

## PALYNOLOGICAL AND PLANT MACROFOSSIL DATA ON LATE PLEISTOCENE SHORT-TERM CLIMATIC OSCILLATIONS IN NORTH-EASTERN HUNGARY

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**ABSTRACT.** Study of pollen, fossilized Bryophyta and charcoal in the Pleistocene part of a 4.30 m core from Nagy-Mohos lake, NE Hungary, has provided a palaeoenvironmental record for the period between c. 8800–22000 years BP. Our investigation attempted to detect small scale climatic fluctuations and to reconstruct the succession of the local peat-forming communities.

During the Upper Pleniglacial the basin was surrounded by coniferous forest-steppe vegetation. Based on the palynological record, two phases of climatic improvement can be distinguished between 20000–22000 and 16000–17000 BP when the percentage of arboreal taxa increased. These data coincide with the malacological and macrocharcoal records from the Hungarian loess profiles. Forest fires were an important factor in the evolution of both terrestrial and aquatic vegetation. An increased frequency of fires during the course of the Late Glacial/Postglacial transition led to the burning of the mire surface and a subsequent slump covered the pleistocene layers with c. 1 m thick layer of silty clay.

Lithostratigraphic analysis of the sediment shows alternating accumulation of sedge peat, moss peat and organic lake sediment. Major trends in the hydrosere development were the same as those typical for recent boreal mires, although gradual change towards more oligotrophic and acidic conditions is shown to have been interrupted many times in the course of the development of Nagy-Mohos lake.

**KEY WORDS:** pollen/macrofossils, Late Pleistocene, Hungary

### INTRODUCTION

This paper presents the results of pollen, fossil Bryophyta and macroscopic charcoal analyses from a basin mire site located in NE-Hungary (Fig. 1).

Climate is often used to account for stratigraphic and palaeoecological changes in peat-lands. The climate signals can be difficult to recognize because of changes in the peat record brought about by autogenic succession or by any of a variety of local factors that might affect the water table and could cause comparable changes to the record (Vardy 1997). These difficulties have generated some debate for a long time (see Frenzel 1983, Janssen 1973, Middeldorp 1984). Generally, it is hard to distinguish internally driven successional changes from those caused by extrinsic factors, such as climate, without an independent climatic record for comparison. Examples of such records which have to be taken into account are the palaeoclimatic model simulations (Berger 1978, Kutzbach & Guetter 1986, Kutzbach *et al.* 1993, 1998), the  $\delta^{18}\text{O}$  records of ice cores (Imbrie *et al.* 1984, Dansgaard *et al.* 1993) and palaeoclimatic reconstruction based on palaeontological databases (Huntley 1993, Bond *et al.* 1993; Guiot *et al.* 1993, Peyron *et al.* 1998, Atkinson 1987, Sümegi 1989, Kordos & Ringer 1991).

Direct comparison with radiocarbon dated pollen diagrams from the region under investigation has priority, however. Unfortunately, we are short of radiocarbon

dated Late Pleistocene pollen diagrams from the Carpathian Basin and the adjacent Precarpathian region (Willis *et al.* 1995, 1997, Borsy *et al.* 1991, Jankovská 1980, Rybníček 1983) and none of them provides data concerning the key period of the last glaciation, that is the LGM (last glacial maximum).

This paper is intended as a first step towards a more detailed understanding of the palaeoenvironmental changes that have taken place in the final phase of the last glaciation. Nagy-Mohos lake is a unique area in NE Hungary, where peat deposits extending back c. 22000 years BP are preserved giving us an opportunity for palaeoecological investigation.

The principal aims of this study are the reconstruction of former local vegetation and environmental conditions, delineation of trends in hydrosere development and its relation to the observed changes in the terrestrial vegetation. Special interest is paid to the triggering mechanism of mire vegetation rearrangement.

### SITE DESCRIPTION

The study site is located mountainous region of north-eastern Hungary at an altitude of 294 m asl. This area is characterized by gently rolling hills that are geo-



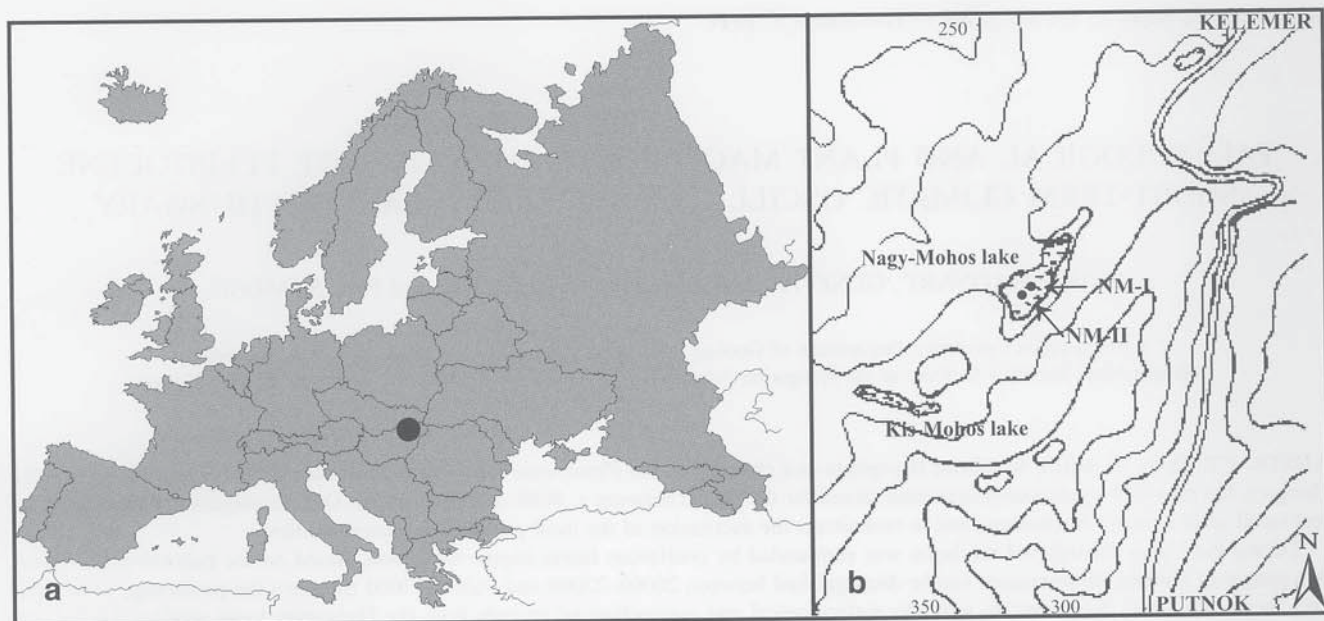


Fig. 1. Site location maps. (a) Location of Nagy-Mohos Peat Bog in Europe (b) Position of the coring site within the Kelemér region, NE-Hungary and location of cores NM-I and NM-II

logically complex and rarely exceed 400 m in elevation. The basin and the north-western slopes are underlain by Tertiary clay and clay-marl, while to the south and east the deposit is composed of Tertiary glauco-arenite and sand. An upper Tertiary deposit of coarse, unconsolidated sandy-gravel consisting of quartzitic cobbles covers much of the bedrock above 300 m. The accumulation of ground water in the upper horizon of the underlying impermeable clay has played an important role in the formation of the peat basin, resulting in frequent deposits of surficial sandy gravel over the waterlogged, and hence extremely plastic, clay horizon.

