INTERGLACIAL VEGETATION AND SOIL DEVELOPMENT

By

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Abstract.

Ecological relationships of the vegetational successions of 3 interglacial stages in Denmark, the Harreskovian, the Holsteinian and the Eemian, are discussed. The distribution of the light-plants, the mull-plants and the acid-humus plants suggest common features, but important differences appear with respect to the Holsteinian interglacial stage. Open forest dominated in the early protocratic phases. Mull-vegetation dominated in the mesocratic phase of the Harreskovian and the Eemian interglacial stages, and open forest and heath vegetation expanded in the oligocratic phase. In the Holsteinian interglacial stage the protocratic phase passed directly into an oligocratic phase. Paludification increased in the latest, telocratic phases. The vegetational successions of the interglacials were strongly conditioned by the influence of the vegetation on its substratum.

The pollen diagrams from interglacial deposits now enable us to recognize 3 interglacial stages in Denmark. The two younger ones, the Eemian and the Holsteinian, may be fixed stratigraphically, but the position of the older one, the Harreskovian, is somewhat uncertain. This interglacial stage is probably of the same age as the Cromerian, the occurrences of which in northern Europe are too widely scattered for a certain correlation (cp. GRÜGER, 1968). The pollen diagrams of the interglacials just mentioned are distinguished by many characteristic features (ANDERSEN, 1965).

In Denmark the interglacial stages represent stable intervals between the glacial stages of disturbance and chaos. The vegetation invaded the virgin soils and stable plant communities had a chance to develop until the new glacial released its destructive forces. Thus the interglacial plant successions reflect the relationship of vegetational development and environment on a longtime scale.

Ecological interpretations of the vegetational developments of the Eemian and the Harreskovian interglacial stages in Denmark were mentioned formerly (ANDERSEN, 1964 and later). The Hosteinian is now also known from a lake deposit representative of the entire interglacial, and a comparison with the ecological conditions of the other interglacial stages may be of interest. The lakes concerned were sufficiently large for pollen from the ajacent land areas to suppress pollen from the shore vegetation and regional vegetational conditions are thus reflected (cp. TAUBER, 1965). However, as the sediments contain pollen from all the plant communities of the surrounding areas, the plant distribution in relation to topography and soils cannot be determined immediately.

The interglacial pollen diagrams were based on the directly determined percentage curves. The interpretations of these diagrams may have been influenced by the unequal pollen representation of the various plants. The pollen productivity of the trees is now better known, as pollen productivity rates were calculated for the most important trees (ANDERSEN, 1967). The interglacial pollen analyses were corrected according to these figures in a preliminary attempt to improve the correspondance between pollen percentages and vegetational composition. The pollen representation of the less important vegetational components such as the shrubs and the herbaceous plants is still unknown. Because of their lower size, the pollen dispersal of these plants is less effective than that of the trees. Hence, the pollen counts for the anemophilous shrubs and the herbs, which are mainly represented by anemophilous taxa, were divided by two and those for the insect-pollinated shrubs were doubled prior to the percentage calculations. The original pollen diagrams are shown in ANDERSEN, 1965.

In the pollen diagrams the most important vegetational components are arranged according to certain ecological requirements in correspondance with earlier practice, a procedure which may emphasize general trends of development (ANDERSEN, 1966). The figures show the average percentages of the plants in the various pollen zones. This method may have oversimplified the results, however, it also facilitates a survey of the many details. There is a near similarity between the pollen frequencies of the various plants at the different sites within the interglacials. Consistent differences of this kind are explainable by differences in soil conditions or climate, and the trends of development are always identical. Such a close correspondance in the pollen content of the sediments from widely separated lakes shows that the pollen analyses reflect general vegetational features and emphasizes that the trends of development are of a fundamental character and cannot be explained by merely trifling or accidental events. The corrected pollen diagrams contain the same general features as those earlier mentioned, but the relative importance of various plants has changed somewhat.

