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LATE HOLOCENE HISTORY AND VEGETATION DYNAMICS OF A FLOODPLAIN ALDER CARR: A CASE STUDY FROM EASTERN BOHEMIA, CZECH REPUBLIC

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Abstract: Vegetation development in the lowland floodplain alder carr "Na bahně" (eastern Bohemia, the Czech Republic) has been studied by means of pollen and macrofossil analyses and combined with vegetation analysis performed over the last 70 years. Local successional changes started with an oxbow lake (160 cal BC) which has later terrestrialised (630 cal AD). Then it changed from a typical alluvial fen into a *Sphagnum*-dominated spring mire (950 cal AD) supplied by water arising from a river terrace surrounding the locality from three sites. In the centre of this wetland a small patch of alder carr developed (100 cal. AD), showing some tendency towards cyclic succession. The alder carr alternated several times with an open *Carex* fen (1100 cal AD to recent). The last fen-to-alder carr transition has been documented by direct observation during this century. Possible autogenic and allogenic factors driving the succession are discussed. The model of autogenic cyclic succession corresponds well with direct field observations and can be used to interpret alder carr structure, its dynamics, and function.

INTRODUCTION

Woodlands dominated by *Alnus glutinosa* occur usually on wet minerotrophic (*Alnion glutinoso-incanae* according to Zürich-Montpellier phytosociological system) or organic substrates (*Alnetea glutinosae*; the term "alder carr" is usually confined for this type). The phytosociological classification of alder carrs is well-established in Europe (DÖRING-MEDERAKE 1991, PRIEDITIS 1993, 1997), but little is known about their long-term dynamics (JENÍK 1980). Alder carrs have a limited distribution, being restricted to floodplains where the natural hydrological regime has not been strongly modified by human action.

Numerous palaeoecological studies found alder carrs to be a successional stage that is later replaced by climax forests (TALLIS 1983, WALKER 1970), but others found them to be rather stable and long-persisting systems (MAREK 1965). Fortunately, in wetland woodlands several approaches such as direct observations, dendrochronology, pollen and macrofossil analysis can be combined (FOSTER et al. 1996, DELCOURT & DELCOURT 1991) to determine the factors responsible for long-term vegetation changes. However, some limitations should be taken into account:

(1) The peat deposits under alder carrs usually undergo mineralization. Peat is aerated in the root layer of the alder and as a result, mineralization speeds up (JENÍK 1980, BENNETT &

Birks 1990). The originally flat surface of the fen, therefore, develops into hummocks and hollows. This is the case of most alder carrs described in literature. The hummocks can be up to 1 m high (Prieditis 1997). In extreme cases peat is mineralized nearly completely. Mineralization of the peat may be one of the factors responsible for the occurrence of stratigraphic hiatuses recorded in the stable, wet climate of the Middle Holocene (Rybníček & Rybníčková 1987). The peat under alder-carr communities is preserved only exceptionally, when a stable water level prevents aeration so that anoxic conditions are maintained throughout the year. This particular situation can be found indicated by a flat, permanently wet soil surface, without hummocks and hollows microtopography on the site of the present study (Klimešová & Klimeš 1996).

(2) Floodplain environments have been changing markedly during the Holocene in Central Europe, because of changing periods of sedimentation and erosion (Opravil 1983, Ellenberg 1996, Brown 1997). Periods of low sedimentation were characterized by the development of soils, fens, and cultural horizons, whereas periods of prevailing accumulation resulted in these layers being covered by gravel and clay, often with embedded trunks (Růžičková & Zeman 1994). During erosional periods, the fens developing in terrestrialized oxbows are often destroyed, resulting in the loss of pollen and macrofossils-containing sediment needed for the study of the history of alluvial alder carrs. Well-preserved, long-term palaeoecological records are therefore quite rare in contemporary floodplains (Döring-Mederake 1991, Prieditis 1993, 1997).

