Retarded wetland succession: anthropogenic and climatic signals in a Holocene peat bog profile from north-east Hungary

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Summary

1 Pollen, plant macrofossil and humification data supplemented by chemical and physical analyses of a Holocene peat sequence from Nagymohos, Kelemér, north-east Hungary, have been used to study local wetland vegetation dynamics and upland vegetation development in the early and mid Holocene. An attempt was made to distinguish between autogenic successional processes and allogenic environmental forces.

2 Holocene sedimentation began *c.* 7500 cal. BC. The basin was occupied by a shallow open lake with substantial input of inorganic material until *c.* 6200 cal. BC, when floating reedswamp vegetation encroached on the lake surface. This turned to *Carex* fen within *c.* 100 years. *Sphagnum* transitional bog became established by *c.* 5300 cal. BC.

3 The local mire water table in the *Sphagnum* bog phases was elevated between *c.* 5700–6000 cal. BC, *c.* 5000–5250 cal. BC and *c.* 4500–4700 cal. BC. The most distinctive feature of the record is the coincidence of upland vegetation changes with reconstructed wet-shifts in mire hydrology. The upland pollen data imply selective exploitation of *Ulmus* and *Corylus* coupled with burning and soil erosion during the second and third wet periods.

4 Succession from shallow open lake to *Sphagnum*-bog is an autogenic process, although superimposed allogenic perturbation (human induced soil erosion and climate change) modified the expected progression from wetter to drier and from minerotrophic-water dependent to oligotrophic communities.

Key-words: geochemistry, human activity, humification, plant macrofossils, pollen record, wetland community succession

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Introduction

Hydroseres are the only vegetational successions that leave behind them, in the form of partially preserved remains, a substantial record of the plant communities that have contributed to them (Walker 1970). Owing to the accumulation of organic sediments, a common feature of all wetland ecosystems is a gradual infilling, and the associated ecological changes are regarded as autogenic processes. Environmental forces may however act allogenically over an even shorter time-scale, and alter the course of succession.

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A recent palaeoecological study (Singer *et al.* 1996) has compared long-term records of wetland vegetation dynamics with regional, climate-forced terrestrial vegetation changes and shown that the rates of autogenic processes may be slow compared with the effects of both hydrologically significant climatic changes and anthropogenic disturbances. Therefore, major shifts in the wetland hydrosere were always induced by such allogenic factors, but responses were constrained by the state of basin infilling.

The early Holocene (*c.* 11500–5000 cal. BP) was a dynamic period in the development of both dryland and wetland ecosystems (Roberts 1998). In spite of its relative climatic stability with higher than present summer temperatures in Central Europe (Huntley & Prentice 1993) neither type had reached equilibrium when the first Neolithic groups entered the foothills of

the Northern Carpathians. Palaeoecological analysis of a peat sequence from a wooded *Sphagnum* mire in north-east Hungary allowed us to examine whether these early cultural groups interfered with the composition of wetland vegetation and thereby disrupted autogenic succession. We investigated changes in the wetland species assemblages and their interaction with the adjacent upland in order to determine the main successional trends in mire development and the factors that drove them.

Plant macrofossil and aquatic/wetland pollen records were compared with upland pollen data. Peat humification data were used to detect changes in mire surface wetness (Aaby & Tauber 1975), while the geochemical record allowed the detection of prehistoric erosional events (Engstrom & Wright 1984).

A sedimentary sequence spanning the entire Holocene from another *Sphagnum* mire (Kismohos) 300 m to the south of our site described the long-term relationship between human activity and land degradation through analysis of the pollen and geochemical records (Willis *et al*. 1998). We use this study as a reference for the early Holocene upland vegetation development and erosional activity in the region, although the time resolution is somewhat coarser.

SITE DESCRIPTION

Nagymohos (48°24′44″ N, 20°24′32″ E), a 1.4-ha valley mire, is located in the north-eastern Middle Mountains of Hungary at an elevation of 294 m a.s.l. (Fig. 1a). Gently rolling hills around the mire consist of sedimentary rocks, mainly Tertiary sands, and rarely exceed 400 m in elevation. The basin is underlain by Tertiary clay marl that is poor in mineral nutrients. The accumulation of groundwater in the upper horizon of the impermeable clay played an important role in the formation of the basin, which was probably caused by a landslide in the Upper Pleniglacial, *c.* 25 300 cal. BP (Schréter in Zólyomi 1931; Magyari *et al*. 1999).

The mire flora is impoverished and the hollow-hummock structure underdeveloped compared to north-west European *Sphagnum* mires (Matus *et al*. 2000). The largest peat–forming association today is Betulo pubescenti-Sphagnetum recurvi (Type 2 in Fig. 1c) that replaced the once dominant Scirpo-Phragmitetum sphagnetosum in the last decade (Matus *et al*. 2000). In raised-bog areas a *c.* 100 cm thick water column separates the *Sphagnum* carpet from the underlying peat.

The climate is continental temperate with annual precipitation below 600 mm. The high amplitude temperature fluctuations together with the frequent drought years in this area (Kakas 1960) do not favour development of an ombrotrophic raised bog. Most of the surface is dependent on minerotrophic spring and surface water, as reflected by the relatively high pH (6), conductivity (77 μS cm^{-1}) and Ca (11 mg L^{-1}) and Mg (0.9 mg L^{-1}) concentrations (Gyulai *et al*. 1988). Oligotrophic associations (Eriophoro-Sphagnetum, Type 4 in Fig. 1c) are restricted in area and show somewhat lower values (pH: 4.1; electric conductivity: 60 μS cm^{-1}; Ca: 10 mg L^{-1}; Mg: 0.9 mg L^{-1}).
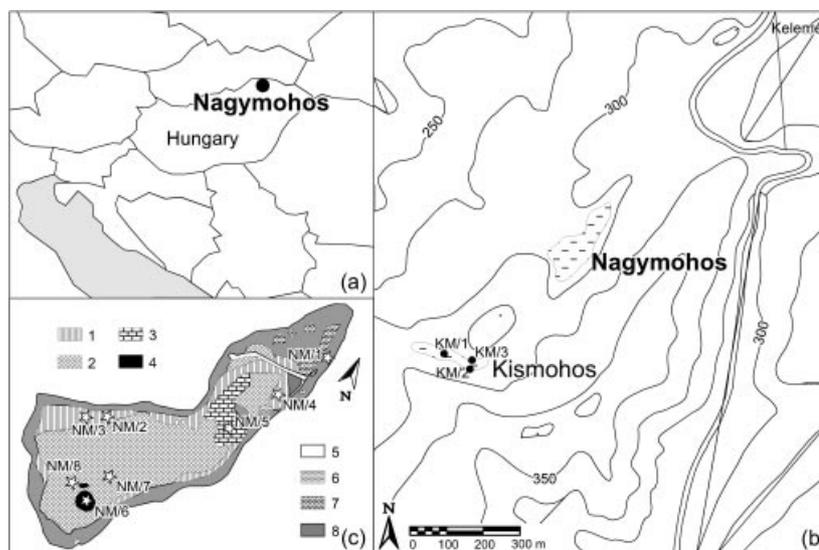
Fig. 1 Nagymohos site: (a) location in Central Europe; (b) Kelemér Region also showing Kismohos site; (c) Vegetation map redrawn form Matus *et al*. (2000) showing the major mire-forming associations after Lájer (1998). 1 Salici cinereae-Sphagnetum (NM/2–4); 2. Betulo pubescenti-Sphagnetum recurvi (NM/7, KM/2); 3. Carici lasiocarpae-Sphagnetum + Eriophoro angustifolii-Sphagnetum (NM/5, KM/1); 4. Eriophoro vaginati-Sphagnetum recurvi (NM/6, 8); 5. Lemnetum; 6. Caricetum acutiformis-ripariae (KM/3); 7. Calamagrostis-Phragmites lawn (NM/1); 8. Calamagrosti-Salicetum cinereae (NM/1). Codes in parentheses indicate surface pollen samples (locations as in b, c) taken from each type.