	Harreskov IG							Holstein IG									Eem IG						
Zones	1	2	3	4	5a	5b	6	1	2	3	4	5	6	7	8	9	1	2	3	4	5	6	7
Hedera			×	×	×	×					×			×				×	×	×	×	×	
Ilex		×	×	×	×	×	(×)		×	×	×	×	×		×	(×)	(×)	(×)	×	×	×	×	(×)
Buxus					×								×	×	×	×						×	(×)
Viscum				×		×												×		×	×	×	
Vitis													×			×							
Pterocarya															×	×							
Osmunda	(×)	×	×	×	×							×	×	×	×			×		×	×	×	(×)
Cladium							(×)										×	×	×	×	×	×	(×)
Trapa																				×	×		
Stratiotes																		×	×				(×)

Table I. The occurrence of plants that are important climatic indicators.
(×) Presumably rebedded.

Forekomsten af planter, som er vigtige klimaindikatorer.
(×) Formodentlig omlejret pollen.

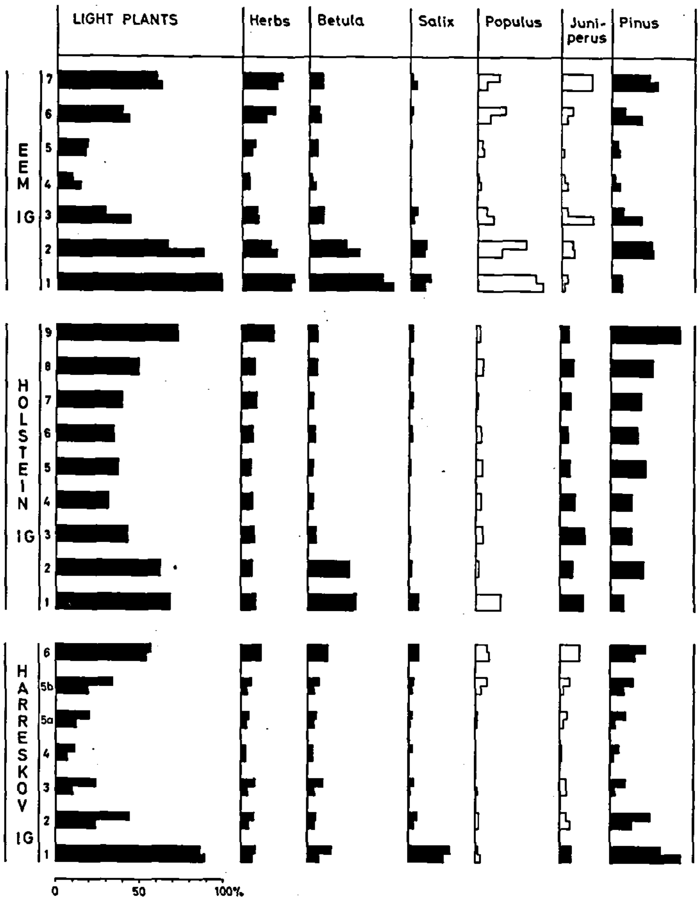

Fig. 1. Average percentages of the pollen of light-plants. The following sites are represented. Harreskovian: Ølgod (upper half of the columns), Harreskov (lower half of the columns). Holsteinian: Vejlby. Eemian: Herning (upper half of the columns), Hollerup (lower half of the columns). The black columns indicate percentages and the white ones percentages × 10.

Gennemsnitsprocenter af pollen af lysplanter. Følgende lokaliteter er vist. Harreskov Interglacialtid: Ølgod (øverste halvdel af søjlerne), Harreskov (nederste halvdel af søjlerne). Holsten Interglacialtid: Vejlby. Eem Interglacialtid: Herning (øverste halvdel af søjlerne), Hollerup (nederste halvdel af søjlerne). De sorte søjler viser procenter og de hvide procenter × 10.

During the late- and early-glacial phases which bordered upon the interglacials destructive forces influenced the vegetation, and hence only the interglacial successions themselves that were dominated by the forest are mentioned here. There is some evidence that the climate was rather uniform during the interglacial stages. The pollen finds of some plants, which are important climatic indicators are shown in table I. The sediments from the earliest and the last pollen zone in each interglacial contain in some cases small amounts of rebedded pollen, and some of the pollen finds from these zones may be considered unreliable. The occurrence of *Hedera* and *Ilex* as shown in the table indicate an atlantic climate, and the other plants shown suggest that the climate was as warm as or probably warmer than that of Denmark to-day during a greater part of the interglacials, except for the earliest and the last pollen zones, the climate of which may have been somewhat cooler.