The locality "Na bahně" (E Bohemia) is an example of an alluvial alder carr having well-preserved and relatively long palaeoecological record. The topography of the surroundings suggest the locality was originally an oxbow lake (Sitenský 1891, Mikyška 1926). Numerous springs at the foot of the terrace, situated around the locality on three sides, ensure a stable water regime and permanently high water level. The vegetation cover of the locality has been repeatedly studied over the last 70 years (Mikyška 1926, 1964, Klimešová & Klimeš 1996), so a comparison between palaeoecological and phytosociological data can be made.

MATERIAL AND METHODS

The study site

The alder carr "Na bahně" covers an area of about 1 ha below the youngest (Weichselian) terrace on the left bank of the Orlice River, about 8 km E of its entrance to the Labe (Elbe) River (240 m a.s.l., 50°12' N, 15°58' E; Fig.1). The terrace, about 5 m high, surrounds the alder carr, from the S, SE, and SW. It is covered with a mixed forest dominated by *Quercus robur*. In the north, the alder carr is bordered by wet abandoned meadows, which are gradually being invaded by alder. At the foot of the terrace several strong springs are situated, stabilizing the water regime of the locality. Their discharge is independent of year-to-year climatic variability and of smaller fluctuations of the nearby river's water level (personal observations during the last 10 years). The site is situated about 150 m from the present river channel. Peat accumulation has recently resulted in the doming over of the surrounding terrain. This has led to a certain degree of emancipation of the locality from the direct influence of the river.

The bedrock of the locality and its surroundings is Cretaceous (Turonian) calcareous marl covered with acid sandy and gravel sediments. The mean annual air temperature is 7.8 °C, and annual precipitation is 602 mm (1901 to 1950, Nový Hradec Králové Meterological Station, 8.5 km E of the locality; Veselký 1961).

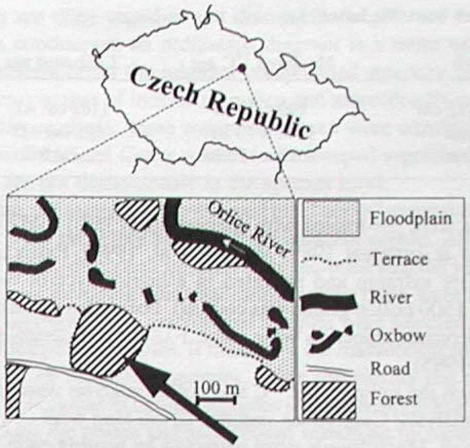

Fig. 1. Location of the study area within the Czech Republic.

The site under study is dominated by *Alnus glutinosa*, with scattered *Betula pubescens* trees. The following plants prevail in the herb layer (ordered according to their decreasing frequency): *Cardamine amara*, *Solanum dulcamara*, *Lycopus europaeus*, *Urtica dioica*, *Thelypteris palustris*, *Myosoton aquaticum*, *Calamagrostis canescens*, *Cirsium oleraceum*, *Chrysosplenium alternifolium*, *Oxalis acetosella*, *Athyrium filix-femina*, *Carex elongata*, *Mentha aquatica*, *Poa palustris*. Phytosociologically, the alder carr belongs to a nitrophilous variant of *Carici acutiformis-Alnetum* (Sádlo, pers. comm.).

Data collection

A series of exploratory borings was performed in the early spring of 1997 at the centre of the locality. Peat from nearly 2.5 to about 5 m thickness was found in the area recently covered by alder carr. Fine-grained mineral flood loam with organic detritus underlay the peat. The peat deposit reaches its maximum depth approximately 16 metres from the edge of the eroded terrace.

Sediment sequence 5 m long was taken with a Russian-type corer (Jowsey 1966) of 5 cm in diameter for litho-stratigraphic examination, ^{14}C dating, macrofossil and pollen analysis. The sediments were analyzed for their components according to Abby & Berglund (1986).