Surveying the existing literature on mire terminology, it is apparent that there is a wide variation in conditions used to distinguish fen from bog. Physical and chemical parameters alone suggest that Nagymohos is a poor fen (Sjörs 1950) or mesotrophic acid mire/transitional bog (Overbeck 1975; Succow & Lange 1984), although its surface vegetation and morphology are similar to continental raised bogs (Osvald 1925; Kulczyñski 1949): henceforth we use 'transitional bog' (Overbeck 1975) that corresponds with mesotrophic bog in the recent terminology suggested by Wheeler & Proctor (2000).

The surrounding hills are covered by Quercion vegetation with Querco-Carpinetum forest to the northwest, and Querceteum petraeae-cerris to the south-east of the mire.

Nagymohos was selected because it occupies a relatively small basin receiving a predominantly local and extra-local pollen rain (Jacobson & Bradshaw 1981) and it is located along the southern latitudinal limit of floating *Sphagnum* mires in Europe (Ellenberg 1988) and therefore might be particularly sensitive to climate change and anthropogenic disturbance. In addition, the hypothesis that *Sphagnum* mires in the Carpathian Basin are fortuitous survivors from the last glacial period (Rybníèek 1984) can be tested.

Methods

RADIOCARBON DATING, PHYSICAL PROPERTIES, HUMIFICATION AND GEOCHEMICAL ANALYSIS

Two sediment cores were collected from the southern mire basin (Fig. 1b) during the winter of 1998 using a modified Russian corer (Aaby & Digerfeldt 1986). From the Holocene part of the cores, eight samples of 2–5 cm vertical thickness were submitted to the Nuclear Research Centre of the Hungarian Academy of Sciences, Debrecen for standard ^{14}C dating (Hertelendi *et al*. 1989). Radiocarbon ages were calibrated using the calibration program of Stuiver *et al*. (1998). The calibrated age vs. depth plot for the period with continuous peat accumulation, between *c.* 4300–7500 cal. BC, is the outcome of weighted least-squares line fitting, where the number of terms is three.

For the determination of sediment organic content 1 cm^3 subsamples taken at 4 cm intervals were weighed and the percentage weight loss following ignition was determined using conventional methods (Dean 1974).

Humification measurements were made on 1 cm^3 subsamples taken at 4 cm intervals using the colorimetric method of Aaby & Tauber (1975).

Chemical elements were analysed in 4 cm sections. Dried samples were digested with 65% nitric acid and 25% hydrogen peroxide using a modified technique of Bengtsson & Enell (1986). Acid-soluble concentrations were measured by inductively coupled plasma atomic emission spectrometry (ICP-AES).

PLANT MACROFOSSIL AND POLLEN ANALYSES

Half of the core was cut into 5 cm slices except close to major stratigraphic boundaries, where 2–3 cm subsamples were taken to prevent distortion of macroscopic remains representing different peat types. Subsequently 10 cm^3 subsamples of peat were sieved through a 250-μm mesh. Our aim was to determine the proportions of woody, herbaceous (Monocotyledons, *Eriophorum vaginatum*, *Typha/Phragmites*), bryophyte and unidentifiable organic material (UOM). Epipphia of *Daphnia* sp. (*Cladocera*) and *Carex* seeds were also counted and identified. For the bryophyte analysis, 2 cm^3 subsamples were separated from the peat slices and sieved through a 300-μm mesh. Estimation of relative species abundances followed the five-point scale approach of Walker & Walker (1961).

Sample preparation, pollen counting and charcoal analyses procedures were as described in Magyari *et al*. (1999) for samples taken at 2–4 cm intervals. In the pollen diagrams, all taxa are represented as percentages of total land pollen. Subdivision of the upland pollen diagram was carried out by numerical zonation using optimal splitting techniques that minimized sum-of-squares and information content (Birks & Gordon 1985). Rarefraction analysis was used to estimate E(*Tn*), the number of terrestrial pollen and spore taxa in *n* grains at each sample, as a measure of temporal changes in palynological diversity (Birks & Line 1992). All the numerical analyses and plotting of the pollen diagram were carried out using PSIMPOLL 2.27 (Bennett 1992).

Surface pollen samples

To model the relationship between wetland microfossil composition and surface mire vegetation, eight surface samples were collected together with three from the neighbouring Kismohos such that all major vegetation units were represented (Fig. 1).

Results

CHRONOLOGY

Results of the radiocarbon measurements are presented in Table 1, from which two hiatuses are apparent. The first, associated with a thin layer of burnt macrocharcoals and a subsequent change in peat stratigraphy (see later) from *Sphagnum* to fen peat shows *c.* 1700 years difference in age between adjacent samples, deb-6574 and deb-5973, and the second *c.* 950 years difference between 119 and 115 cm. The 'Kismohos' palaeoecological data (Willis *et al*. 1997, 1998) suggests that the first coincides with a peat cut in the early Middle Age when Barbarians were using that lake for rope production, whereas the second probably represents an unsuccessful attempt to drain the mire in the early 20th century (Gyulai 1995).