Fig. 1 shows the occurrence of the light-plants in the 3 interglacial stages. These plants require good illumination duing their entire life cycle and indicate a vegetation sufficiently open for the light to penetrate into its deepest layers. They are indifferent to the soil conditions and often appear as pioneer plants. The first column, which indicates the total light-plant percentages, shows the characteristic distribution mentioned earlier by the author for the Harreskovian and the Eemian interglacial stages. The trend of change suggests an open-forest vegetation in the early phases of the interglacials, a forest with a dense crown cover in their middle parts, and increasingly open forest in their late phases. The light-plants remained frequent in the Holsteinian interglacial stage, and it appears that a universal dense forest cover did not develop.

The subsequent columns in fig. 1 show that the identical light-plants characterized the open-forest vegetation of the 3 interglacial stages. The light-plants included in the early phases relics of the preceding late-glacial periods such as the herbaceous plants, *Juniperus* and *Salix*, and new immigrators such as *Betula*, *Populus* and *Pinus*. These pioneer trees rapidly conquered the land, but their shade was insufficient for a complete suppression of the late-glacial relics. The same plants contributed to the re-increase of the light-plant curve in the late phases of the interglacials.

Fig. 2 shows the occurrence of the mull-plants in the 3 interglacial stages. These plants require a mull-soil rich in nutrients. The trees and shrubs of the group form a closed crown canopy, and pollen of mull-soil herbs are very rare in the lake sediments.

The mull-plants occurred in a characteristic manner. Their frequencies increased in the early phases, they had maximum frequencies in the middle phases and their frequencies decreased in the late phases. The mull-forest dominated the vegetation in the Harreskovian and the Eemian interglacial stages, but its frequencies in the Holsteinian did not reach the high values characteristic of the other interglacials.

In contrast to the great uniformity of the light-plant flora, the mull-flora varied considerably in the 3 interglacial stages. This fact is difficult to understand, but there may be reason to think that the conditions of survival during the glacial stages and immigration were of some importance. The unpretentious light-plants presumably had large survival areas, and they migrated quickly, whereas the selective and demanding mull-plants probably were more restricted during the glacial stages, and they spread more slowly than the light-plants. Hence it seems likely that the immigrational opportunities of the mull-plants varied in the 3 interglacial

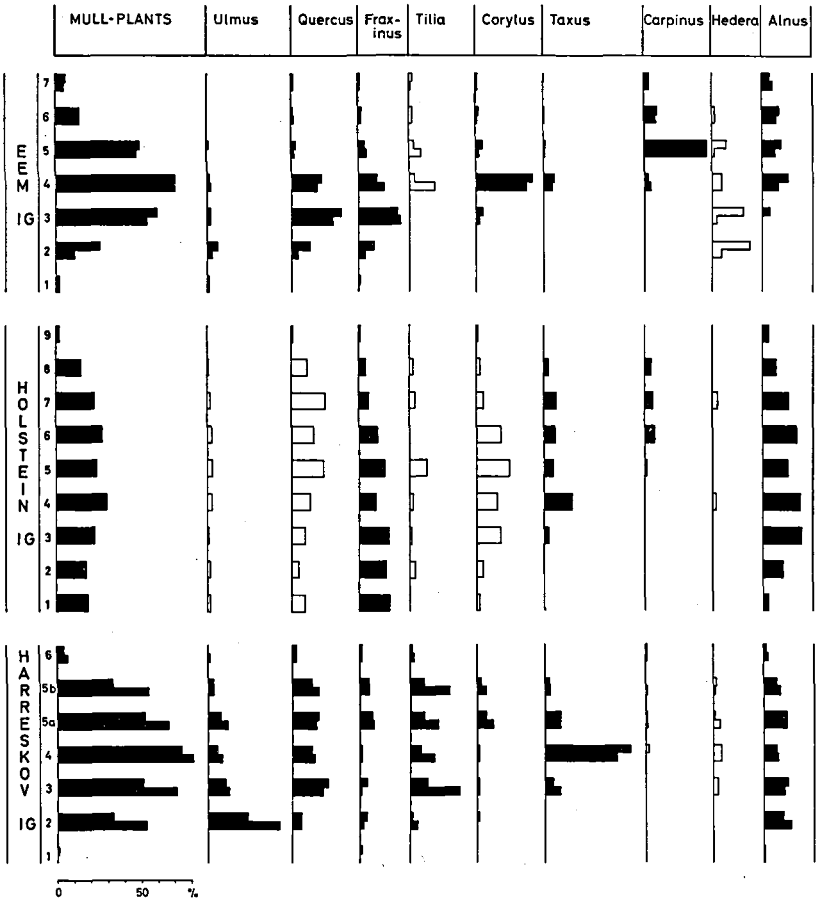

Fig. 2. Average percentages of the pollen of mull-plants and *Alnus*. Otherwise as fig. 1.
Gennemsnitsprocenter af pollen af muldplanter og el. Ellers som fig. 1.

stages, and due to restricted survival refuges and great areal transformations they may have been subjected to change in genotypical constitution and competitive ability.