Three levels were radiocarbon-dated. A few pieces of alder wood were selected for each radiocarbon analysis. One sample (Lu4529) was dated by decay counting and two others by AMS method at the Radiocarbon Dating Laboratory, Department of Quaternary Geology, Lund, Sweden. Age calculations were based on a ^{14}C half-life of 5568 years. The results were calibrated (after Stuiver & Reimer 1993) and are reported on the calibrated calendar time scale (cal AD, cal BC).

The samples used for pollen (and other microfossil) analysis were prepared by modified acetolysis method (Erdtman 1943). As the lower part of the core had more or less a mineral

Table 1. Radiocarbon dates from "Na bahně" site.

Lab. No.	Depth	Measured ^{14}C age	Calibrated age	Method
LuA-4528	110–112 cm	890 ± 90 BP	1168 cal AD	AMS
Lu-4529	330 cm	1440 ± 70 BP	635 cal AD	decay
LuA-4551	450 cm	2020 ± 110 BP	2 cal BC	AMS

character, the samples were pre-treated with concentrated (35%) cold hydrofluoric acid (HF) for 24 hours (Faegri & Iversen 1989, Moore et al. 1991). Extracted microfossils were lightly stained by 0.3% safranin and mounted in a liquid glycerol-water mixture. In each sample an average of 1500 pollen grains was counted. For pollen identification, the following keys as well as a reference collection were used: Faegri & Iversen (1989), Moore et al. (1991), Punt (1976–1995).

The core from which the samples for ^{14}C and pollen analysis were taken was subsampled also for macrofossil analysis: Contiguous samples 20 cm long were cut, and the fresh volume of each was determined. Macrofossils were extracted by heating each sample for 5 minutes in a 5% potassium hydroxide (KOH) solution and sieved with running water. Sieves with mesh sizes of 200 µm, 300 µm and 700 µm were used. The residues were examined under a dissecting stereomicroscope. For the macrofossil diagram, the absolute number of each taxon was recalculated to a standard volume of 500 cm^3 of fresh sediment.

Plant nomenclature follows Tutin et al. (1964–1980) and Frey (1995), pollen nomenclature follows ALPADABA (*Alpine Palynological Data-Base*, housed at the Geobotanical Institute, Bern).

Data analysis

In the pollen diagram local elements were distinguished from regional ones according to the following method (after Rybníčková & Rybníček 1971 and Hulme & Shirriffs 1994): Taxa present in both the pollen and macrofossil data-sets were considered as local ("gravity component" of the pollen spectra according to Faegri & Iversen 1989), whereas pollen taxa not present among the macrofossils were considered to be of extralocal, regional, or extraregional ones. Pollen belonging to one or several strictly wetland species was considered as part of the local component, even if it was not recorded as a macrofossil. Broad pollen types, which include at least one species growing in mesic or dry habitats, were excluded from the local diagram to avoid possible misinterpretations. Percentage values were calculated on the basis of the regional pollen sum (for the list of regional pollen types see the Appendix). Concealed, corroded, degraded, and well preserved, but indeterminable pollen grains were included under "varia". Printing of the diagrams was performed with TILIA computer program, written by E.C. Grimm (Springfield).

Zonation of the pollen and macrofossil diagrams was made visually, using both the presence and the abundance of the taxa. A more formalized approach to delimit the zones was also applied, using detrended correspondence analysis – DCA (Hill 1979, ter Braak & Šmilauer 1998). DCA belongs to a group of multidimensional scaling methods designed to detect the underlying pattern in the data. It is an extension of correspondence analysis (CA), eliminating the arch effect that is produced by CA if data are sampled along long gradients (Wartenberg et al. 1987). DCA results, presented as ordination diagrams, show the overall trends in the data. Similar samples are close together and dissimilar samples are far from each other. If data are more or less continuous, an ordination diagram is a more useful tool than cluster analysis, because it reflects better the inherent complicated structure in the data.

Log-transformed percentages of individual pollen and macrofossils taxa were used as input data in our case. Before analysis, some macrofossil taxa were combined into higher pollen taxa; e.g. all macrofossil finds of *Carex* species were lumped together because pollen grains of individual species are not determinable at the species level.

