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RECONSTRUCTION AND INTERPRETATION OF THE LOCAL VEGETATIONAL SUCCESSION OF A LATEGLACIAL DEPOSIT FROM USSELO (THE NETHERLANDS), BASED ON THE ANALYSIS OF MICRO- AND MACROFOSSILS

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SUMMARY

Analysis of plant micro- and macrofossils from a sequence from Usselo (The Netherlands) allows a detailed reconstruction of local developments during a period of more than one and a half millennia, starting before the Bølling period and lasting till the end of the Allerød period. The sequence started in an oligotrophic shallow pool with a very low organic production in a barren sandy landscape. An early phase with *Gloeotrichia* type may be connected with the ability of N-fixation of these blue-green algae. This capacity may have initiated nutrient availability. Characeae played an important role on the initially sandy substrate. These pioneers opened up the site for other aquatics and helophytes, e.g. *Potamogeton alpinus, Carex rostrata, Phragmites australis, Equisetum fluviatile,* followed by *Menyanthes trifoliata, Myriophyllum spicatum* and various *Carex* species. This sequence indicates a gradual eutrophication of the site, accompanied by an increase in production of organic matter (interrupted during the Older Dryas), as substantiated by the organic/inorganic ratio of the substrate. The tendency towards eutrophication ended when the vegetation at the mire surface lost its contact with the ground water. The sequence ended with a vegetation type dominated by *Sphagnum* and the occurrence of oligotraphentous Thecamoeba.

These changes in local vegetation are explicable without resort to temperature fluctuations. The nutrient status of the habitat, and the water level (the latter influenced by sand and organic sediment deposition) were apparently the most important factors in the vegetation succession.

1. INTRODUCTION

The Lateglacial deposits near Usselo (52°12′ N, 6°49′ E) were studied palynologically for the first time by VAN DER HAMMEN (1951). During the last few decades many deposits of Lateglacial age have been studied intensively in N.W. Europe. Recent overviews of the final phase of the Last Ice Age in Europe have been given by IVERSEN (1973), GODWIN (1975), OVERBECK (1975) and LOWE et al. (1980). Reconstructions of fluctuations of the mean July temperatures during the Lateglacial period have been made, based mainly on pollen diagrams in which the arboreal/non-arboreal pollen ratio plays an important role (see e.g. VAN DER HAMMEN et al. 1967). These display some remarkable differences with reconstructions of temperature fluctuations based on the analysis of remains of Coleoptera (COOPE 1970, 1977; LAMB 1977). To attack this problem G. R. Coope (Birmingham) and T. van der Hammen (Amsterdam) planned a detailed palynological-palaeobotanical study and a study of Coleoptera of one Lateglacial sequence from Usselo. In 1975 the deposits of Usselo were exposed again by an excavation specially carried out for this purpose. The sample site is a channel infill of an early Lateglacial cut-off, the stratigraphy showing a sandy gyttja deposit followed by a peat deposit, which was covered once more by a sandy deposit. These deposits were studied in detail and a number of papers are in preparation, dealing with among others, the possible temperature fluctuations during the period concerned. The detailed stratigraphy and lithology of the profile will be discussed in a later paper. The present paper deals with the reconstruction and interpretation of the local vegetation succession, based on a selection of frequency curves of microfossils and macrofossils from the aquatic and fen stages of the infill sequence.

2. METHODS

Sampling was done by means of metal boxes, 50 and 100 × 10 × 15 cm, open at one side. The sharp edges of the boxes were pushed into the exposed profile, carefully cut out and returned to the laboratory where separate subsamples for the analysis of microfossils and of macrofossils were taken.