Ulmus immigrated early in the interglacials and spread rather quickly. This tree was widespread in the Harreskovian but rather restricted in the other interglacials. *Quercus* immigrated rather quickly too. One may question its position within the mull-plants, as the oak species, *Quercus petraea* especially, thrive on mor soil. Oak rather clearly joins the mull-plants in the interglacials, however. The tree was quite frequent in the Harreskovian and the Eemian, and like *Ulmus* restricted in the Holsteinian. *Fraxinus* expanded quickly too, and this tree was particularly common in the Holsteinian interglacial stage. *Tilia* had its widest occurrence in the Harreskovian. This tree immigrated in the Eemian at a late point of time, where *Corylus* was already widespread, and it could apparently not expand. However, *Tilia* occurred widely south of Denmark at that time. The *Taxus* distribution was strange. It occurred with highest frequencies in the Harreskovian and the Holsteinian interglacial stages, but *Corylus* played its part in the Eemian. *Carpinus,* finally, consistently immigrated later than the other mull-plants, and a slow immigration was apparently characteristic of this tree. The hornbeam was most common in the Eemian interglacial stage.

The distribution of *Hed*era shows its relationship with the mull-plants. This tree climber was in the Eemian particularly frequent in the early phase, where it was favoured by the good light conditions. It was most frequent at Herning, a fact suggestive of a more atlantic climate at this site than at Hollerup, the other site.

The *Alnus* frequencies are shown together with those of the mull-plants. Alder grows on soils that are too wet for mull formation, but like the mull-plants it requires a soil influenced by mineral salts. This tree expanded early in the Harreskovian and the Holsteinian interglacial stages and surprisingly late in the Eemian. Its frequencies were very uniform except for a slight decrease in the late interglacial phases.

Fig. 3 shows the distribution of the plants characteristic of acid-humus soil such as mor or acid peat. Several of the acid-humus plants tend to promote acdification and humus accumulation.

The distribution within the interglacials of the acid-humus plants differs from that of the other plant groups discussed above, as they were most frequent in the later phases, however, the acid-humus vegetation expanded earlier in the Holsteinian than in the other interglacials. The acidophilous floras were greatly similar in the 3 interglacials. In this respect they resemble the light-plants.

Picea was an early pioneer in the Harreskovian interglacial stage but did not expand at that time. It was suppressed by the mull vegetation and increased in the late interglacial. *Picea* immigrated at an early time in the Holsteinian too, expanded early in that interglacial and decreased somewhat in the late phase. In the Eemian *Picea* immigrated and spread at a late point. This tree is known in western Europe from the early Cromerian and Holsteinian interglacial stages, and it quickly immigrated to Denmark. It did not survive the Saalian glacial stage in western Europe, however, and in the Eemian it had to migrate from the east with the result that its immigration in Denmark was delayed considerably.

Like *Picea, Frangula* occurred early in the Harreskovian and the Holsteinian. This occurrence of *Frangula* is remarkable, as the shrub is not known from such early stages of the Eemian interglacial stage and the Postglacial. The other acidophilous plants had rather uniform distributions in the 3 interglacials. *Ilex* may grow on a mull soil, but this shrub is particularly frequent in open mor-forest, and its pollen is prominent in postglacial mor from Denmark (IVERSEN, 1964). *Ilex* was particularly common in the Holsteinian, where its frequent occurrence suggests wide-