The area falls into the continental temperate climatic zone. The annual rainfall is between 650–700 mm. The mean annual temperature is 9.5°C (July: 20°C; January: -3°C, see Kakas 1960). The microclimate of the basin is somewhat cooler, the mean temperature deviation between the bog surface and the summit is 2.5–3°C, while the relative humidity is 25–30% higher above the mire surface (Gyulai *et al.* 1988).

Slopes surrounding the basin are covered with *Quercus-Carpinetum* forest. The recent vegetation of the mire is composed of *Scirpo-Phragmitetum sphagnetosum* as the dominant community, *Carici cinereaesphagnetum* prevails in the marginal zone, and *Eriophoro-Sphagnetum* patches are restricted to only two localities (Czente 1985).

## METHODOLOGY

Peat cores were retrieved using a 5 cm diameter Russian corer and a 5 cm diameter modified Livingstone piston corer (Aaby &

Diegerfeld 1986, Wright 1967). The position of the boreholes is shown on Figure 1. Borehole NM-I was taken from the deepest part of the basin and was used for pollen analysis and radiocarbon examinations. Borehole NM-II is situated south of borehole NM-I, closer to the marginal fen zone of the recent bog. This latter sequence was used for the Bryophyta and charcoal analysis. The length of section sampled from the two cores was 3 m.

From the Pleistocene layers four bulk samples were submitted for radiocarbon dating at the Nuclear Research Centre of the Hungarian Academy of Sciences, Debrecen, Hungary (Hertelendi *et al.* 1989).

The detailed description of the peat cores follows the system described by Troels-Smith (1952) and the stratigraphic description of the profiles is shown in Table 1.

Samples for pollen analysis were collected using a 1 cm<sup>3</sup> volumetric subsampler mostly at 4–8 cm intervals. Pollen samples were prepared following the method described by Berglund and Ralska-Jasiewiczowa (1971) with exotic pollen (Stockmarr 1971) added to each sample in order to determine the concentration of pollen and charcoal abundance using Clark's point count method (1982).

Pollen and spores were identified with the aid of keys (Moore *et al.* 1991, Reille 1992). A minimum of 300 terrestrial pollen grains per sample were counted. Since the aim of our investigation was the reconstruction of the mire-forming vegetation and its relation to changes in the terrestrial vegetation pollen percentages were calculated in two different ways. For the description of changes in the terrestrial vegetation, the percentage calculation is based on the sum of all terrestrial taxa including Poaceae (Fig. 4), although this taxon is considered to have had its centre of occurrence on the mire surface (pollen grains of *Glyceria* and *Molinia* types were identified as occurring in large quantity). On the other hand, the pollen curve of the Poaceae shows parallel changes with that of *Artemisia* and other characteristic steppe species (described later in this paper) suggesting that at least part of the Poaceae pollen derived from the terrestrial vegetation. To avoid overrepresentation of arboreal species in the terrestrial diagram, we decided to include the Poaceae in both percentage calculations. The second diagram (Fig. 2) depicts the curves of the peat-forming wa-



Table 1. Core recovery data and lithological notes

Depth range sampled (cm)	Troels-Smith symbols	Comments
Profile NM-I		
250–318	Ag2Lf1As1	Light grey silty clay
318–320	Sh4	Dy
	hum 4, nig 4, elas 1	
320–350	Ld2Tb1Th1	Dy mixed with <i>Sphagnum-Carex</i> peat
	hum 3, nig 3, elas 2	
350–360	Th2Ld1Dh1	Charred <i>Carex</i> peat
	hum 4, nig 4, elas 1	
360–372	Tb(Spha)3Dg1	Dark brown, humified <i>Sphagnum-Carex</i> peat
	hum 4, nig 4, elas 2	
372–399	Tb(Spha)2Dg1Th1	Brown <i>Sphagnum-Carex</i> peat with dryness increasing upwards
	hum 3, nig 3, elas 4	
399–410	Ld2Tb1Dg1	Dark brown Hypnaceae- <i>Carex</i> peat mixed with dy
	hum 3, nig 3, elas 2	
410–412	Sh4	Charred, highly compressed and decomposed organic debris
	hum 4, nig 4, elas 1	
412–422	Tb(hyp)2Th1Dg1	Dark brown Hypnaceae-sedge peat mixed with <i>Pinus cembra</i> twigs
	hum 2, nig 3, elas 2	
422–426	Dg3Sh1	Charred <i>Pinus cembra</i> twigs, branches and nutlets mixed with dark brown Hypnaceae peat
	hum 3, nig 3, elas 1	
426–431.5	Sh4	Blackish-brown, strongly decomposed organic silt
	hum 4, nig 4, elas 1	
431.5–450	Gg2As1Ag1	Light grey silty clay mixed with gravels
Profile NM-II		
250–318	Ag2Lf1As1	Light grey silty clay
318–320	Sh4	Dy
	hum 4, nig 4, elas 1	
320–341	Ts2Th2Ld1	Blackish-brown <i>Sphagnum-Carex</i> peat
	hum 4, nig 4, elas 3	
341–347	Tb(hyp)1Ld1Th1	Dark brown Hypnaceae peat with dy
	hum 3, nig 3, elas 2	
347–390	Th2Dh2Tb1	Blackish-brown, highly compressed, humified <i>Carex</i> peat with a burnt layer between 365 and 366 cm
	hum 3, nig 3, elas 3	
390–405	Ts2Dg1Th1	Dark brown <i>Sphagnum-Carex</i> peat
	hum 3, nig 3, elas 1	
405–415	Tb(hyp)2Ld1Dg1	Blackish-brown Hypnaceae- <i>Carex</i> peat mixed with dy
	hum 3, nig 3, elas 2	
415–416	As 4	Light grey silty clay
416–425	Tb(hyp)2Th1Dg1	Dark brown Hypnaceae-sedge peat mixed with <i>Pinus cembra</i> twigs
	hum 3, nig 3, elas 2	
425–427	Dg3Sh1	Charred <i>Pinus cembra</i> twigs, branches and nutlets mixed with dark brown Hypnaceae peat
	hum 3, nig 3, elas 1	
427–435	Sh4	Blackish-brown organic silt
	hum 4, nig 4, elas 1	
435–450	Gg2As1Ag1	Light grey sandy gravel mixed with clay