The subsamples for microfossils were taken every 0.5 cm. Some subsamples (in coarse sand) were very poor in pollen (Σ-pollen < 100) and were discarded. The subsamples were treated with KOH and subsequently acetolysed according to FAEGRI & IVERSEN (1975). For the separation of organic material from sand and clay a bromoform-alcohol mixture (specific gravity 2) was used. The material was embedded in glycerine jelly and sealed in with paraffin wax. All suitable subsamples were analysed for pollen, Algae, Fungi, Rhizopoda and other palynomorphs (cf. VAN GEEL 1978; VAN GEEL et al. 1983). Frequencies in subsequent spectra were calculated as percentages of Σ-pollen (the sum of pollen of *Betula, Salix, Hippophaë, Juniperus, Pinus, Artemisia, Helianthemum, Plantago, Rumex, Thalictrum,* Chenopodiaceae, Ericales, Poaceae and Cyperaceae). In most of the samples the counted number of Σ-pollen was between 300 and 600. In this way the microfossil curves were not influenced by changes in the sediment accumulation rate. Several palynomorphs were recorded which often are neglected by palynologists, viz. certain Cyanophyta, Chlorophyta and Thecamoeba. In the diagram these taxa are indicated by a "Type number" which refers to descriptions and illustrations by VAN GEEL (1978), VAN GEEL et al. (1981), VAN GEEL et al. (1983) and VAN GEEL (in prep.).

The subsamples for macrofossil analysis (size c. 5 cc) were boiled in 5% KOH for 5–10 min and separated from the finer material using a 140 μm mesh sieve. Seeds, fruits and other macrofossils were counted and the volumes of mosses, vegetative remains of Phanerogams and charcoal were estimated as volume percentages of the sieved residue. The organic/inorganic volume ratio of the residue was also estimated. It should be emphasized that the number of macrofossils per sample is influenced by the sediment accumulation rate.

3. LITHOLOGY

The sample series Usselo I was taken at a point in the excavated profile which showed the most complete sequence of the Lateglacial deposits. Samples (indicated next to the lithological column of fig. 1) represent 0.5 cm each.

The lithological description of the entire section is as follows.

samples	description
1– 58	coarse sand with some charcoal in samples 22, 23 and 42, 43
59– 65	loamy sand
66– 72	peaty sand
73–140	peat
141–155	sandy peat, sand diminishing from base to top
156–162	coarse sand
163–167	sandy gyttja
168–189	gyttja
190–199	sandy gyttja
200–206	gyttja
207–208	sandy gyttja
209–227	coarse sand
228–245	loamy sand with iron fibres
246–270	coarse sand
271–273	loamy sand
274–276	fine sand
277–279	loamy sand
280–291	fine sand

The present paper deals with a part of the section, viz. sample 74 to sample 260. The non-treated lower part of the section does not belong to the pool deposit (algae almost absent; terrestrial fungal spores present). The upper boundary of the part of the section treated here was fixed at the Allerød-Younger Dryas transition (sample 73), characterized by a temperature fall and – locally – by a rise of the water table, reflected here in the covering of *Sphagnum* peat by a sandy pool deposit. This deposit was formed under mesotrophic conditions (*Scenedesmus* spec., *Calliergon stramineum, Drepanocladus exannulatus*).

In a forthcoming paper the complete set of analysed data (from local and regional sources) of the whole sequence will be presented, in combination with morphological descriptions, illustrations and ecological data of a series of "extra" palynomorphs and macrofossils, e.g. fungal spores, algae and invertebrates.

4. DATING

VAN DER HAMMEN (1951) studied the Lateglacial sequence at Usselo. The site was revisited in 1955 in order to take samples for dating at the ^{14}C laboratories in Copenhagen and Groningen. A profile was exposed by digging and the position of the samples was determined by the stratigraphic sequence: sandy deposits preceding the gyttja of the Bølling period (Ib), a sandy deposit of the Older Dryas period (IC), Allerød peat (II) and sandy deposits of the Younger Dryas (III). Some pollen samples were taken for comparison with standard Lateglacial pollen zones. They were analysed by Dr. H. Krog (Geol. Survey Denmark). The dating resulted in a detailed ^{14}C-chronology of the Lateglacial period (LANTING & MOOK 1977). At the right-hand side of *fig. 1* the approximate age of some zone boundaries is given in years B.P., based on the 1955 sample series. Using these data the duration of successive phases (subzone A3-zone C) of the succession can be estimated. These estimations are rather rough because of interpolation of ^{14}C dates. As soon as ^{14}C dating of very small samples becomes possible, using a Van de Graaff accelerator, fruits and seeds will be selected for more precise datings of several relevant levels.