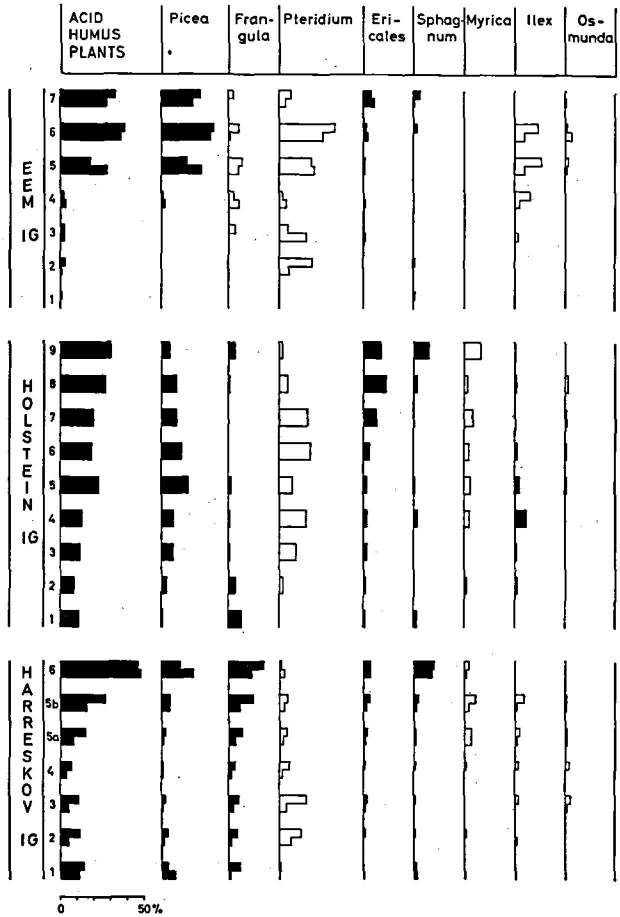

Fig. 3. Average percentages of the pollen of acid-humus plants. Otherwise as fig. 1.
Gennemsnitsprocenter af surbundsplanter. Ellers som fig. 1.

spread mor vegetation. Like *Hedera,* the *Ilex* frequencies from the Eemian suggest a climatic difference between the two sites represented. The occurrence of *Osmunda* suggests a warm climate in the late phases, as this fern is of a southerly distribution to-day. *Osmunda* spores characterize acid peat in the Postglacial (IVERSEN, l.c.). The decrease of *Ilex, Osmunda* and *Pteridium* in the latest pollen zone of the various interglacials was presumably due to decreased temperature.

The many differences in the interglacial vegetational successions are not surprising in view of the length of the time spans and the vicissitudes caused by the great climatic changes and areal transformations. The distri-

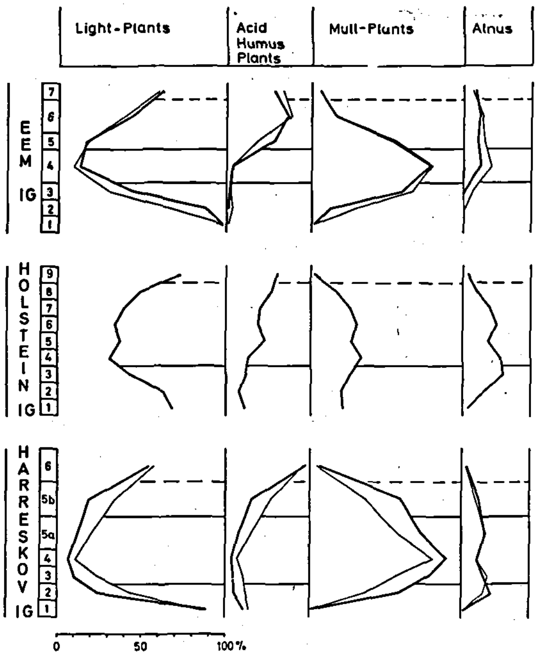

Fig. 4. Curves for the average pollen percentages of light-plants, acid-humus plants, mull-plants, and *Alnus*. The following sites are represented. Harreskovian: Ølgod (thin line), Harreskov (thick line). Holsteinian: Vejlby. Eemian: Herning (thin line), Hollerup (thick line).

Kurver for gennemsnitsprocenterne af lysplanter, surbundsplanter, muldplanter og el. Følgende lokaliteter er vist. Harreskov Interglacialtid: Ølgod (tynd linie), Harreskov (tyk linie). Holsten Interglacialtid: Vejlby. Eem Interglacialtid: Herning (tynd linie), Hollerup (tyk linie).

butional patterns of the light-plants, mull-plants and acid-humus plants show some common features but important differences exist too (cp. fig. 4).