Table 1 Radiocarbon dates from the Holocene sediments of Nagymohos. Calibrated ages were calculated using the calibration programme of Stuiver *et al.* (1998)

Laboratory number	Depth below peat surface (cm)	$\delta^{13}C$ (PDB) [‰]	^{14}C age years BP	Calibrated range years BC/AD (2σ)	Best estimated age of the 2σ calibrated range (BC/AD)
deb-5881	110–115	−30.60	235 ± 45	1527–1954 AD	1661 AD
deb-6583	119–120	−28.09	1300 ± 35	679–747 AD	713 AD
deb-6575	127–128	−28.91	2010 ± 45	57 BC – 42 AD	5 BC
deb-6574	127–130	−28.77	2975 ± 55	1284–1116 BC	1200 BC
deb-5973	130–133	−27.90	4270 ± 70	3033–2625 BC	2888 BC
deb-5969	140–145	−27.62	5515 ± 45	4457–4258 BC	4350 BC
deb-5882	220–225	−27.59	6833 ± 90	5920–5526 BC	5675 BC
deb-5991	280–285	−29.76	8650 ± 110	7952–7485 BC	7586 BC
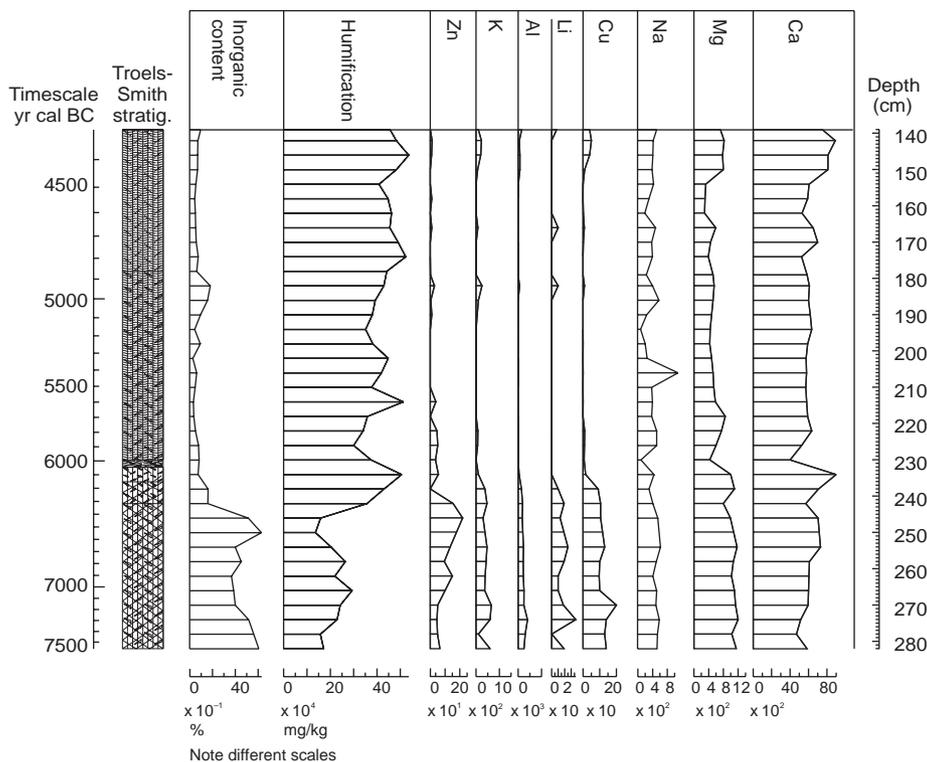
Fig. 2 Inorganic content, peat humification and geochemical element concentrations. Nagymohos peat bog, Kelemér, north-east Hungary.

Since peat accumulation was continuous over the early and mid Holocene, we used the lower part of the sequence to examine the role of allogenic and autogenic factors in mire development.

INORGANIC CONTENT AND PEAT HUMIFICATION

There is an increasing number of studies demonstrating that shifts in peat humification can be linked with past changes in the surface wetness of peat bogs (Aaby & Tauber 1975; Chambers *et al.* 1997; Anderson 1998). When the water table is deep, the surface organic matter spends longer in the aerated acrotelm and decay rates, measured by the concentration of humic acids, are therefore relatively high (Clymo 1983). Figure 2 shows relatively low humification at the base of the

diagram, but since this corresponds to the shallow lake phase where the above principles do not apply this cannot be used in the interpretation of past hydrological changes.

Above 245 cm, there is a rise in the humification curve accompanied by a substantial decline in the sediment inorganic content and preceding the change from lake mud to fen peat. Since inorganic content of the sediment then remains low, fluctuations in humification probably reflect changes in surface wetness (Blackford & Chambers 1995). Marked decreases between 222 and 230 cm, 190–196 cm and 155–160 cm may indicate wet-shifts in the succession between about 6000–5700, 5250–5000 and 4700–4500 cal. BC. Peak humification at 234 cm, 214 cm and 174 cm may represent the culmination of dry phases at *c.* 6100, 5580 and 4800 cal. BC.

Table 2 Frequency distribution of selected wetland microfossils in the surface samples taken from Nagymohos and Kismohos. Location of surface samples is shown in Fig. 1. Percentage calculation is based on the terrestrial pollen sum from which *Betula* was excluded

	KM/1	KM/2	KM/3	NM/1	NM/2	NM/3	NM/4	NM/5	NM/6	NM/7	NM/8	Description
Salix	0.57	1.76	0.73	13.3	1.67	8.78	1.50	2.88	0	0	1.12	Modest freq. when dominates
Solanum dulcamara	0	0	0.73	0	0	1.58	0	0	0	0	0	In disturbed fen associations
Lysimachia vulgaris	0	0	4.90	0	0.84	0.53	0	0	0	0	0	In disturbed fen & fenwood
Mentha-type	0	0	0	1.04	0	0	0	0	0	0	0	Characteristic for the mire fringe
Lemna	0	0	0	7.44	0	1.58	0	0	0	0	0	High freq. in open water spots
Sparg./Typha ang.	0	0	0	18.3	0	0	0	0	0	0	0	Note high freq. in NM/1
Typha latifolia	0	0	0	2.39	0	0	0	0	0	0	0	Note high freq. in NM/1
Phragmites	2.79	1.47	0.73	1.72	4.07	3.61	7.75	0.74	0	3.33	1.12	Characteristic of fen associations
Cyperaceae	5.16	1.18	9.93	8.63	0	0.53	0	0	4.31	0.68	0.56	High in perennial fen, fenwood & *Eriophorum*-dominated spots
Thelypteris palustris	0.29	0.30	1.45	0	0	1.58	0.76	0	0	1.36	0	Low freq. when locally present
Filicales undiff.	0	0.30	0.73	1.04	0	1.58	1.50	0	0.89	0.68	0	No definite pattern, but more frequent in fen associations
Sphagnum	43.9	5.10	11.1	1.38	7.09	12.2	7.09	7.53	36.9	26.4	11.5	Highest freq. in oligotrophic raised-bog associations
Tilletia sphagni	1.97	0.30	0	0	0.84	2.09	0	0	0	0	0	Related to pools
Assulina seminulum	17.1	1.47	5.56	0	0	5.56	24.7	2.17	14.6	13.7	0.56	Highest freq. in oligotrophic raised-bog associations
Amphitrema flavum	0	0	0	0	0	0.53	0	1.46	0	0	0	Sporadic appearance only
Arcella discoides	3.86	1.76	1.45	0	1.67	0	0	0	0	0	0	Characteristic of the 'Kismohos'

The increasing mineral content of the peat between 182 and 190 cm may have artificially lowered the measured humic acid concentrations and thus makes interpretation less reliable in this section.