5. RESULTS

Fig. 1 shows a schematic summary diagram for Σ-pollen taxa at the left-hand side, from which a chronostratigraphical sequence can be deduced. It comprises the changing relative frequencies of *Betula, Juniperus, Hippophaë, Pinus* and the total of upland herbs. The boundaries of the regional zones Ia, Ib, Ic and II according to FIRBAS (1949) and also the boundaries of (sub)zones for the local vegetational succession are indicated next to the lithological column. The ratio of organic and inorganic material in the samples is indicated in the next column. Next to this ratio the curves of indicative local vegetation elements and some invertebrates are presented, showing from left to right the taxa associated with the local succession. Horizontal orientation lines are drawn at distances of 20 samples (10 cm), from sample 251 upwards. The curve of Poaceae pollen was included in the diagram to show the maximum in subzone A4, which corresponds with epidermis fragments with stomata of *Phragmites*. For practical reasons (reduction of the length of *fig. 1*) some maxima were cut off (viz. of *Gloeotrichia* type, Characeae and *Carex paniculata* type).

6. RECONSTRUCTION AND INTERPRETATION OF THE LOCAL DEVELOPMENT

Three major zones can by distinguished, viz. zone A, representing the aquatic and reed swamp phase, zone B representing a sedge fen stage and zone C corresponding with an oligotrophic acid *Sphagnum* fen. Some subzones of A and B could be distinguished, but it should be born in mind that the exact place of the (sub)zone boundaries is more or less arbitrary because of the overlapping ecological amplitudes of the taxa involved.

Subzone A1 (sample 260–245)
The algae *Botryococcus braunii* and, somewhat later, *Pediastrum* spec. and *Debarya* spec. characterize this zone which is very poor in other aquatic plants. Considering the A.P./N.A.P.-ratio (arboreal/nonarboreal pollen, see schematic summary diagram at the left side of *fig. 1*), the vegetation around the pool had a very open character and the sediment (coarse sand) indicates that erosion and deposition by wind and water played an important role.

Subzone A2 (sample 244–209)
This subzone is especially characterized by blue-green algae of the *Gloeotrichia* type (see VAN GEEL et al. 1983, p. 313). During the earliest phase of the Lateglacial the raw, unleached soils, pools and lakes in N.W. Europe must have been very poor in nitrogen compounds (see e.g. IVERSEN 1973, p. 26; OVERBECK 1975, p. 414) and in humus. In this situation blue-green algae apparently could play a pioneer role thanks to their nitrogen-fixing ability and they gradually made conditions suitable for other aquatic plants. The algae *Euastrum insulare* var. *lacustre*, *Cosmarium* cf. *botrytis* and *Cosmarium turpinii* var. *eximium* (Desmidiaceae) occurred during a short phase (sample 237). According to P. F. M. Coesel (Amsterdam, pers. comm., 1983) these pioneer species are capable of rapid vegetative reproduction. Oospores of Characeae in a layer of loamy sand indicate that these pioneer algae were among the earliest colonizers of the sandy bottom of the pool. The absence of oospores in a layer of coarse sand of the samples 229 to 216 is apparently a consequence of very rapid deposition of this layer. Subsamples for microfossils in this layer were also very poor.

Subzone A3 (sample 208-151; c. 650 years)
The transition of subzone A2 tot subzone A3 is correlated with a change from sandy sediments to a sandy gyttja, confirmed by the change in the organic/inorganic ratio. *Gloeotrichia* shows a decline and the sharp rise of oospores of Characeae indicate that the pioneer role of the blue-green algae is taken over by representatives of the Characeae. Spores of *Spirogyra* are of regular occurrence too. In the upper part of subzone A3 *Potamogeton alpinus*, *Carex rostrata* and *Scorpidium scorpioides* indicate mesotrophic conditions. The sparse occurrence of some aquatic bryophytes, a.o. *Drepanocladus exannulatus* and cf. *Amblystegium riparium* confirm that indication. In the upper three samples of subzone A3 the high representation of *Carex rostrata* and *Potamogeton alpinus* indicates the increased density of these species at the start of the infilling of the pool.