In the scatter diagram, the samples were grouped into "zones" using the following procedure: Three pollen samples were randomly selected from adjacent depths. All other pollen samples located in the range of the three chosen samples were included into the selection. The selection process was continued by including aditional samples until there were no overlapping zones in the selected pollen samples. Then, macrofossil samples were selected from the same depths as the previously-selected pollen samples. If necessary, the macrofossil selection was continued in the same way as that of the pollen samples. After completing the macrofossil selection, the pollen selection was adjusted to include samples from corresponding depths. This iterative procedure continued until the pollen and macrofossil selections included contiguous samples from the same depths. Finally, the same procedure was performed for samples so far not included into any selection. Thus, an equal number of non-overlapping envelopes, which included samples from the same depths, was obtained for pollen and macrofossils. The whole procedure was repeated 100 times in order to determine alternative zonations.

RESULTS

The results of the pollen and macrofossil analyses are presented in the form of diagrams (Figs. 2 and 3). Four local zones were distinguished on both pollen and macrofossil diagrams. Absolute ages of the zone boundaries can be roughly estimated by linear interpolation from three available radiocarbon dates (Tab. 1).

If the pollen and macrofossil data are used simultaneously for DCA analysis, only two zones can be distinguished in the ordination diagram (Fig. 4). Further division would result in an overlap of envelopes, including samples belonging to individual zones. The lower zone corresponds to the visually delimited zone NBL-1 (oxbow lake phase; 160 cal BC – 610 cal AD). The remaining samples form a group that can be further divided if the taxa are weighted or if a different approach gives more weight to the dominant taxa. For example, zone NBL-2 is differentiated from the other zones by the abundant *Filipendula* and *Caltha* macrofossils and *Filipendula* pollen, zone NBL-3 by *Equisetum* and *Sphagnum* spores, and zone NBL-4 by abundant *Cyperaceae* pollen and *Betula* fruits.

Zone NBL-1 (oxbow lake phase; 160 cal BC – 610 cal AD)

This zone is characterized by the findings of indicators of permanent water bodies, suggesting that a small oxbow lake has been present. According to the finds of aquatic plant remains (*Myriophyllum spicatum*, *Ranunculus* subgen. *Batrachium*, *Potamogeton*, *Nuphar lutea*, *Ceratophyllum demersum* and *Nymphaea alba*) its depth was about 1.5 m. The occurrence of *Nympheaceae* and *Ceratophyllum* has been confirmed by the findings of trichosclereids and leaf-spines, respectively (determination after van Geel 1978). The high diversity of aquatic macrophyte vegetation indicates that the oxbow lake was not completely shaded by trees (Prach et al. 1996). The occurrence of *Mougeotia* zygospores (chlorococcal algae) indicate permanent, shallow-water conditions as well (Jankovská & Komárek 1982).

