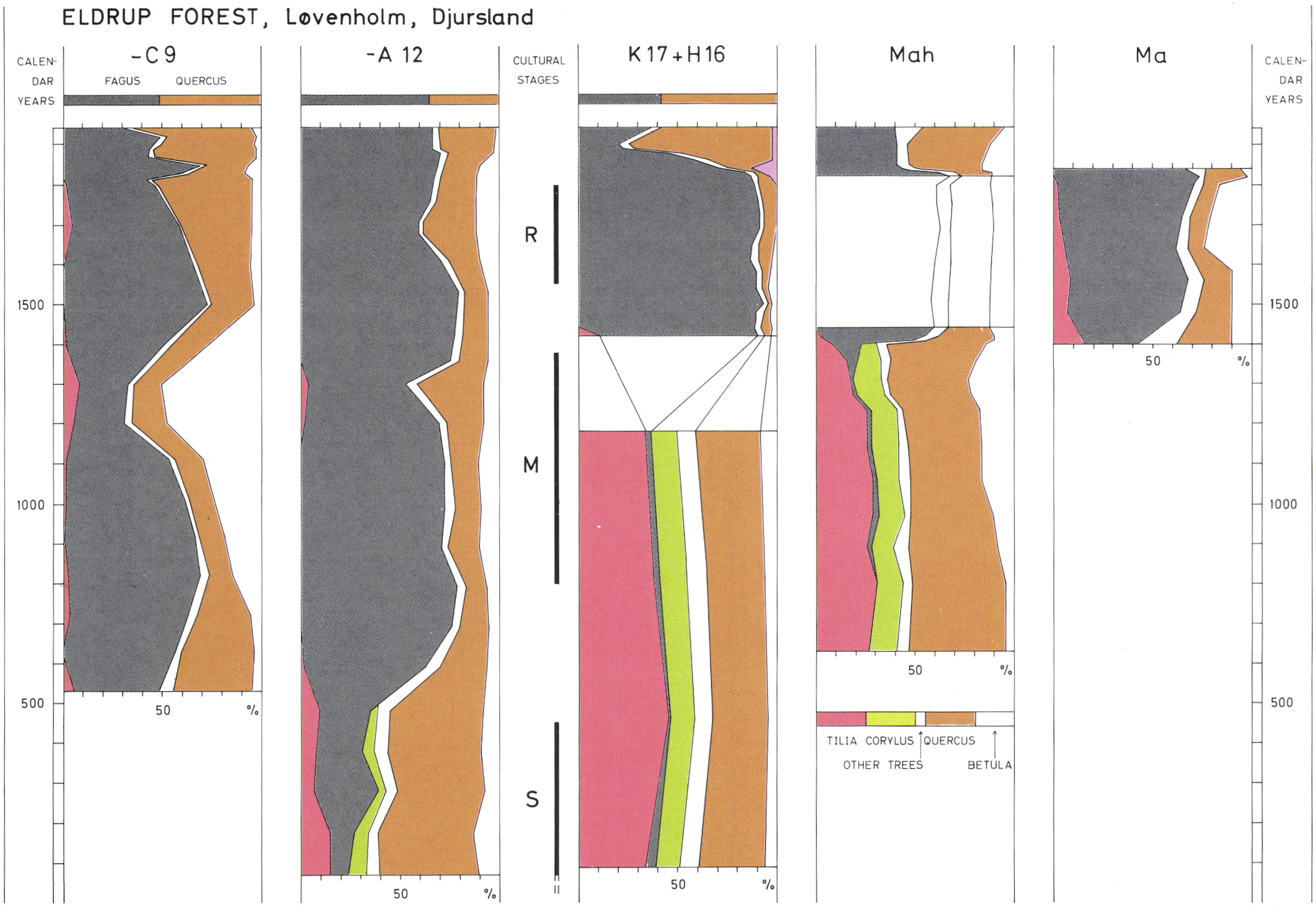


PLATE XXVII. Synchronized tree pollen diagrams from soil section -C9, the *Molinia* hollow (Mah), and the soil section at the Matrikel bank (Ma). Only the humus layers are shown for the soil sections. Otherwise as Plate XXVI.

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