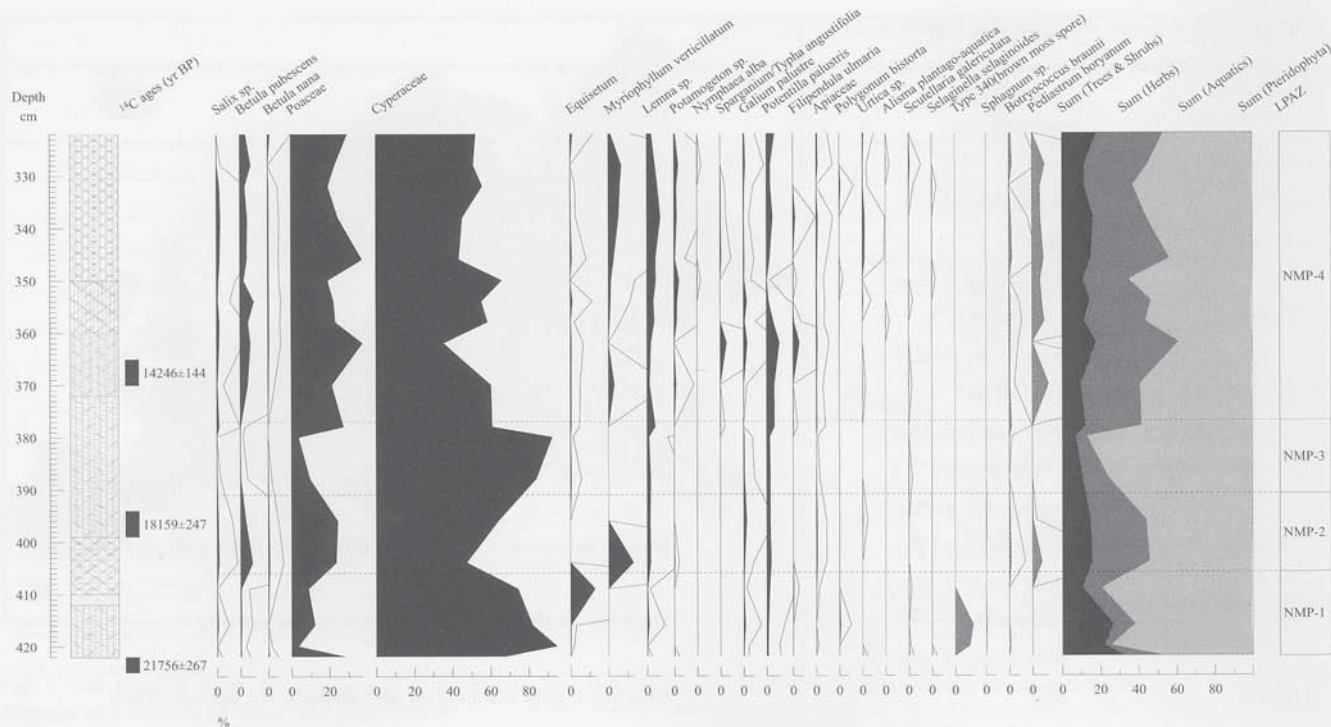


Fig. 2. Percentage pollen diagram of selected peat-forming taxa

ter plants. The percentage calculation is based on the sum of their pollen grains and Pteridophyta spores. The percentages of Bryophyta spores and algae were determined by relating their absolute values to this sum.

The pollen diagrams were prepared using PSIMPOLL Ver. 2.25 (Bennett 1992). Zonation of both the terrestrial and aquatic diagrams was performed using statistical procedures in which the results were subjected to optimal splitting by information content (Birks & Gordon 1985). They were then used to guide decisions as to the number and position of the pollen assemblage zone (LPAZ) boundaries.

For the fossil Bryophyta analysis, half of borehole NM-II was cut into 2–3 cm sections. 1 cm<sup>3</sup> subsamples from each interval were sieved through a 250 µm mesh. Estimation of species abundance followed the method described by Dickson (1986), while the overall moss abundance of each sample was determined using a ten-point scale. Zonation of the diagram was performed by visual inspection.

For the identification of charred wood fragments, both a binocular microscope and scanning electron microscope were used. Identification of wood fragments was made with the aid of keys (Greguss 1972, Schweingruber 1978) and modern reference specimens.

## RESULTS

### RADIOCARBON CHRONOLOGY AND RATES OF PEAT ACCUMULATION

The results of the radiocarbon measurements are shown in Table 2. Unfortunately, measurements of the uppermost sample have not yet been performed, so we could gain only an extrapolated age for the top sample

Table 2. Radiocarbon dated sediment samples

Mean depth (cm)	Depth range (cm)	Age	Standard	$\delta^{13}\text{C}$ (PDB) deviation	Dated material
		( <sup>14</sup> C yr BP)			
424.0	422–426	21756	267	-27.22	wood
396.5	394–399	18159	247	-25.56	peat
367.5	365–370	14246	144	-27.22	peat

(c. 8800 BP). Based on the <sup>14</sup>C data, a 110 cm layer of peat represents 13000 years. Assuming continuous accretion this would lead to an extraordinarily low rate of peat accumulation (0.076 and 0.074 mm yr<sup>-1</sup>). On the other hand, accumulation rates between dated samples are almost equal suggesting very low, but fairly even accretion between 14246 and 21756 years BP.

These dates make us wonder if there are long periods without appreciable peat accumulation or we are faced with an ecosystem characterized by very low peat forming ability.

A stratigraphic survey of the peat profiles revealed three distinct layers of desiccation:

412–413 cm – observed in both profiles, micro- and macrocharcoals are present

392–394 cm – observed in NM-II

360–362 cm – observed in both profiles, microcharcoal present

It is very likely that these horizons designate periods



with reduced peat accumulation, with the rate of decay probably even exceeding the rate of addition of dry matter, resulting in a net loss, causing reduction in the peat thickness.