Selaginella selaginoides probably did not grow in the water, but on the moist embankment, macro- and microspores being transported and embedded in the sediment.

The above mentioned change from minerogenic to more organogenic sediment at the base of subzone A3 coincides with and is related to marked changes in the vegetation of the area around the pool at the start of the Bølling period (the transition of Ia to Ib: see schematic summary diagram). *Betula* pollen shows a rise and *Hippophaë* (a nitrogen fixer) and *Juniperus* became important elements in the regional vegetation. This vegetation cover apparently prevented the strong erosion/deposition by wind and water which occurred during the preceding period as shown by the changes in lithological data.

The Older Dryas period (upper part of A3; zone Ic of Firbas) is characterised by a rise of herbs, a decline of *Juniperus* and *Betula* and the deposition of a more sandy sediment as a result of a relatively short phase of rapid erosion and eolian deposition. This is often explained as the effect of a decline of mean summer temperatures, though the Coleoptera from this site show no evidence of such a temperature decline (G. R. Coope, pers. comm. 1984). Alternative explanations (VAN GEEL & KOLSTRUP 1978; HUNT & BIRKS 1982) draw attention to possible effects of temporary drier climatic conditions, but in the present study local aquatic plants do not show marked changes during the Older Dryas period, apart from the relatively low representation of Characeae, *Potamogeton alpinus* and *Carex rostrata* in some samples.

Subzone A4 (sample 151–138; c. 150 years)
This subzone represents the phase of vegetative infill of the pool. Initially *Potamogeton alpinus* played a role, but soon it was completely replaced by *Carex rostrata, Phragmites australis* and *Equisetum fluviatile* (specific determination based on macrofossils). Gemmules of fresh water sponges occur in the upper part of subzone A4 and in A5. According to R. W. M. van Soest (Amsterdam, pers. comm. 1983) these epiphytic organisms are restricted to the submerged parts of helophytes. The stratigraphic position of the gemmules and the spectrum of co-occurring plants in the Usselo section fit perfectly with the idea of a transition (in space and time) from the aquatic to the fen stage. In a late Holocene deposit (VAN GEEL et al. 1983, p. 301) the same phenomenon was observed.

The transition of zone Ic to II shows the characteristic decline of herbs and rise of *Betula* pollen. Bud scales indicate that tree-birch species are concerned here. The possible cause(s) of the sudden extension of birch forest (rise of summer temperatures, rise of winter temperatures, an increase of winter rainfall and immigration) will be discussed in forthcoming papers. The sudden extension of birch forest is – at the Usselo sample site – concomitant with a relative lowering of the water table and with the transition from strongly minerogenic to organogenic sediment.

Subzone A5 (sample 138-132; c. 50 years)
Carex rostrata, Phragmites australis and *Equisetum fluviatile* show a sharp decline and filamentous algae of the *Zygnema* type show a rise at the transition of zone A4 to A5. Zone A5 is dominated by *Menyanthes trifoliata. Myriophyllum spicatum* becomes a local element in samples 133 and 132. These phenomena suggest a transition from the aquatic environment to a situation of shallow pools intermingled with small cushions of essentially terrestric vegetation (e.g. *Carex vesicaria*), with the actual sample site in a pool. This situation will have caused a rise in the nutrient status of the pools through increased mineralisation and run off, which would explain the occurrence of filamentous algae and *Myriophyllum spicatum*. Characteristic of this alternating wet-dry situation is *Hydrocotyle*

vulgaris (sample 133), while *Utricularia* (sample 131) occurred in the mesotrophic shallow pools mentioned.

Zone B

This zone represents a sedge fen stage. Algae are almost absent, apart from spores of representatives of Zygnemataceae (*Mougeotia* and *Zygnema* type), indicating that at some levels open water still prevailed, at least during spring.