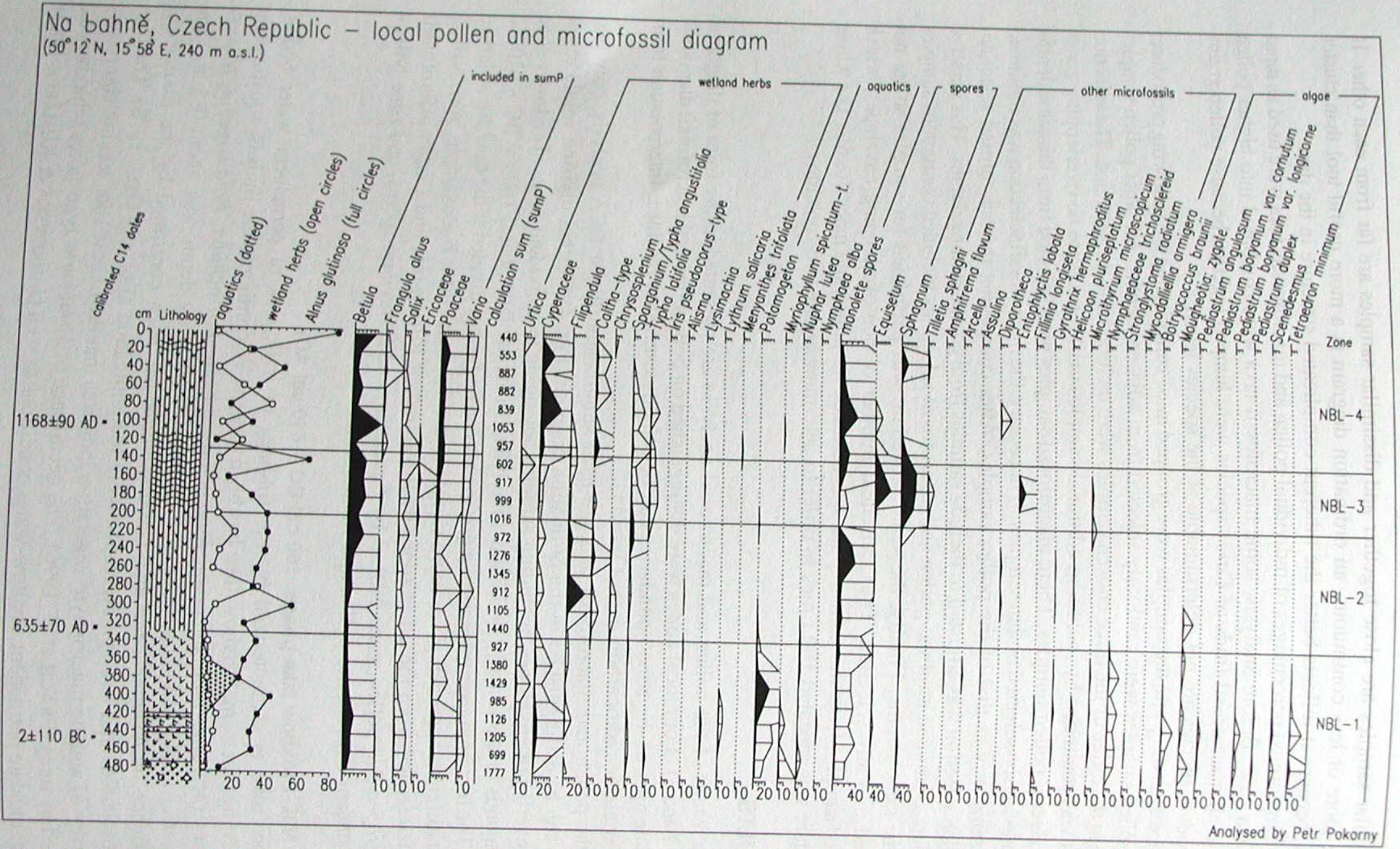

Fig. 2. Percentage of pollen diagram from the alder carr "Na bahně". Only the taxa representing local vegetation elements are selected following the procedure described in the Methods section. Pollen types that do not fall into the local pollen types are listed in the Appendix. For sediment description, see Fig. 3.