GEOCHEMISTRY

The principal aim of geochemical analysis was to provide a record of past soil erosion within the catchment, since many studies (Mackereth 1966; Bennett *et al.* 1992; Szalóki *et al.* 1999) have demonstrated that increases in the concentration and/or accumulation rate of elements such as K, Na, Mg, Al and Ca reflect the inwash of clastic minerals associated with such disturbance.

The geochemical diagram for the early and mid Holocene part of the Nagymohos profile (Fig. 2) indicates high Al and K frequencies in the early Holocene with a sharp decline at 234 cm (*c.* 6100 cal. BC), just before lake mud is replaced by reedswamp and fen peat, followed by low, but detectable levels until 220 cm (5700 cal. BC). The overlying *Sphagnum* peat is devoid of clastic elements for a short period during which sediment inorganic content declines. Transient peaks in K and Al are seen between 182 and 190 cm (4420–5090 cal. BC), 139 and 152 cm (4300–4450 cal. BC) and at 166 cm (*c.* 4680 cal. BC) and their allogenic source is indicated by the coincidental rise in sediment inorganic content.

Li, Zn and Cu mirror the Al and K curves, suggesting that all these elements arrive via the allogenic input of mineral matter into the lake.

WETLAND VEGETATION DEVELOPMENT

Ordination and numerical comparison of fossil and surface wetland microfossil spectra

Frequencies of the surface wetland pollen and testate amoebae species for use in the numerical comparisons are given in Table 2. PCA was used to highlight the ecological characteristics of the different zones. The covariance matrix of the joint data set (surface plus fossil assemblages) with matrix sample vectors normalized to unit length was subjected to ordination (Prentice 1980). Figure 3 shows sample scores on the first three principal component axes plotted against depth, whereas Fig. 4 displays sample scores and component loadings of the most important taxa as revealed by PCA. Fossil spectra indicated by their depths were considered to have similar ecological characteristics to surface assemblages to which they were close in the biplot. Five mire-forming associations (1–5 in Fig. 4) were identified and used in the reconstruction of the wetland succession.
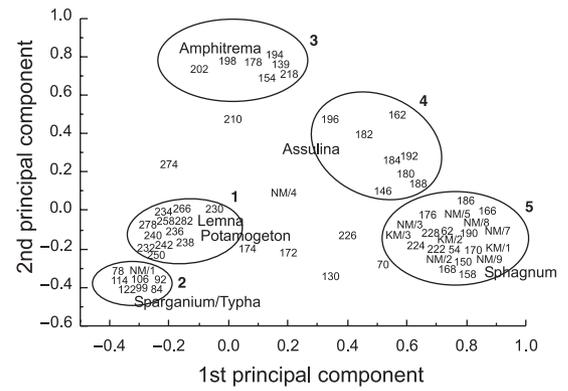
Wetland vegetation dynamics

Table 3 shows the reconstructed development taking into account the results of the macro- and microfossil
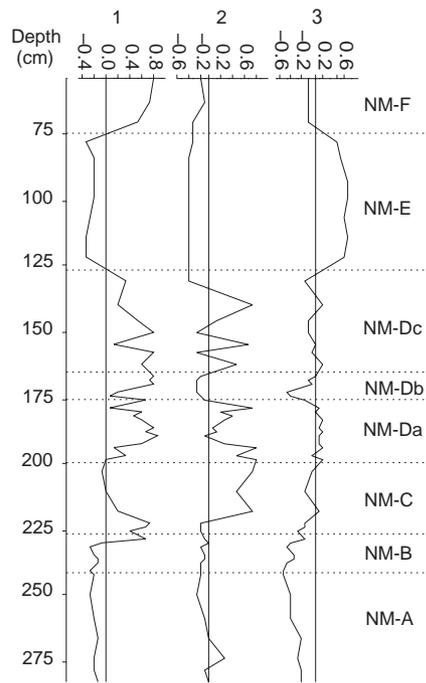
Fig. 3 Stratigraphic plot of the sample scores on the first three principal components of the Nagymohos wetland pollen data set. Phases of the mire development (A–F) are shown.

Fig. 4 Principal component biplots of wetland pollen spectra with sample scores and component loadings of the most important pollen and spore types plotted on the first and second principal axes. Analysis included 65 fossil and 11 surface samples from Nagymohos and Kismohos (Fig. 1).

analyses (Figs 5, 6), the ordination (Figs 3, 4) and the autoecology of different mire-forming taxa.

Shallow lake (NM-A; 7500–6150 cal. BC). Both the plant macrofossil and pollen analysis suggest an aquatic vegetation of lemnoids (*Lemna minor*) and elodeids (*Potamogeton natans, Myriophyllum spicatum*) with marginal reeds (*Sparganium/Typha angustifolia* and *Phragmites*-type). The presence of algae is indicative of an initial water depth of at least 1.5–2 m and mesotrophic conditions (Van Geel 1978). Irregular finds of *Sphagnum* leaves (Fig. 6) along with other water mosses suggest a shoreline moss carpet.