Subzone B1 (sample 132-119; c. 150 years)

The transition of zone A to zone B is characterised by the decline of more eutraphentous aquatic taxa and a rise in Cyperaceae. Overall conditions were temporarily dry enough to permit, for the first time, the occurrence of fire, evidenced by the presence of charcoal. The occurrence of *Calliergonella cuspidata* fits with this picture. Strictly locally aquatic conditions persisted, which is substantiated by the occurrence of *Scorpidium scorpioides, Drepanocladus aduncus* and *Calliergon giganteum*.

Subzone B2 (sample 119-109; c. 100 years)

Drepanocladus fluitans, D. aduncus and high amounts of *Scorpidium scorpioides* reflect a period in which a hummock-hollow complex will have been present at the site. The decline of *Menyanthes* might indicate that progressively more oligotrophic conditions developed.

Subzone B3 (samples 108-78; c. 300 years)

The gradual disappearance of aquatic mosses point to the development of more terrestrial conditions. *Calliergon stramineum, C. megalophyllum, Meesia triquetra, Carex limosa* and the Thecamoeba *Amphitrema flavum* are indicative of a still lower nutrient status (oligo/mesotrophic). *Carex paniculata* type (comprising the species *C. paniculata, C. appropinquata* and *C. diandra*) is abundant in the lower part of this subzone. In view of the above mentioned hydrological and trophic conditions prevailing in this stage the latter species seems the most probable. Many partly charred remains of local plants and recurrent charcoal concentrations show that several fires swept the area, which confirms the prevailing drier conditions. *Carex vesicaria*, which played an important role in the local vegetation, might have been stimulated by the elevated input of minerals as a result of these fires.

Zone C (sample 78-74; c. 50 years)

The sharp rise in the remians of *Sphagna* and the co-occurrence of *Meesia triquetra*, in combination with a maximum of *Amphitrema flavum* and the presence of *Assulina* spec. (Thecamoeba) illustrate the development to a wet oligotrophic *Sphagnum* fen. Instrumental in this development will have been the gradual rise of the surface of the mire, which will have reduced the influence of run-off and superficial seepage water from the surroundings. Moreover the vegetation became isolated from the minerotrophic ground water. In the meantime the process of leaching of the surrounding coversand area which had taken place during the Allerød period (development of "Usselo-soils"; zone II of the diagram) will have resulted in a lower nutrient status. The presence of fruits of *Carex* sect. *Acutae*, which is also characteristic for zone C, cannot be ecologically interpreted with certainty, as the species concerned have different ecological demands.

7. DISCUSSIONS AND CONCLUSIONS

The first colonizers of the open water were *Botryococcus braunii* and *Pediastrum* spec., taxa which can occur in conditions that in the context of the present paper can be called oligotrophic (ROSÉN 1981). A phase with remains of *Gloeotrichia* type may be connected with the ability of these blue-green algae to fix nitrogen, which was of great importance in an environment which must have had very low amounts of nitrogen compounds. FJERDINGSTAD (1954) and KORDE (1966) interpreted the abundant occurrence of certain blue-green algae in lake deposits as an indication of warm climatic phases, but the occurrence in the Usselo section is most probably explained in terms of trophic conditions. A paleoclimatological interpretation would be rather uncertain. According to P. F. M. Coesel (Amsterdam, pers. comm. 1983) this fossil occurrence of *Gloeotrichia* type has its parallel in a recently dug sandy pool in the Dutch calcareous coastal dune area. There *Gloeotrichia echinulata* occurs every late summer in pioneer conditions, almost in the absence of other aquatic plants.