Quickly spreading trees and shrubs with unpretentious requirements to climate and soils apparently characterized the vegetation of the early phases in all of the 3 interglacials. *Betula, Pinus, Populus, Juniperus* and *Salix* were the most important light-plants. The mull-vegetation had not expanded yet, and the acid-humus plants were of restricted importance. This vegetation belonged to the fresh soil left by the glaciers, and as mentioned by IVERSEN (1958) this protocratic phase resembled the conditions in the early Postglacial strongly.

The biological transformation of the soil begins with the mull formation. Its topmost layers are mixed with the vegetational litter and a rapid biological decomposition of the organic waste products maintains a favourable nutrient status. Vegetation characteristic of mull became dominant in the Harreskovian and the Eemian interglacial stages. *Ulmus, Quercus, Taxus* and *Tilia* predominated in the Harreskovian, and *Quercus,* *Fraxinus, Corylus* and *Carpinus* were the most important mull-plants in the Eemian in these mesocratic phases. The mull-vegetation was less prominent in the Holsteinian interglacial stage. *Fraxinus,* characteristic of damp sites, was the only important mull-plant at that time, and the mull-plants of the drier sites such as *Ulmus, Quercus, Tilia, Corylus* and *Carpinus* were restricted. This situation can hardly be explained by immigrational and evolutional features, and it appears that deficient formation of mull on the well drained soils was an important cause. Like *Fraxinus,* the commonness of *Alnus* in this interglacial suggests richer conditions on the low lying sites.

Mull is a stable soil, however, the dominant mull-vegetation from the Harreskovian and the Eemian interglacials decreased and the acid-humus plants and the light-plants expanded. This change cannot have been due to an unfavourable climate, and it seems more likely that the mull-soil did not resist degeneration and that an accumulation of acid humus began. Lime preserves a basic reaction in the mull-soil, but is dissolved by the surplus of carbon dioxide produced by the biological activities (VOGEL, 1959) and removed by seeping rain water. When the lime is dissolved, the acidity increases, other soluble minerals are leached, and the base saturation of the mull decreases. In this stage an accumulation of strongly acid humus may be initiated by the presence of plants with a litter resistant to decomposition. *Picea* needles are particularly unfavourable, as they are left on the surface by the rainworms and resist decomposition (BORNEBUSCH, 1943; WITTICH, 1953; OVINGTON, 1953; HANDLEY, 1954). Due to a higher acidity the soil mixing fauna disappears in mor, the breakdown of the waste products becomes incomplete, and the plant nutrients become withheld (MÜLLER, 1878; BORNEBUSCH, 1930; ROMELL, 1935). *Picea* is known to promote mor accumulation in soils deficient in lime, and the decrease of the mull-vegetation in the interglacials coincided with an expansion of this tree (cp. ANDERSEN, 1966). As open vegetation expanded simultaneously with *Picea* it appears that the soil was unable to support dense *Picea* forest. The change to mor conditions probably promoted podsolization of the formerly calcareous soils with formation of an impenetrable hard pan as the result. Such a shallow soil dries easily in elevated places and water collected in depressions promotes paludification, and as *Picea* is sensitive to drought and swamping, such conditions probably restricted this tree and favoured the expansion of heath and bog vegetation with plants such as *Pinus, Betula, Populus, Juniperus, Frangula, Ilex, Myrica, Osmunda,* and the Ericales in this oligocratic phase of the interglacials (ANDERSEN, l.c.).

Unlike the other interglacials, the acidophilous plants expanded at an early phase in the Holsteinian interglacial stage, whilst the light-plants remained frequent, and the mull-vegetation was restricted to the moist sites. Thus the mesocratic phase was suppressed, and the protocratic phase passed directly into an oligocratic phase in this interglacial. This strange development is somewhat difficult to understand. The most likely explanation of this situation would be a widespread occurrence of sandy soils poor in lime, which were leached very quickly and changed into podsolized mor soils, a development which would have been promoted by the occurrence og *Picea*. Similar vegetational features characterize the Holsteinian deposits of North Germany (HALLIK, 1960), but it may be noticed that mull-plants such as *Quercus, Ulmus, Tilia* and *Corylus* occurred abundantly at Holsteinian sites on calcareous soils in England with insignificant *Picea* occurrence (WEST, 1956; KELLY, 1964; SHACKLETON and TURNER, 1967). In the Post-glacial, where *Picea* was absent from Denmark, retrogression set in at a late time, even on the sandiest soils (IVERSEN, 1964).