Humification values (Troels-Smith 1952) are very high throughout the sequence suggesting, a low peat-forming ability of the former plant assemblages, probably as a result of the prevailing environmental conditions at that time. Whatever the background process acting upon the rate of peat formation, however, this 110 cm long profile provides us with a sequence of palaeoecological information, the interpretation of which is limited.

#### HYDROSERAL DEVELOPMENT OF THE PEAT-FORMING PLANT ASSEMBLAGES

The results of the palynological and bryological examinations appear in Figures 2 and 3. Four main phases of hydroseral development were distinguished on the basis of observed changes in the pollen diagrams with additional subdivisions according to the Bryophyta local assemblage zones (LBAZ).

Zones NMP-1 (430–406 cm), NMB-1 (430–409 cm)

Following its formation, the basin was invaded by brown moss communities dominated by *Calliergon richardsonii*, *Warnstorfia sarmentosa* and *Scorpidium scorpioides*. This plant assemblage has a very restricted distribution nowadays in the higher mountains of Europe, in Scandinavia and in the boreal zone of NE Europe. In the

pollen diagram Cyperaceae reaches extremely high percentages (above 70%) together with high abundance of brown moss spores. Unfortunately, we couldn't identify the moss spores at species level. However, most of them correspond to spore type 340 in Van Geel (1981) who found manifest maxima correlated with the transition phase of pool to fen in the Netherlands. In our case the abundance of these spores coincides with dominant macroremains of *Warnstorfia sarmentosa* and *Calliergon richardsonii* providing evidence of a terrestrial phase following the formation of the basin. Rainwater gradually accumulated on the ground providing a suitable habitat for the colonization of these species.

There were no pollen grains of aquatic species found in this part of the sequence indicating the absence of open water. Frequent macroremains of *Pinus cembra*, branch, trunk, twig and seed fragments, point to the establishment of Arolla pine stands on the mire surface. In the understorey *Betula nana* and *Betula pubescens* occurred, but their presence is confirmed only by pollen grains. In the herb layer *Potentilla palustris*, *Potentilla erecta* and *Galium palustre* prevailed. The scattered occurrence of *Polygonum bistorta* and *Selaginella selaginoides* point to the presence of wet arctic meadows in the basin. The character of the mire-forming vegetation was minerotrophic, strongly alkaline and well supplied with nutrients.

At the end of this phase the pollen diagram shows characteristic changes. An increased charcoal concentration coupled with a peak in the curves of *Equisetum* sp.,

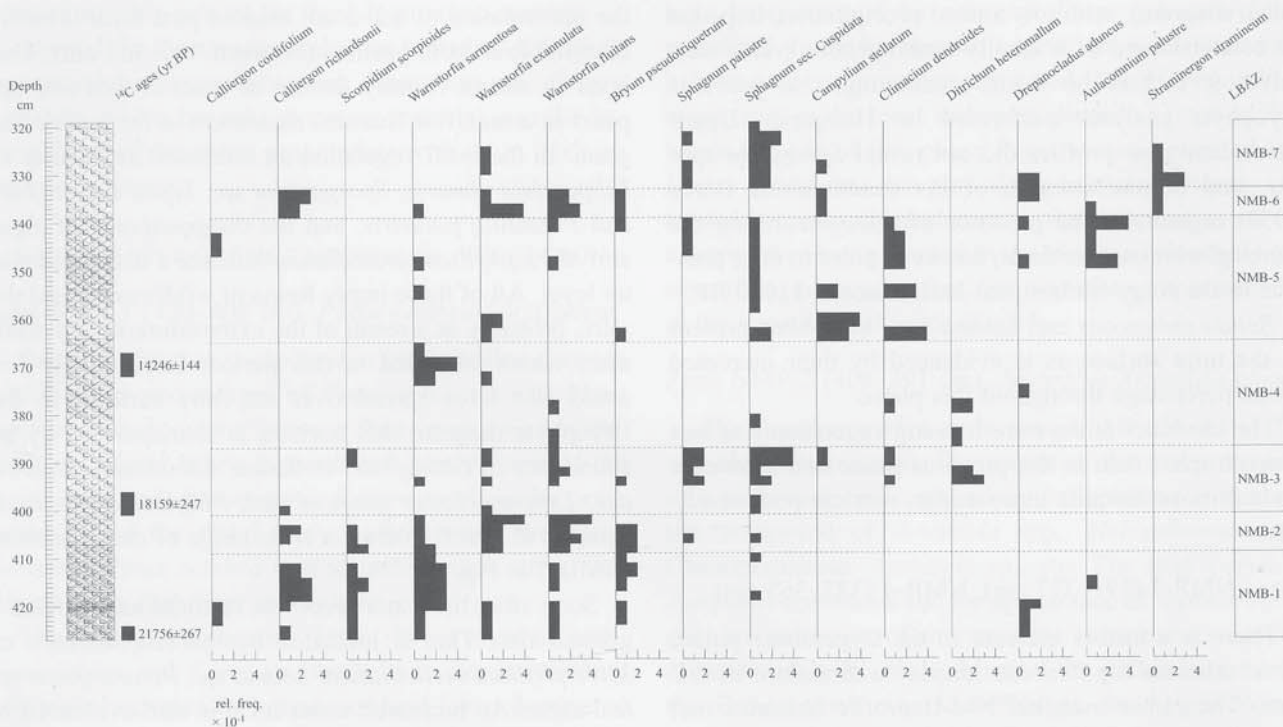


Fig. 3. Pleistocene Bryophyta diagram of Nagy-Mohos lake (selected taxa)



*Filipendula ulmaria* and a decrease of pine in the dry-land vegetation (described later) imply increased fire activity and desiccation of the mire surface. The number of charred wood fragments in the sediment also increased in this horizon.

Zones NMP-2 (406–391 cm), NMB-2 (409–401 cm) and NMB-3 (401–387 cm)

Following the burning of the canopy layer the vegetation development of the mire proceeded to raised-bog pool characterized by an abundance of Poaceae (presumably *Glyceria* sp. and *Molinia* sp. were the major components). Macroscopic remains of *Warnstorfia fluitans*, *W. exannulata* and *Sphagnum* cf. *cuspidata* indicate shallow-water conditions with the permanent water table close to the margin of the basin, while the high percentage of *Myriophyllum verticillatum*, *Pediastrum boryanum* and the uninterrupted presence of *Botryococcus braunii*, *Potamogeton* sp., *Stratiotes* sp. and *Lemna* sp. also suggest shallow open water conditions in the deepest part of the peat-basin. Towards the close of this phase Cyperaceae, *Sphagnum* cf. *cuspidata* and *Sphagnum palustre* became more abundant, *Warnstorfia fluitans* disappeared and by phase NMB-3 fen species were much less in evidence. All these changes reflect a succession from raised-bog pool to transitional bog. The composition of both the pollen spectra and the sediment during this phase might be taken as reflecting a move to less nutrient-rich oligo-mesotrophic conditions, but even if the geological setting of the basin provided a suitable environment for raised bog formation, the extreme continental climate of the area (as reflected in the terrestrial pollen diagram), with low annual precipitation, impeded the establishment of a wholly ombrogenous (rainwater-fed) bog. It may be worth mentioning, that previous Bryophyta analyses performed on Hungarian Upper Pleistocene peat profiles did not reveal *Sphagnum* species, and on the strength of his examinations Boros (1952) argued for the presence of *Sphagna* during the Würm glaciation. Our finds, however, point to their presence in the Nagy-Mohos peat-basin since c. 21000 BP.