Characeae appear as a pioneer vegetation on a loamy-sandy substrate. They maintain their position throughout the aquatic phase, especially in the lower part of subzone A3. In the declining phase of the Characeae two *Potamogeton* species, viz. *P. alpinus* and *P. praelongus* appear. The next step in the succession is characterized by the dominance of helophytes: first *Carex rostrata*, then *Equisetum fluviatile*, *Phragmites* and finally *Menyanthes*. This latter phase is accompanied by the appearance of *Myriophyllum spicatum*. This whole sequence generally indicates a progression from an oligotrophic to a mesotrophic situation (*table 1*), with the exception of the somewhat "early" occurrence of fruits of *Potamogeton praelongus*. The succession described corresponds with the usual hydrosere of isolated, originally oligotrophic fens on mineral subsoil (e.g. SEGAL & GROENHART 1967). The synsystematic sequence can be described as: Charetalia → Magnopotamion → Magnocaricion → Phragmition. In locally dispersed pools elements of the Parvopotamion occurred. This sequence reflects the abovementioned process towards water which is progressively shallow and richer in nutrients, and a more organic sediment with a thicker layer of sapropelium. As a cause of the rise in N- en P-compounds the increase in exogenous animal life and bacterial and algal N-fixation can be suggested, together with the accumulation of water- or air-transported exogenous organic and inorganic compounds, processes accompanying a denser vegetation. This tendency towards eutrophication is continued up to the phase where the mire vegetation loses its contact with the minerotrophic ground water. The development of the fen vege-

Table 1. Ecological preferences of the dominant aquatic macrophytes in the succession.

	substrate	$PO_4^{3-} - p$	NH_4^+ NO_3^-	other water characteristics
Myriophyllum spicatum	med. (coarse) min. to fine org. (9)	mean 1.29 ± 0.04 mg/l (10)		eutrophic (6/7) lightnr. 5 (8) eutrophic to mesotrophic (9/11)
Menyanthes trifoliata	deep org. or anaerobic mud (9)		N-number 2 (8)	mesotrophic (7, 11) oligotrophic to dystrophic (9)
Phragmites australis	min. to org. (9) humic mud and peat (11)	mean 1.15 ± 0.04 mg/l (10)	N-number 5 (8)	eutrophic (7) eutrophic to oligotrophic (9) eutrophic to mesotrophic (11)
Equisetum fluviatile	fine min. to sand (and thin peat) (9) peaty or humic mud (11)	mean 0.72 ± 0.03 mg/l (10)	N-number 5 (8)	eutrophic (7) eutrophic to oligotrophic (9) meso-eutrophic (11)
Carex rostrata	org. (9)		N-number 3 (8)	mesotrophic (7) mesotrophic to oligotrophic (9/11) up to 0.5 m deep (9)
Potamogeton praelongus	min. to org. (9)		N-number 4 (8)	eutrophic (6/7) lightnr. 8 (8) mesotrophic to eutrophic (9) mesotrophic (11) 50–80 cm deep (11)
Potamogeton alpinus	org. to min. (9) prefers < 5 cm sapropelium (10)	opt. 0.01 mg/l max. 1 mg/l (5) mean 0.46 ± 0.02 mg/l (10)	N-number 2 (8)	oligotrophic (7/11) lightnr. 7 (8) mod. eutrophic to oligotrophic (9)
Characeae (spec. div.)	sand without sapropelium (1)	< 20 µg/l total P (4)		clear (1,2), unpolluted (2), oligtrophic (3)

(1): SEGAL & GROENHART 1967
(2): SEGAL 1966
(3): MELZER 1976
(4): FORSBERG 1964
(5): NOBEL 1980
(6): MEIJER & DE WIT 1955
(7): ARNOLDS & VAN DER MEIJDEN 1976
(8): ELLENBERG 1979
(N-number from 1 = very poor up to 9 = very rich)
(lightnumber from 1 = deep shadow up to 9 = full light)
(9): HASLAM et al. 1975
(10): DE LANGE 1972
(11): OBERDORFER 1962

tation is subsequently characterised by elements of the Caricion davallianae. The Bryophyte succession in zone B is very similar to the successions described for quaking mires in peat digging areas (SEGAL 1966). The presence of both *Carex vesicaria* and taxa indicating nutrient-poor conditions (*Amphitrema flavum, Carex limosa, Meesia triquetra*), combined with the recurring influx of minerals resulting from the fires that swept the area, point to a fluctuating nutrient input, described by VAN WIRDUM (1979) as "poikilotrophic". The gradual lowering of the nutrient status of the site finally resulted in the dominance of *Sphagna* with *Carex limosa* and oligotraphentous Thecamoeba.