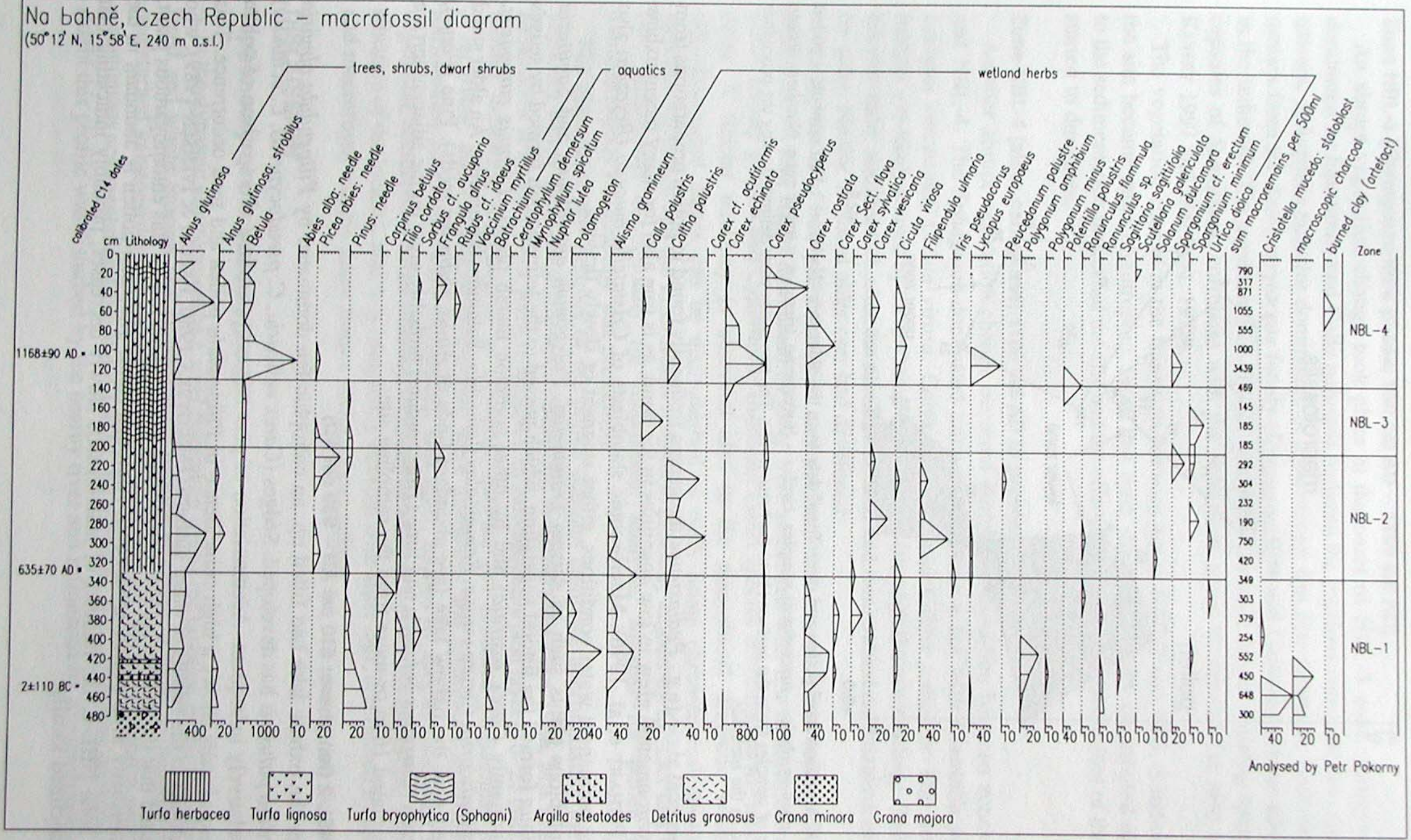

Fig. 3. Macrofossil diagram from the alder carr "Na bahně". Absolute number of findings was recalculated to a standard volume of 500 cm^3 of fresh sediment. If not stated differently, all findings represents seeds.