Floating reedmace mat (NM-B; 6200–5900 cal. BC). By around 6200 cal. BC, the lake had become overgrown by a floating-mat of *Typha latifolia* and *Thelypteris palustris* at the sampling point. Both are present in the pollen diagram (Fig. 6) and the fall of the pollen concentration values (Fig. 6 right) coincidentally suggests that a very rapid peat formation accompanies the establishment of the reedmace mat.
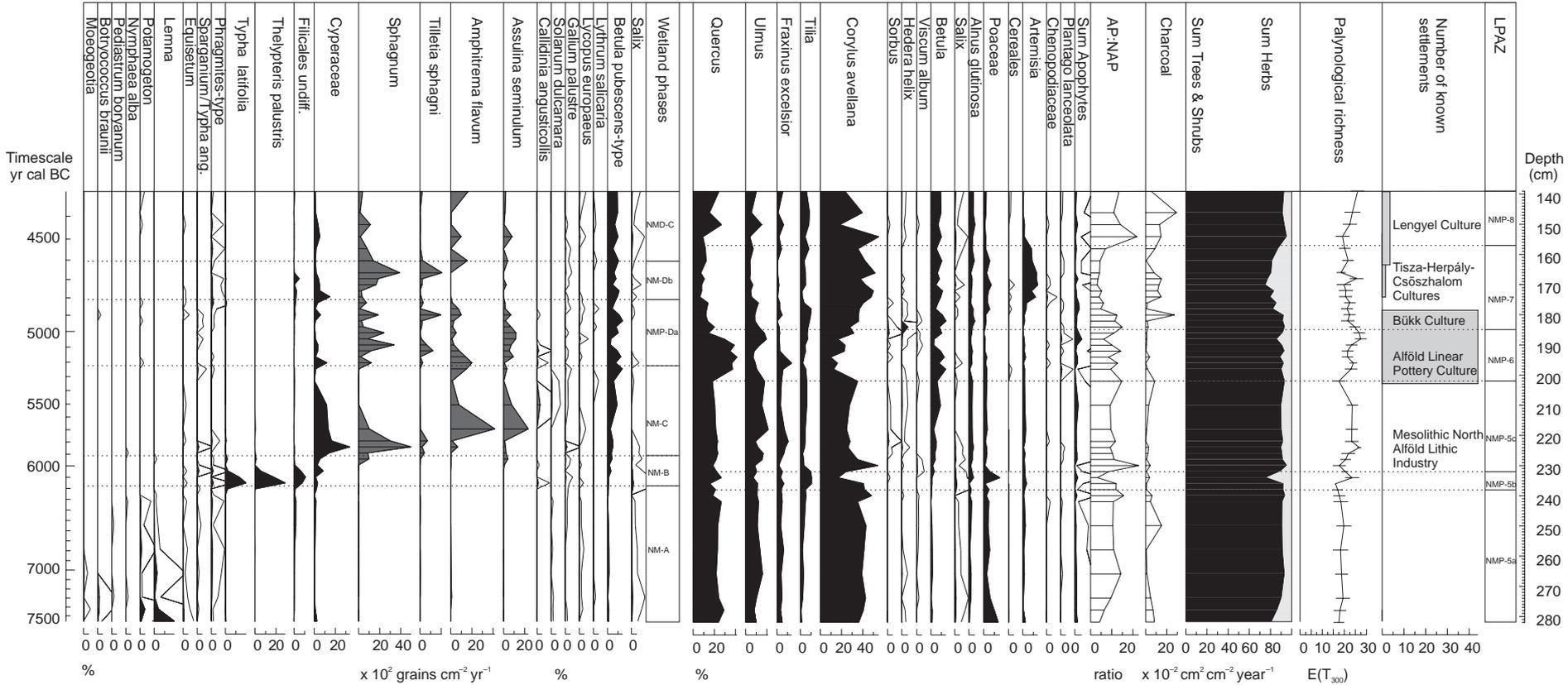
Thelypteris palustris was then replaced by other fern species, before *Meesia longiseta* colonized areas previously occupied by ferns, and *Typha latifolia* was eradicated from the mat surface (Fig. 5, 6).

Carex fen (NM-C; 5900–5300 cal. BC). Poor-fen conditions are indicated by the emergence and sudden advance of *Sphagnum palustre*. This phase therefore also marks the development of a floating *Sphagnum*-lawn that isolated the mire from the influence of groundwater and seepage water thereby blocking the availability of dissolved nutrients from these sources (Ingram 1992).

Table 3 Hydroseral development of Nagymohos in the Holocene. Determination of the subfossil associations is based on the plant macrofossil (with special regard to the Bryophyta and *Carex* constituents) and the wetland pollen diagrams

Age (year. cal AD/cal. BC)	Phases of wetland development	Fossil associations
c. 1660 AD–present HIATUS 2nd historical peat cut	Transitional bog (NM-F)	Scirpo-Phragmitetum Sphagnetosum, Betulo-Sphagnetum
? AD–5 cal. BC HIATUS 1st historical peat cut	Shallow pond + raised bog hollow (NM-E)	Potametum + Scirpo-Phragmitetum Sphagnetosum
4300–4500 cal. BC	*Sphagnum* bog (NM-Dc)	Carici lasiocarpae-Sphagnetum
4500–4650 cal. BC	*Sphagnum–Eriophorum* bog (NM-Dc)	Eriophoro vaginati-Sphagnetum
4650–4820 cal. BC	Raised bog hollow (NM-Db) (fluctuating water table!)	Carici-Sphagnetum
4820–5250 cal. BC	*Sphagnum–Eriophorum* bog (NM-Da)	Eriophoro vaginati-Sphagnetum
c. 5250 cal. BC	Dry peat surface (NM-Da)	
5250–5300 cal. BC	Transitional *Sphagnum* bog (NM-Da)	Carici lasiocarpae-Sphagnetum
5300–5900 cal. BC	*Carex* fen (NM-C)	Carici acutiformi-Sphagnetum
5900–6200 cal. BC	Floating bulrush mat (NM-B)	Thelypteridi-Typhetum latifoliae
6200–7500 cal. BC	Shallow non-calcareous lake (NM-A)	Potametum natantis + Sphagno-Utricularion

Fig. 5 Plant macrofossil and bryophyte relative frequency diagram of Nagymohos, Kelemér. Sediment components are plotted as percentage total organic constituents. Number of seeds and other macroscopic remains is given as items per 10 cm³ sediments; U.O.M., unidentifiable organic matter.

Transitional Sphagnum-bog (NM-D; 5300–4300 cal. BC). Typical *Carex*-fen species were much less in evidence by *c.* 5300 cal. BC. The prevailing mesotrophic transitional *Sphagnum*-bog association was similar to Carici lasiocarpae-Sphagnetum currently found in hollows on the mire surface (e.g. NM/5). This was followed by the appearance of *Eriophorum vaginatum* (phase NM-Da). Several wetland microfossils, e.g. *Sphagnum* and *Tilletia sphagni*, Cyperaceae, *Amphitrema flavum* and *Assulina seminulum*, show fluctuations indicating that small-scale hydrological changes occurred within the transitional bog phase.

Both the peat stratigraphy and the radiocarbon dates corroborate a stratigraphic hiatus at around 4300 cal. BC (Fig. 6), which denotes the onset of phase NM-F (see Table 3).