*Betula pubescens* and *B. nana* may have been present on the mire surface as is evidenced by their increased pollen percentage throughout this phase.

The character of the mire-forming vegetation was less minerotrophic than in the previous phase and showed a gradual move towards more acidic, nutrient-poor conditions.

Zones NMP-3 (391–377 cm), NMB-4 (387–365 cm)

There is a further increase in the Cyperaceae pollen curve, whereas the Poaceae display a minimum in this zone. The rather marginal NM-II profile indicates that development of the *Sphagnum* carpet came to an end at the beginning of this phase. The number of moss leaves

decreased, only a characterless assemblage of *Ditrichum heteromallum*, *Climacium dendroides* and *Warnstorfia sarmentosa* can be reconstructed. This part of the mire was most probably occupied by Magnocaricion communities favoured by only some moss species adapted to drier substrates, e.g. *Climacium dendroides*, *Plagiomnium ellipticum* and *Ditrichum heteromallum*. Peat samples from this zone were dominated by *Carex* leaves and utricles of *C. rostrata* and *C. nigra* were identified in profile NM-II, while, in addition to the abundance of sedge remains, *Sphagnum* leaves were encountered in NM-I continually. The subjective palaeoenvironmental inference is of drier conditions prevailing on the mire surface that must have led to the transition of the marginal areas into rich fen vegetation, while the *Carex-Sphagnum* carpet could have survived only in the wetter central areas of the mire. The rising curve of *Pinus* sp. in the terrestrial pollen diagram (Fig. 4) suggests its simultaneous spread in the valley and probably in the marginal areas of the mire. Macroscopic remains, however, were not found in these layers.

Zones NMP-4 (377–320 cm), NMB-5 (365–339 cm), NMB-6 (339–333 cm), NMB-7 (333–320 cm)

At the beginning of this zone the appearance of *Myriophyllum verticillatum*, *Potamogeton* sp., *Stratiotes* sp., and decrease of Cyperaceae point to the presence of shallow open water in the centre of the basin, for which further evidence is provided by the lithological changes in profile NM-I, with the introduction of strongly humified fine-grained detritus gyttja (dy).

A subsequent change in the lithostratigraphy, that is the intercalation of a 2–3 cm charred peat layer is easily discernible in both profiles (between 360–362 cm). This layer is almost entirely devoid of macrofossils and appears as a manifest charcoal maximum in the pollen diagram. In the local vegetation an increased abundance of *Filipendula ulmaria*, *Sparganium* sp., *Typha angustifolia* and *Potentilla palustris*, and the disappearance of algae and *Myriophyllum verticillatum* indicate a decreased water level. All of these imply frequent wildfires around the mire, probably as a result of the extraordinarily dry summers which prevailed in this period. Occasionally fire could also have spread over the mire surface. In the Bryophyta diagram this horizon is characterized by an abundance of *Campylium stellatum*, *Climacium dendroides*, *Drepanocladus aduncus* and *Plagiomnium ellipticum*, all of which tolerate a wide range of damp habitats (NMB-5 in Fig. 4).

Soon after, the water level was restored and showed a gradual rise. This is indicated by the reappearance of *Myriophyllum verticillatum*, *Lemna* sp., *Potamogeton* sp. and algae. An increased water level is also evidenced in the sequence of NM-II, where the changes in the Bryophyta species suggest the formation of a raised-bog pool