The soils degenerated presumably first on the high and well drained sites, as seepage of ground water in low areas delay mor formation (HESSELMANN, 1926; PEARSALL, 1950). Hence the mull-vegetation presumably persisted longest on the damp soils, and *Alnus*, which grew on the wet sites was less affected than the mull-plants. However, podsolization causes a surficial seepage of the rain water through the leached layers, and it seems that even the wet sites became depauperated, as the *Alnus* frequensies decreased in the latest stages of the interglacials. Such a development presumably also caused the decrease of the mull-vegetation of damp soils in the late Holsteinian interglacial stage.

As mentioned above, a temperature decrease is indicated in the latest pollen zone of each interglacial stage.The Ericales and *Sphagnum* were particularly frequent in this last phase and suggest an expansion of bogs at that time. This last phase resembles the telocratic phase of IVERSEN (1958).

The soil development was reflected by the lake sedimentation in the Harreskovian and the Eemian interglacials, as mentioned in ANDERSEN, 1966. The lake deposits from the Holsteinian site are uniform throughout the interglacial stage. Their eutrophic diatom flora (FOGED, 1960) suggests that this large lake mainly received ground water that had passed through deep and unleached layers.

The vegetational successions of the interglacials suggests instability of the vegetation throughout long periods. The delayed establishment of the mull-forest gave room for a wide occurrence of open forest in the early phases of the interglacials. The mull-forest could not maintain itself, and with the lapse of time, the forest caused itself a depauperization and acidification of the upper soil layers, which extended so far that the dense forest receded and more open vegetation types expanded. Easily leached soils seem to have been of a wide extent in the Holsteinian interglacial stage, and mor formation and podsolization apparently progressed so quickly in this interglacial that dense forest remained to be of restricted occurrence. This process was probably promoted by the early presence of *Picea*.

TANSLEY wrote in 1939 (p. 226), "Even climatic climax communities, though seemingly permanent so long as the existing climatic complex persists, may contain within them the seeds of their own decay. They may, for example, gradually bring about changes in the soil on which they are growing, changes that will ultimately prevent their own regeneration. But though we may suspect their occurrence, of the details of such events we have as yet very little knowledge." The interglacial plant successions in relation to soil development emphasize the importance of events of the kind TANSLEY spoke of.

DANSK SAMMENDRAG

INTERGLACIAL VEGETATION OG JORDBUNDSUDVIKLING

Pollendiagrammerne fra interglacialaflejringer viser tilstedeværelsen af 3 interglacialtider i Danmark. Interglacialtiderne udgør tidsrum med stabile forhold imellem istidernes perioder med ødelæggende virksomhed, og interglacialtidernes vegetationssukcessioner gør det derfor muligt at studere den langsigtede balance mellem vegetationen og kårforholdene.

Pollendiagrammerne fra søaflejringerne afspejler den regionale vegetation. En korrektion af pollenprocenterne i overensstemmelse med nyindvundne erfaringer gør det muligt at forbedre overensstemmelsen mellem pollenanalyserne og vegetationens sammensætning.

Klimaet var ret ensartet i de tre interglacialtider. Forekomsten af vedbend og kristtorn tyder på et atlantisk præget klima, og varmekrævende planter forekom i de fleste af pollenzonerne, måske med undtagelse af den første og sidste i hver interglacialtid (table I).

Planterne der udgjorde den interglaciale vegetation er delt i 3 økologiske grupper: lysplanter, muldplanter og surbundsplanter.

Lysplanterne (fig. 1) viser en karakteristisk fordeling: høje værdier i de tidlige stadier, lave værdier i de midterste stadier og stigende værdier i de sene stadier af interglacialtiderne; men lysplanterne forblev udbredte i hele Holsten Interglacialtiden. Lysplantefloraen var ensartet i de tre interglacialtider. Muldplanterne (fig. 2) havde en modsat fordeling: lave værdier i de tidlige stadier, høje værdier i de midterste stadier og faldende værdier i de sene stadier. Muldvegetationen var af begrænset udbredelse i Holsten Interglacialtiden. Muldfloraens sammensætning var højst uensartet i de tre interglacialtider. Dette skyldtes muligvis til en vis grad indvandringshistoriske og udviklingshistoriske årsager. Surbundsplanterne (fig. 3) afveg fra lysplanterne og muldplanterne: de var sjældne i de tidlige stadier, og deres udbredelse tiltog henimod de sene stadier. Surbundsfloraen var ligesom lysplantefloraen ensartet i de tre interglacialtider.