UPLAND VEGETATION DEVELOPMENT

Five local pollen assemblage zones (LPAZ) have been recognized and are labelled NMP-5 to NMP-9. NMP-1 to NMP-4 have been allocated to LPAZs of the Pleistocene part of the sequence and have been published elsewhere (Magyari *et al.* 1999). Note that in Fig. 6 only the early and mid-Holocene part of the sequence is displayed.

The upland pollen diagram demonstrates that a mixed oak forest of varying composition was present around the basin from *c.* 7500–4300 cal. BC. Total arboreal pollen (AP) frequencies exceeding 80% indicate that during phase NMP-5 the landscape was densely forested. Well-drained hilltops most probably supported oak–lime woods whereas the slopes could have been occupied by stands of *Ulmus*, *Fraxinus excelsior* and *Quercus* with an admixture of *Corylus avellana* in the shrub layer.

The dominance of hazel in the pollen diagram suggests that the lake basin was encircled by hazel scrub.

Evidence for changes accompanying the transition from NMP-5a to NMP-5b is ambiguous. The marked increase in the accumulation rate of charred particles around 6600 cal. BC is followed by only a small rise in *Corylus* and an eventual lowering of *Quercus* rather than a decrease in total AP. The preceding increase in the inorganic content of the sediment implies that the charcoal came from inwash. Increased *Tilia* values during a short transitional period (between *c.* 6200–6000 cal. BC) indicate that it expanded in the woodland at the expense of the surrounding *Corylus* scrub, which regained ground around 6000 cal. BC.

The next change was the first elm decline at *c.* 5850 cal. BC. This was balanced by a rise in *Fraxinus* and *Hedera* and the first appearance of light-demanding species such as *Sorbus*. Reversal of the *Ulmus* and *Fraxinus* curves implies that open areas arising from the removal or death of *Ulmus* trees were invaded by *Fraxinus*, then gradual regeneration of the *Ulmus* stands took place. The duration of this process is estimated at 100–150 years.

Between 5700 and 5300 cal. BC the mixed oak forest regained its natural state with a gradual rise in hazel, but a sharp decline in *Corylus* and *Ulmus* at around 5250 cal. BC implies selective exploitation of these species. The slight increase in the charcoal accumulation rate around 5300 cal. BC and the prevalence of macro-charcoal in the sediment (Fig. 6) suggest small-scale fires around the basin, although the decline in *Corylus*, *Ulmus* and *Tilia* and the contemporaneous rise in *Quercus* imply that fire was used only to thin the hazel scrub. The gradual decline in *Ulmus* accompanied by a *Fraxinus* rise lasted until 5100 cal. BC.

Fig. 6 Wetland microfossil (left) and upland pollen (right) diagram of selected taxa for the early and mid Holocene. The number of known settlements within 50 km radius of the mire is indicated on the right. LPAZ, local pollen assemblage zones.

Fig. 7 Composite diagram of selected palaeo-environmental proxy data, Nagymohos, Kelemér, north-east Hungary. The number of known settlements within 50 km radius of the mire and cold (humid) intervals of the early and mid Holocene are shown on the right. Phases of alpine glacier movements are according to Patzelt (1977); cold/humid phases in Central Europe are taken from Haas *et al*. (1998); the phase of δ ^{18}O minimum is shown according to Johnsen *et al*. (1992) and Bond *et al*. (1997); TOC, total organic carbon; its minima in Lago di Mezzano are from Ramrath *et al.* (2000).

Between 5100 and 5000 cal. BC, the composition of the upland vegetation became similar to that of the early sixth millennium cal. BC except that less dense conditions allowed a more diverse herbaceous flora. A third distinct *Ulmus* decline appeared around 5000 cal. BC followed by the expansion of *Hedera helix* and *Sorbus* as the canopy opened up. The decline in elm was compensated by a rise in *Corylus* and *Tilia* with both AP: NAP (non-arboreal pollen) and total AP remaining high, implying that woodland clearance was not important. The fourth elm decline was accompanied by substantial lowering of the arboreal pollen around 4900 cal. BC, when a steep rise in the microcharcoal concentration also indicates forest fires (Fig. 7). *Corylus* was the only species to gain from the repeated forest fires. For the first time the herbaceous flora was characterized by *Artemisia* and Poaceae with small quantities of *Triticum* and *Secale* type pollen grains present.

A second phase of forest regeneration started around 4500 cal. BC, but a hiatus in the sediment accumulation around 4300 cal. BC, resulting from prehistoric peat cutting, prevents any further reconstruction.

Discussion

The rise of *Sphagna* to dominance in the macrofossil diagram at the beginning of phase NM-C marks an important shift in the functioning of the mire ecosystem with decay rates becoming predominantly influenced by the position of the water table (Clymo 1992). In this system hydrological change can result both from climate change and from other factors such as introduction of an outlet that drains surplus water or cutting of the surface peat.

PEAT BOG PALAEOHYDROLOGY

In attempting to reconstruct the hydrological changes at Nagymohos, we make a number of assumptions.
1. High humification indicates a dry period, while low values point to a raised water table.
2. Increases in Cyperaceae pollen suggest a shift from drier to wetter conditions or strong fluctuation of the mire water table. Most of the peaks in the Cyperaceae pollen record could be correlated with macrofossil finds of *Carex* seeds and *Eriophorum* macro-remains, and thus identified to species (*Carex rostrata*, *C. lasiocarpa*, *C. acutiformis*, *C. paniculata*, *Eriophorum vaginatum*, see Table 4). These *Carex* species indicate an above- or near-ground water table, whereas *Eriophorum vaginatum* in the Carpathian Basin appears in drier mire associations characterized by frequent water level change (Lájer 1998).
3. The spore production of *Sphagnum cuspidatum* is positively correlated with past mire surface wetness

Table 4 The relationship between Cyperaceae pollen frequency peaks and plant macrofossil assemblages in phase NM-B. Note that the number of seeds applies a 10-cm³ sample

Cyperaceae pollen peaks	Cyperaceae macrofossils in the same layers
173 cm	*Carex* sp. (2 seeds), Monocots. undiff. (15%)
180 cm	*Carex paniculata* (2 seeds) + *Eriophorum vaginatum* (70%), Monocots. undiff. (5%)
196 cm	*Eriophorum vaginatum* (45%), Monocots. undiff. (75%)
223 cm	*Carex* cf. *acutiformis* (11 seeds) *Carex lasiocarpa* (2 seeds), Monocots. undiff. (75%)