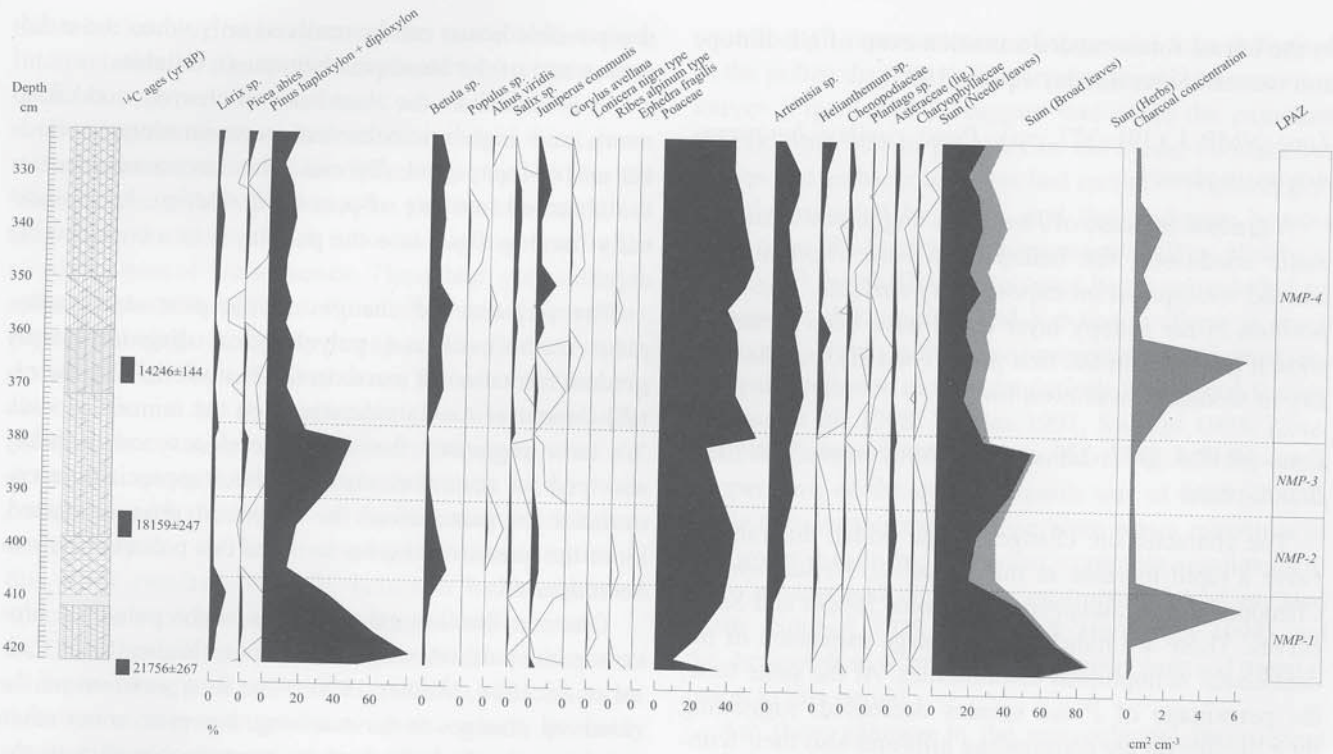


Fig. 4. Percentage pollen diagram of selected terrestrial taxa

in zone NMB-6. A similar hydrosereal succession from raised-bog pool to transitional *Sphagnum* bog had taken place earlier. (It was discernible in the second phase (NM-2) of the mire development). The sporadic occurrence of *Selaginella selaginoides* and *Polygonum bistorta*, however, suggest that in spite of the gradual climatic improvement, the microclimate of the basin ensured suitable habitat for these high-arctic species.

Around the Pleistocene/Holocene boundary the development of the *Carex-Sphagnum* carpet was cut off by a landslide, which brought inorganic material into the basin and buried the entire peat surface with c. 1 m thick inorganic sediment.

#### DEVELOPMENT OF THE TERRESTRIAL VEGETATION

##### Zone NMP-1 (430–406 cm), *Pinus cembra-Larix* phase

*Pinus haploxylon + diploxylon* in the pollen diagram depict added percentages of *Pinus sylvestris* and *Pinus cembra*. Distinguishing between the two species was difficult in several cases, because bad preservation of the grains obscured characteristic features such as the ornamentation of the distal body wall between the sacchi. However, *Pinus cembra* was identified more often, and was possibly dominant in this zone.

The high percentage of *Pinus* (80%) together with *Picea abies* and *Larix* sp. imply that the surrounding hills were occupied by boreal parkland forest dominated by *Pinus cembra* and *Pinus sylvestris* in the canopy layer and with a sporadic admixture of *Larix* sp. and probably

*Picea abies*. Charred *Pinus cembra* wood was frequently encountered in this phase (see Fig. 4) indicating its presence on the mire surface. In the understorey, characteristic species of northern boreal *Pinus-Larix* forest (Nikolov & Helmisaari 1992), such as *Lonicera* sp., *Ribes* sp. and probably *Betula nana* occurred.

The drier habitats of the neighbouring slopes could have been covered by scattered *Pinus sylvestris-Larix* woodland. In the herbaceous vegetation, cold continental heliophilous communities appeared, but played only a minor role in the local and more distant vegetation. Towards the end of this phase *Pinus* species retreated and *Larix* spread into that part of the habitat previously occupied by pines. This change in the composition of the canopy layer was preceded by an increased charcoal concentration, suggesting that fire played an important role in the vegetation changes (Fig. 4).

##### Zone NMP-2 (406–391 cm), *Juniperus-Artemisia* phase

The abundance of trees decreased (AP= 24–30%), *Picea abies* disappeared. The retreat of the forest resulted in a park landscape covered by heliophilous communities composed of *Artemisia* spp., *Helianthemum* sp., *Chenopodiaceae*, *Anthemis* sp., etc. The high curve of *Juniperus communis* and the appearance of *Ephedra fragilis* are indicative of an extremely continental subarctic climate within the basin. Most of the pollen comprising the *Betula* curve was identified as *Betula pubescens*. This species most probably formed sparse stands with *Larix* sp. and *Pinus sylvestris* similar to those prevailing



in the boreal forest-tundra transition zone of NE Europe and western Siberia today (Sirois 1992).

Zone NMP-3 (391–377 cm), *Pinus cembra*-*Juniperus*-*Artemisia* phase

A gradual increase of *Pinus* spp. suggests warmer climatic conditions, but heliophilous herb vegetation remained widespread on exposed, dry surfaces. The composition of the canopy layer could have been similar to what it had been in the first phase (NM-II), but the density of woodland was even lower.

Zone NMP-4 (377–320 cm), *Helianthemum*-*Artemisia*-*Betula* phase

The characteristic changes in the pollen diagram involve a rapid increase in the *Artemisia*, *Helianthemum*, *Chenopodiaceae*, *Juniperus communis*, *Betula* and *Salix* curves. These are indicative of a large expansion of the continental heliophilous communities. At the same time, the percentage of *Pinus* species decreased, suggesting their decline on the surrounding hills and also their withdrawal from the mire surface. The landscape became more open. Sparse *Betula* woodland (most probably *B. pubescens* and *B. pendula*) and *Larix* occurred on the moister surfaces together with *Pinus cembra*. The characteristic short-term fluctuations of the late-glacial climate are discernible in the pollen diagram, but only in the form of percentage fluctuations in the vegetation components.

## DISCUSSION

### RELATIONSHIP BETWEEN THE HYDROSERAL DEVELOPMENT AND CHANGES IN THE TERRESTRIAL VEGETATION

From the plant macrofossil and pollen composition we have reconstructed a boreal wooded rich-fen vegetation at the sampling sites in the basal layers. Arolla pine fens are widespread in Western Siberia today, and are characterized by a well-developed ground layer of moisture-loving herbs and Hypnaceae mosses (Botch & Masing 1983, Eurola *et al.* 1984). In this vegetation the biomass is considerable, but in general, the rate of decay almost compensates the production of organic matter. Therefore, Arolla pine fens are usually underlain by thin, highly decomposed peat of a thickness that rarely exceeds 40–50 cm. These recent observations are well in agreement with the surprisingly low peat accumulation rate calculated for this period, approximately 21700–19500 years BP, but conceivably there is a time lag between the <sup>14</sup>C dated basal macroscopic wood horizon and the overlying peat, as is the case in several palustral sequences (e.g. Dionne 1979). However, the question of

this possible hiatus can be resolved only when the radiocarbon age of the basal peat becomes available.

As is clear from the abundance of charred wood fragments and high microcharcoal concentrations towards the end of this period, fire must also have accounted for the observed low rate of peat accumulation, by periodically burning down into the peat layer to a considerable depth.

The sequence of changes in the peat stratigraphy, plant macrofossil and palynological diagrams imply gradual formation of marsh in the basin following the establishment of Arolla pine stands on the mineral ground. We have suggested that *Pinus cembra* wood probably survived for several centuries without appreciable accumulation of peat before the paludinal process started, since the question, of what initiated this process needs to be addressed.