Lysplanterne indvandrede hurtigt og havde stor udbredelse i de tidlige stadier af interglacialtiderne, hvor muldvegetationen endnu ikke havde bredt sig. De vigtigste lysplanter var birk, fyr, asp, enebær og pil. Jordbunden var frisk og sure humuslag stærkt begrænsede i disse protokratiske stadier (se fig. 4).

Muldbund var af stor udbredelse i Harreskov og Eem Interglacialtiderne, og den tætte og mørke muldskov fordrev næsten helt lysplanterne i de mesokratiske stadier. De vigtigste muldplanter i Harreskov Interglacialtiden var elm, eg, taks og lind, og i Eem Interglacialtiden eg, ask, hassel og avnbøg. Ask, som trives bedst på fugtig jordbund, var den hyppigste muldbundsplante i Holsten Interglacialtiden, og muldbundens træer og buske fra den højere jordbund manglede næsten helt. Dette tyder på, at muldbundsdannelse udeblev på den høje jordbund i denne interglacialtid.

Muld er en stabil jordbund, men de opløselige mineraler, først og fremmest kalken, opløses efterhånden og bortfjernes ved udvaskning. I denne tilstand kan muld let omdannes til mor, og tilstedeværelse af planter med vanskeligt omsætteligt affald, især gran, kan fremkalde en ændring til mortilstand, hvor sammenblandingen af jordbunden ophører, og stærkt sur humus pålejres. Lysplanternes tiltagen sammen med gran tyder på, at denne ikke dannede tæt skov. Dette skyldtes sandsynligvis, at podsolering med dannelse af vandstandsende al-lag bevirkede udtørring af den flade jordbund på de høje steder og forsumpning i lavninger, som begge er ugunstige for granen. I hvert fald bredte en åben vegetation med fyr, birk, asp, enebær, kristtorn og en række surbundsplanter sig sammen med granen i dette oligokratiske stadie.

Muldbundsskovens begrænsning til fugtig bund og surbundsvegetationens tidlige udbredelse i Holsten Interglacialtiden kan forklares ved en hurtig udvaskning og mordannelse på den høje bund på grund af en stor udbredelse af sandet og kalkfattig jord. Gran var tidligt til stede og kunne fremme en sådan udvikling. Det mesokratiske stadie blev således undertrykt, og det protokratiske stadie gik direkte over i det oligokratiske.

Mordannelse og podsolering skete sandsynligvis først på de høje jorder, som udvaskedes først. Podsoleringen fremkalder et overfladisk afløb af afstrømningsvandet, og tilbagegangen af el i interglacialtidernes sene stadier tyder på en fattiggørelse af de lavestliggende voksesteder. En lignende udvikling fremkaldte sandsynligvis tilbagegangen af muldbundsskoven på lavtliggende jordbund i Holsten Interglacialtiden.

Søudviklingen i Harreskov og Hollerup fra kalkrig til kalkfri sedimentation skete samtidig med muldbundsvegetationens tilbagegang og tyder også på mordannelse og podsolering. Den eutrofe diatoméflora i den store sø ved Vejlby fra Holsten Interglacialtiden tyder på, at denne sø modtog grundvand, der passerede uudvaskede dybtliggende jordlag.

I interglacialtidernes allersidste del skete der sandsynligvis en temperaturnedgang, og en tiltagen af lyngplanter og Sphagnum tyder på højmosedannelse. Dette stadie minder om det telokratiske stadie.

Interglacialtidernes vegetationsudvikling tyder således på, at den tætte skovvegetation ikke var stabil i længden. Vegetationen fremkaldte åbenbart selv ændringer i jordbunden, som betingede en udvikling henimod mere åbne og fattige vegetationstyper. Granens tilstedeværelse var sikkert af væsentlig betydning for dette udviklingsforløb. I Holsten Interglacialtiden var jordbundsforholdene åbenbart af en sådan karakter, at denne udvikling skete væsentlig hurtigere, sandsynligvis under påvirkning af granens tidlige tilstedeværelse.

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