(Cronberg 1991). In the Nagymohos pollen diagram *Tilletia sphagni* is synchronous with *Sphagnum* (Fig. 7) similarly to the observation of Dickson (1973) who revealed the same relationship in his peat bog pollen sequence. Van Geel (1978) found that *Tilletia sphagni* spores were abundant in *Sphagnum cuspidatum* capsules, but not in other *Sphagnum* species. He concluded that *Tilletia sphagni* preferentially infects *Sphagnum cuspidatum*, and therefore the synchronous maxima indicate that the *Sphagnum* curve is due to the increased spore production by *S. cuspidatum*. Our *Sphagnum* spore maxima probably also reflect *S. cuspidatum* present during the formation of bog hollows.
4. *Daphnia* epiphia indicate the occurrence of temporary shallow-water pools (Van Geel 1978).
5. The testate amoeba *Amphitrema flavum* is an indicator of wet conditions (> 95% peat water content), whereas *Assulina seminulum* indicates relatively dry conditions (78–89% peat water content; Tolonen *et al.* 1992). In the wetland microfossil diagram (Fig. 6) testate amoebae species are plotted as microfossil influxes to avoid possible misinterpretations of the distorted percentage data that may arise from selective destruction during chemical treatment of the pollen samples (Hendon & Charman 1997). Fluctuations therefore represent real changes in the population of individual rhizopods and thus in mire surface wetness.

The *Sphagnum* carpet that developed on the surface of the reedmace mat in phase NM-C was initially rich in various wetland *Carex* species (*C. lasiocarpa*, *C. acutiformis*) implying above-ground water table. Wet conditions are also supported by the great abundance of *Sphagnum* spores and Cyperaceae pollen and by low humification values. The large quantity of *Carex* remains interspersed with the seeds of eutrophic helophytes, such as *Oenanthe aquatica* and *Lycopus europaeus*, suggest that the water was minerotrophic, although these species later decline, and the abundance of *Amphitrema flavum* and *Assulina seminulum* at 218 cm suggests that conditions were already oligotrophic. Above 216 cm (5600 cal. BC), there are declines in both wetland microfossils and bryophytes and a rise in humification. *Solanum dulcamara* pollen frequencies were high and its presence is confirmed by seeds between 205 and 210 cm (Fig. 5). This nitrophilous species frequently appears in mesotrophic and eutrophic fens, fenwoods and marshes (Simon 1992; Braun & Tóth 1994), and together with the disappearance of testate amoebae indicates a drier peat surface

and temporary nutrient enrichment. Excess nitrogen was most probably supplied by enhanced decomposition of the surface peat as aerobic surface conditions were established (Kuhry & Vitt 1996). Three lines of evidence therefore imply a dry shift at *c.* 5580 cal. BC.

The end of this dry period is marked by a layer of strongly humified organic material at 197 cm (*c.* 5300 cal. BC), probably representing a previous desiccation event, above which the peat became rich in *Eriophorum vaginatum*. Increased surface aeration usually leads to humification and structural collapse (Hughes 2000) and thus produces unidentifiable organic debris in the peat sequence. Kazda (1995) has demonstrated that surface dehydration is followed by increased nitrogen mineralization, and eventually by a fall in pH. Phosphorus becomes more soluble at low pH (Hughes 2000) and so could have favoured the spread of *Eriophorum vaginatum*.

The subsequent shift to wetter conditions is inferred from the lowered concentration of humic acids that coincides with a minor increase in the Cyperaceae pollen frequencies and the onset of a second prominent *Sphagnum* spore maximum. This wet-shift coincides with an increase in the microcharcoal curve (Fig. 6) and spans *c.* 500 years. From around 5100 cal. BC, however, the inorganic components increase, suggesting an inwash from the surrounding slopes possibly linked to the cause of the second microcharcoal peak curve that appears coincidentally. The wetland vegetation seemingly reacted to the allogenic mineral input with a *c.* 50–80 years time lag. Appearance of *Daphnia* epiphia and *Warnstorfia fluitans* and a slight increase in the Cyperaceae and *Sphagnum* spore frequencies all suggest a wet-shift, and the absence of support from humification may be due to sediment inorganic content causing bias in humic acid measurements (Blackford & Chambers 1993). At around 4820 cal. BC (phase NM-Db), *Eriophorum vaginatum* was replaced on the mire surface by *Meesia longiseta*, whose re-invasion again indicates temporary nutrient enrichment and strong fluctuation of the water table (as at 230 cm) and is accompanied by a peak in humification.

This period of frequent water table oscillation ended at around 4700 cal. BC, when a wet-shift is inferred from the low humification values and increasing abundance of *Sphagnum* spores, followed by the reappearance of *Eriophorum vaginatum* at *c.* 4650 cal. BC and an increase in testate amoebae. Subsequently, declines in *Sphagnum* with a slightly rising humification support a dry shift at around 4450 cal. BC.

PHASES OF HUMAN DISTURBANCE

In the first three millennia of the Holocene represented by the Nagymohos upland pollen diagram, the slopes around the mire supported a mixed deciduous forest of relatively constant species composition despite shifts in dominance and evidence of clearance. A characteristic early Holocene *Corylus* dominance (Huntley 1993; Willis *et al*. 1998) was first interrupted by a short-lived spread of *Tilia* between *c.* 6200 and 6000 cal. BC both here and at Nyírjes-tó (50 km from Nagymohos; Gardner 1999) and by *Betula* at Kismohos (Willis *et al*. 1998). All coincide with infilling of the lake basin, but *Betula* spread on the developing *Sphagnum* carpet at this stage only at Kismohos implying allogenic forcing, probably by a warm and/or humid interval. There is no evidence of human activity from pollen or charcoal records.

The upland vegetation subsequently returned to its previous state, with lime being replaced by hazel in the wetland fringe until *c.* 5850 cal. BC when both elm and hazel may have been selectively exploited (the 1st elm decline). The simultaneous expansion of ash and several light-demanding trees implies the opening up of the closed canopy around the mire. Hazel and ash have a very similar autoecology (Rackham 1980), and would be expected to react to climate change in the same way. Their pollen curves however (Fig. 6) are mirrored, implying that ash was favoured by the declines in elm and could be explained by felling or coppicing of elm and hazel. Mesolithic field camps and stations are known within a 70–100 km radius (Kertész 1993) of the site, and people from these mobile foraging groups could have caused the observed small-scale disturbance.