One can find several examples of the paludinal process in the palaeoecological literature (Weber 1908, Zoltai *et al.* 1988, Walker 1970). The interpretation of the observed changes is far-reaching, however, most often involving the formation of an impermeable skin to the peat surface as a result of burning. Impeded drainage allows rain- and run-off water to accumulate on the surface, while the surface deposit of ash gives rise to temporarily increased nutrient levels that favour the establishment of Hypnaceae mosses. This seems to be a reasonable interpretation of the observed changes in the Nagy-Mohos lake, but other factors may have to be taken into account too. These are the relevant ground water table, micro- and macroclimate, changes in the terrestrial vegetation and possible changes in the geomorphology of the basin.

Tertiary clay formed an impermeable layer at the bottom of the peat basin, so ancient *Pinus cembra* stands rooting on the mineral soil were directly affected by the ground water. Changes in the ground water table could have had detrimental effects on the Arolla pine, a tree which grows well in wet sites, but poorly on undrained soil (Botch & Masing 1983, Nikolov & Helmisaari 1992).

It is well-known, that a varying rate of peat growth causes varying pollen concentrations (Aaby & Tauber 1975, Middeldorp 1982). This is justifiable for the components of the terrestrial vegetation if we assume a constant pollen influx, but does not hold for the local pollen rain. For instance, changes in the local peat-forming vegetation may lead to enormous changes in the local pollen production (Van Geel 1978). The time period embraced by the peat profiles NM-I and NM-II, however, has revealed severe climatic fluctuations that affected both the terrestrial and aquatic ecosystems in several unforeseen ways (Peterson 1979). It follows, that in such an unsettled environment, neither the assumption of a constant terrestrial pollen influx, nor the permanence of



the mire forming vegetation can be guaranteed making interpretation of the pollen concentration curves very difficult.

Bearing the above-stated uncertainties in mind, however, we can suppose that the following may hold for the basal layers (NMP-I) where the pollen concentrations (Fig. 5) were two or three times as high as than in the overlying part of the sequence. These high concentration values are attributable to *Pinus* spp. and Cyperaceae, both taxa being notoriously strong pollen producers (Andersen 1973). Their dominance on the mire surface was also confirmed by their abundant macro-remains. The pollen concentration of undoubtedly terrestrial taxa, e.g. *Artemisia* sp. and *Picea abies*, however, is very low compared with other parts of the sequence, so it seems more likely that the high overall pollen concentration of this phase resulted from the luxuriant local vegetation which was predominated by strong pollen producers.

The subsequent moister phase, with the development of a raised-bog pool environment implies reduced decay, thereby raising accumulation rates which probably reached their maximum when the *Sphagnum* carpet became established on the mire surface.

Although representation of terrestrial taxa is limited in the pollen diagram, both percentage and concentration curves (Figs 4 and 5) suggest that while the paludinal process was still in progress in the basin, heliophilous shrubs and herbaceous plants had spread over places previously occupied by pine, and the landscape became more open. Radiocarbon measurements tell us, that by c. 18400 BP the shallow-water pool had been invaded by *Sphagnum* cf. *cuspidata* and *S. palustre*. There is much evidence from palaeoenvironmental reconstructions and palaeoclimate model simulations for Central Europe (Peyron *et al.* 1998, Kordos 1991, Sümegi 1998, Kutzbach & Guetter 1986) that around 18000 BP the mean temperature of the coldest month was at least  $-20^{\circ}\text{C}$ , while the summer mean temperature was a minimum of  $5^{\circ}\text{C}$  lower than today. Moreover, computer-simulated climate models and climate reconstruction based on land snails (Sümegi 1989, Sümegi & Hertelendi 1998) and the Arvicolidae (Kordos 1991) suggest lowered precipitation in this period.

Are these changes in the macroclimate inconsistent with the marsh formation, taking place in the basin at the same time? At first sight there is an apparent contradic-