Fossil spores of representatives of the Zygnemataceae in the Usselo section could be identified to genus level. Within this group of filamentous algae hardly any appreciable differences in ecology are known, but the curves of the different spore types evidently show that there are differences in habitat preference: spores of *Debarya* and also foveolate/fossulate *Spirogyra* spores occurred in minerogenic sediment, whereas *Mougeotia* spores were found at some levels in the organogenic deposits. *Zygnema* type shows a maximum at the transition of a vegetation type dominated by *Phragmites* and *Equisetum* towards a *Menyanthes* phase.

The characteristic Lateglacial A.P./N.A.P. fluctuations, in combination with the data of the ^{14}C samples taken in 1955, allow a rough estimation of the duration of the successive phases from the start of the Bølling period on. The results of this estimation are:

(sub)zones	duration	predominant vegetation
C	c. 50 years	Sphagnum fen
B3	c. 300 years	
B2	c. 100 years	sedge fen
B1	c. 150 years	
A5	c. 50 years	transition phase with *Menyanthes*
A4	c. 150 years	reed swamp
A3	c. 650 years	aquatic macrophytes and helophytes; Characeae
A1 + A2	uncertain, because of lack of sufficient organic sediment, but probably not longer than 500 years	green and blue-green algae

Comparing recent similar hydroseres in sandy areas in N.W. Europe with the Usselo sequence, the long duration of the aquatic pioneer phase, in relation to the relatively small dimensions of the pool, is striking. An explanation might be found in the above mentioned character of the surrounding barren landscape in the Lateglacial period, viz. its poverty in nitrogen and humus. The influx of exogenous nutrients would have been much slower than in comparable recent situations. In other words, the accelerating influence of the eutrophicating surroundings on the succession rate of the hydrosere may be much greater nowadays. A similar explanation might be given for the long duration of the sedge fen phase as compared with recent data. The lack of exogenous nutrients will have hampered the organic production that finally results in ombrogenic conditions.

A conventional interpretation of the fluctuations of the arboreal/non-arboreal pollen ratio in the Usselo I section would imply relatively cold conditions

Fig. 1: Diagram of selected indicative macro- and microfossils of part of the Usselo section.


USSELO I
SCHEMATIC SUMMARY DIAGRAM FOR Σ-POLLEN TAXA
DEPTH IN CM +N.A.P.
LITHOLOGY
SAMPLES
ZONES LOCAL VEGETATION
ORGANIC/INORGANIC RATIO
BOTRYOCOCCUS
PEDIASTRUM
POACEAE
EQUISETUM
MENYANTHES TRIFOLIATA seeds
CAREX ROSTRATA
SPHAGNUM SPEC.
Charcoal
II
Ic
Ib
Ia
BETULA
PINUS
JUNIPERUS/HIPPOPHAE
HERBS
PEAT
PEATY SAND
GYTTJA
IRON FIBRES
LOAMY SAND
SAND (FINE)
SAND (COARSE)
SCALE FOR MICROFOSSIL CURVES
SCALE FOR MACROFOSSIL CURVES
(unless otherwise indicated)
MICROFOSSILS
MACROFOSSILS
SCALE FOR MOSSES
APPR. AGE IN YEARS B.P.
11000
11800
12000
12400

for the zones Ia and Ic. One of the conclusions of the present study is that the observed strictly local succession can be explained without any cold climatic phase in the period concerned. The trophic situation, and the ground water level (influenced by deposition of sand and of organic mud) were apparently the important ecto- and endogenic factors influencing the vegetation succession. G. R. Coope and miss B. Wilkinson (Birmingham) respectively studied the remains of Coleoptera and Trichoptera larval remains from the Usselo site. Their preliminary conclusions concerning the aquatic phase can be summarized as follows: Even in the lower part of the section the site was not in any way arctic, there are indications that average July temperatures were at least 15 °C. The ecology of the site at the base of the section is of a very barren landscape with damp sand and small pools of standing water. Above that there is a gradual increase in faunal diversity indicating a progressive development of the productivity of the area and a gradual eutrophication of the sampling site rather than an improvement of the climate. These conclusions concur very well with the interpretation of the vegetational succession.

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