The second elm and hazel declines at *c.* 5300 cal. BC clearly demonstrate anthropogenic activity, with the appearance of *Plantago lanceolata* and Chenopodiaceae. There is no significant increase in *Artemisia* and Poaceae indicating pastoral rather than arable farming near the mire (Turner 1964) as in the subsistence economy of the Bükk culture (Lichardus 1974) whose remains are found in the area (Fig. 6). Several mountain-adapted Neolithic groups in Germany and Switzerland used hazel and elm twigs, catkins and branch wood as winter livestock fodder (Favre & Jacomet 1998). From pollen data, Gardner (1999) suggests that Neolithic ALP (Alföld Linear Pottery) groups in the nearby Mátra Mountains were regularly coppicing hazel and hornbeam trees between *c.* 5350 and 4600 cal. BC. The Bükk may have behaved similarly and the absence of a *Quercus* rise at Kismohos (Willis *et al*. 1998) confirms its anthropogenic origin here.

Following a short recovery of the forest around 5000 cal. BC, elm declined again, this time in two steps (3rd and 4th elm declines). A substantial lowering of the total arboreal vegetation, coincident with rises in cereals and *Artemisia*, similar to those in surface samples, point to the establishment of arable fields, probably in the nearby Kelemér valley. A 300-year period of farming and coppicing coincides with the appearance of the late Neolithic Tisza-Herpály Cso''szhalom and Lengyel Cultures in the region. The discrepancy between pollen evidence for intense human activity and the small number of archaeological finds (Fig. 6) stresses the importance of systematic field walking in the evaluation of former population densities (Chapman 1999).

CONTROLS ON WETLAND DEVELOPMENT

Reconstructed palaeohydrological and hydroseral changes can be compared with the coincident upland vegetation alterations and with independent palaeoclimate proxies for Central and south-eastern Europe (Fig. 7). The Nagymohos hydrosere starts with a distinctive shallow-lake phase with floating mat formation over the lake commencing *c.* 6200 cal. BC. Concomitant shifts in both wetland and terrestrial ecosystems (*Tilia* rise) infer allogenic forcing of the wetland vegetation change. Although autogenic processes, such as gradual infilling of the basin and altered base status of the water, can initiate succession, both humification and upland pollen data imply a short-term warm/humid interval at the time of floating mat development. Palaeoclimate proxies from central Italy (Ramrath, Sadori & Negendank 2000), the GRIP ice core and North Atlantic marine core $\delta^{18}O$ minima (Johnsen *et al*. 1992; Bond *et al*. 1997) and the multi-proxy palaeoclimate reconstruction of Haas *et al*. (1998) however, all indicate a cooling event around 6200 cal. BC (Fig. 7). Nevertheless, higher than present lake levels in Italy and Switzerland (Ramrath, Sadori & Negendank 2000) point to a simultaneous precipitation increase in Central and south-east Europe, as might be expected in the warmer period suggested by the *Tilia* rise. Soil erosion, as well as allogenic factors may have been important.

Spread of *Sphagna* over the surface of the reedmace mat occurs autogenically once environmental conditions are adequate for floating-bog development (Walker 1970; Bunting & Warner 1998). The invasion of *Sphagnum palustre* marks the establishment of *Sphagnum*-dominated transitional bog associations on the mire surface, and hydrological changes during this phase were reflected in humification, plant macrofossil and pollen data. The first wet phase between 6000 and 5700 cal. BC coincides with the first elm decline (*c.* 5750 cal. BC) and the upland pollen data indicate the onset of human exploitation (selective coppicing or felling). From this point, the pollen record demonstrates repeated human activity, as well as episodic alterations in the species composition of the peat bog. If wetland succession is autogenically driven the wetland pollen and plant macrofossil sequences should be independent of changes in the upland pollen record, rather than parallel, as seen here (Fig. 7). Linking up the changes in the two data sets is complicated, but one striking feature is the coincidence of consecutive elm declines and

Cyperaceae maxima. Wet shifts were reconstructed between *c.* 6000–5700 cal. BC, *c.* 5250–5000 cal. BC and *c.* 4700–4500 cal. BC, suggesting that both human activity and climate change may have effected the vegetation.

The first decline in *Ulmus* took place in the initial *Carex*-fen phase, when human activity affected only the upland vegetation. Only the Cyperaceae peak and the subsequent appearance of *Solanum dulcamara* indicate temporary nutrient enrichment, whereas a small peak in the aluminium and potassium concentrations hints at human-induced erosion. The second elm decline is further accompanied by a modest rise in charcoal influx and the third and fourth by intensive soil erosion, and temporary nutrient enrichment during the wet-shifts, which coincide with the upland vegetation change.

The various palaeoecological data shown in Fig. 7 corroborate the idea that transitions to higher mire water table were at least partly induced by gradually intensifying human activity. Comparison of the geochemical and wetland vegetation data suggests that repeated erosion occasioned periodic standstills in nutrient sequestration: depletion can be inferred when *Sphagna* are favoured over mesotrophic moss species and *Eriophorum vaginatum* against *Carex* species. The periodic supply of nutrients, together with man-induced water table rises may have delayed autogenic succession for example during the third and fourth elm declines, when mesotrophic mosses (*Warnstorfia exannulata* and *Meesia longiseta*) appeared repeatedly (Fig. 7). Although wet-shifts are confirmed by the presence of *Daphnia* epipphia and rising Cyperaceae pollen (Fig. 7), high humification values suggest that the high water table was not stable, but alternated with periods of relatively dry mire surface conditions.

Short-term climate oscillations may influence upland and wetland vegetation development in addition to effects on woodland ascribed to human exploitation between 5800 and 4500 cal. BC. Based on microvertebrate and malacological data, Kordos (1977) and Hertelendi *et al.* (1992) regarded the mid-Holocene (6000–5000 cal. BC) in the Carpathian Basin as the Holocene climatic optimum with gradually rising summer temperatures, reaching a maximum at *c.* 5500 cal. BC. On the other hand, proxy climate records from Central and south-eastern Europe demonstrated instability even within this time-period. Our first and second wet phases coincide with one of the cold/humid periods in Central Europe (Fig. 7), but the forest disturbance and subsequent secondary succession that was also discernible, is more probably due to human activity. The later wet-shifts do not coincide with Holocene cooling events, and the third and fourth *Ulmus* declines are clearly of anthropogenic origin. All wet-shifts entailed a similar order of species replacements in the mire and coincided with elm declines, suggesting a general mechanism such as the acceleration of run-off from the bordering slopes. Nutrient enrichment and water table rise and/or fluctuation lead to

Carex species and later *Eriophorum vaginatum* temporarily replacing *Sphagna*, whose recovery was recorded as enormous spore production of *Sphagnum* cf. *cuspidatum*. Climate change was certainly involved in the first two wet-shifts, although human activity was probably decisive in triggering wetland vegetation shifts.

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