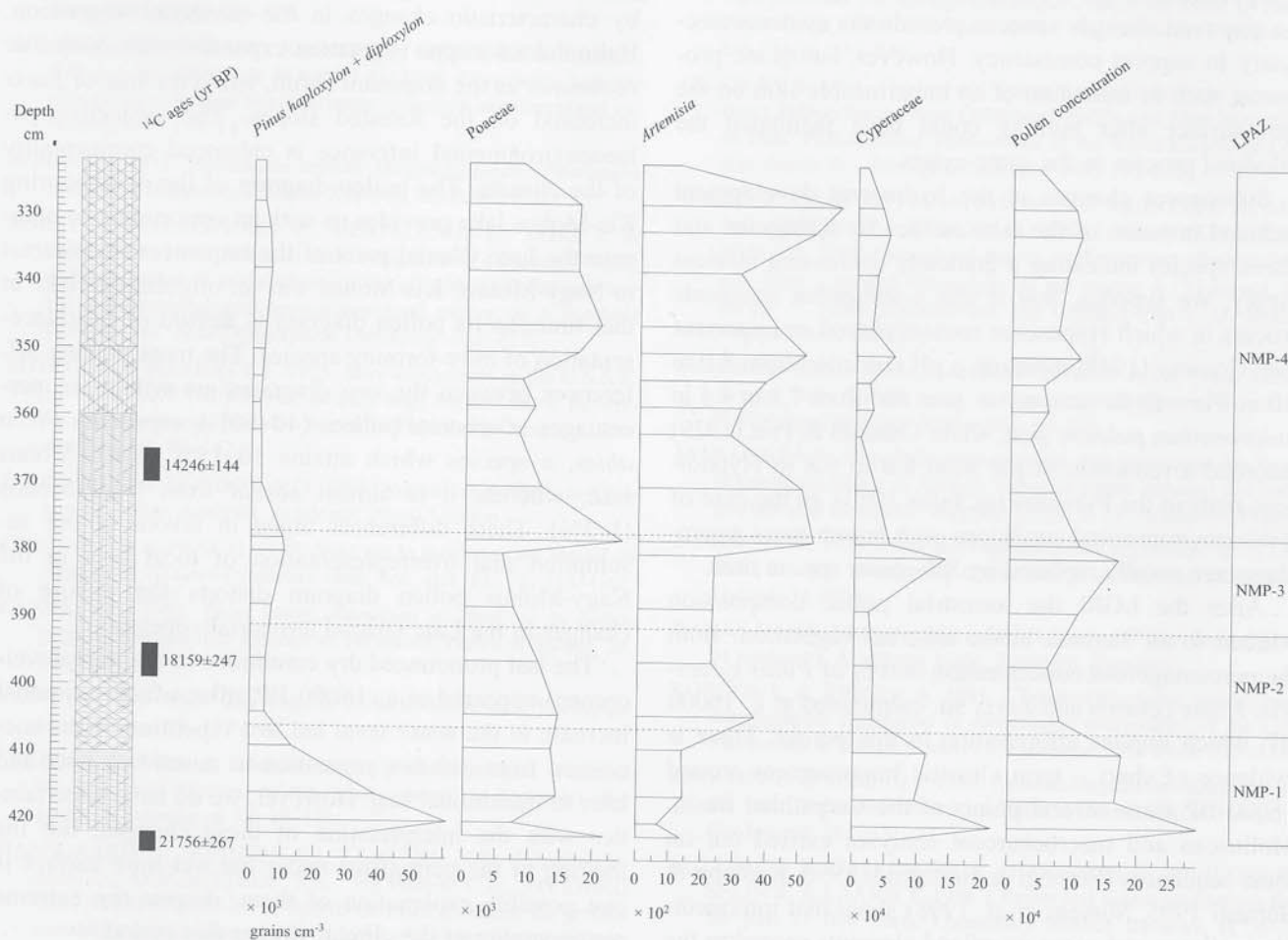


Fig. 5. Pollen concentration diagram of frequent taxa



tion. Usually, colder phases are related to a lowered water table in the palaeohydrological record, but there are examples to the contrary. Inghram (1983) and Glebov & Korzukhin (1992) considered the historical aspects of subarctic and boreal wetlands. How these ecosystems react to climate change is controversial. If permafrost formation is involved in the process, climatic deterioration usually entails impeded drainage, causing permanent waterlogging in the shallow-basin environment. The existence of permafrost in the area of Nagy-Mohos lake has already been proposed by Willis *et al.* (1997) who examined the neighbouring Kis-Mohos lake, with preserved sediment from c. 12500 BP onwards. The principal focus of their study was the relationship between vegetation change and changes in the soil surrounding the basin. They claimed that the microclimate of the basin allowed permafrost to persist until at least 10000 cal. yr BP ( $\approx$  9200–9300 yr BP). This assumption is also reinforced by the pollen record, which shows that the transition from boreal to deciduous forest was delayed by c. 2000 years compared with other sites in SE Europe (Willis *et al.* 1997). If we accept the theory of permafrost formation, both under the mire surface and on the surrounding slopes, impeded drainage coupled with higher run-off rates, leading to the opening up of the vegetation cover, the observed changes seem to provide the evidence necessary to support consistency. However, autogenic processes, such as formation of an impermeable skin on the peat surface after burning could have facilitated the paludinal process to the same extent.

Subsequent changes in the hydrosere development included invasion of the mire surface by *Sphagnum* and *Carex* species indicating a gradually decreasing nutrient supply. We suppose, that it was a somewhat autogenic process in which Hypnaceae mosses played an important role. Conway (1949) mentions a pH reduction from 8.0 to 6.0 in *Warnstorfia exannulata* peat and from 7.3 to 4.4 in *Aulacomnium palustre* peat, while Chouard & Prat (1929) recorded a reduction in pH from 8.0 to 5.8 in Hypnoideae mats in the Pyrenees (in Tallis 1983). In the case of stable environmental conditions such brown moss assemblages are usually replaced by *Sphagnum* spp. in time.

After the LGM the terrestrial pollen composition pointed to an increase in the arboreal vegetation. Both the percentage and concentration curves of *Pinus sylvestris*, *Pinus cembra* and *Larix* sp. culminated at c. 16000 BP, which implies afforestation in this period. There is evidence of short-term climatic improvement around 16000 BP from several points of the Carpathian Basin. Molluscan and macrocharcoal analyses carried out on loess sequences (Sümegei & Hertelendi 1998, Krolopp & Sümegei 1995, Sümegei *et al.* 1998) show that intermediate molluscs and some woodland elements spread to the central part of the basin at that time. The authors supposed that climatic improvement facilitated their migra-

tion. Palynological examination of sediment from an ox-bow lake in the south-eastern part of the Great Hungarian Plain also indicates dense boreal forest stands dominated by *Pinus sylvestris* around 16000 BP (Sümegei *et al.* in press).

The composition of the mire-forming vegetation altered at around 16600 BP and this change coincided with the second dry layer in profile NM-II. We are now seeing the opposite situation from that which confronted us around 18000 BP. Higher temperatures were coupled with the drying up of the mire surface and an invasion by Cyperaceae. Although we have only indirect evidence, it would appear that the triggering mechanism of the hydrosere development was most probably related to changes in the water balance, that is the relation between inflowing and outflowing water. When rising temperatures are not accompanied by a precipitation increase, rain- and ground-water fed basin mires can easily become water deficient, resulting in dry conditions on the mire surface (Inghram 1983). The drying out of the basin surface at that time is therefore most likely to have resulted from either a decrease in moisture draining into the basin, an increase in evaporation from the basin, or some combination of the two.

The beginning of the Late Glacial period is marked by characteristic changes in the terrestrial vegetation. Heliophilous steppe vegetation expanded with *Juniperus communis* as the dominant shrub, while the role of *Larix* increased on the forested slopes. The subjective palaeoenvironmental inference is enhanced continentality of the climate. The pollen diagram of the neighbouring Kis-Mohos lake provides us with an opportunity to compare the Late Glacial parts of the sequences. In contrast to Nagy-Mohos, Kis-Mohos was an oligotrophic lake at that time, so its pollen diagram is devoid of overrepresentation of mire-forming species. The most striking differences between the two diagrams are within the percentages of arboreal pollens (40–50%), especially *Picea abies*, a species which attains 10–15% in Kis-Mohos lake, whereas it is almost absent from Nagy-Mohos (1–3%). These differences argue in favour of our assumption that overrepresentation of local taxa in the Nagy-Mohos pollen diagram distorts the picture of changes in the Late Glacial terrestrial vegetation.

The last pronounced dry conditions in the mire development appeared at c. 14000 BP, after which a gradual increase in the water level led to a repetition of the succession from rich-fen vegetation to raised-bog pool and later to transitional bog. However, we do have uncertainties with the interpretation of these changes, but the melting of the permafrost under the wet mire surface is one possible explanation of them, despite the extreme continentality of the climate during this period.

Summing up, the general conclusion is that the major trends in hydrosere development were the same as those



typical for recent boreal mires, although the gradual change towards more oligotrophic and acidic conditions have been interrupted many times in the course of development of Nagy-Mohos lake.

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