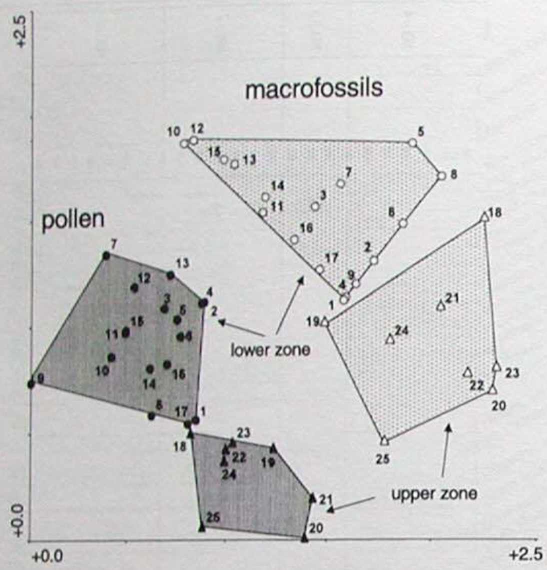

Fig. 4. DCA ordination of pollen and macrofossil data from the alder carr "Na bahně". Full symbols – pollen samples, open symbols – macrofossil samples, circles – lower zone, triangles – upper zone. Numbers denote the order of samples from the surface (1) to the bottom (25). The two zones were delimited using the procedure described in the methods.

Chlorococcal algae (e.g., *Pediastrum*, the genera frequently found in pollen preparations from lake environments) grew in low quantities in the pond, as is true also for many recent oxbow lakes (PITHART et al. 1996). Macroscopic statoblasts of *Cristatella mucedo* (*Bryozoa*) also indicate permanent water conditions, either stagnant or slowly flowing.

Amphibious plants such as *Alisma gramineum*, *Polygonum amphibium*, and *Sagittaria sagittifolia* formed the littoral vegetation, which passed to the telmatic belt formed by sedges (predominantly *Carex rostrata*) and by other common marsh plants (*Lycopus europaeus*, *Lythrum salicaria*, *Cicuta virosa*, *Ranunculus flammula*, *Solanum dulcamara*). An alder stand occurred near the oxbow lake (see abundant finds of *Alnus glutinosa* seeds). Pine (*Pinus*), hornbeam (*Carpinus betulus*), and lime (*Tilia cordata*) probably grew on the adjacent terrace slope situated 16 m or more from the sampling site.

Zone NBL-2 (fen phase; 610 cal AD – 930 cal AD)

After the oxbow lake had filled up, an eutrophic fen dominated by *Filipendula ulmaria* and *Caltha palustris* has developed. Sedges (*Carex vesicaria*, *C. pseudocyperus*, *C. echinata*) were relatively infrequent. Accumulation of peat began at that time. Comparison of pollen and macrofossils shows a high coincidence in *Filipendula* pollen and seed occurrence. This corresponds to the results of other authors (JANKOVSKÁ 1980, FAEGRI & IVERSEN 1989), who concluded that the gravity component prevails in the pollen rain of this entomogamous plant, with unusually high pollen production. Although *Alnus glutinosa* pollen is abundant in the entire zone NBL-2, the number of macrofossils slowly decreases, probably indicating that alder declined locally.

Zone NBL-3 (*Sphagnum* mire phase; 930 cal AD – 1100 cal AD)

An abrupt vegetation change took place at the onset of NBL-3 zone. *Sphagnum* mire, dominated by *Equisetum* and *Calla palustris* replaced the previous eutrophic fen. Among the mosses, *Sphagnum palustre* dominated, *S. squarrosum* was less common. Leaf remains of mosses from the *Amblystegiaceae* family (*Drepanocladus* and *Calliergon*) were also present in the sediment. The occurrence of *Tilletia sphagni*, a parasitic fungus forming spores in the capsules of *Sphagnum*, correlates with the *Sphagnum* spore occurrence (as also noted by KUHRY 1997 and VAN GEEL 1978).

The vegetation change at the transition between zones NBL-2 and NBL-3 indicates that the site became more oligotrophic. From that time, the river activity contributed only little to the sedimentation process at the site and the effect of local springs at the foot of the terrace started to dominate.

Zone NBL-4 (alder carr phase; 1100 cal AD to present)

Another abrupt vegetation change occurred during the transition between zones NBL-3 and NBL-4. The *Sphagnum*-dominated mire changed into a fen with *Potentilla palustris*, *Lycopus europaeus*, *Cicuta virosa*, *Carex echinata*, and *Caltha palustris*. The decline of mosses was likely caused by the invasion of birch trees (through the overshading). The surface became more nutrient-rich after the mosses declined and this enabled colonization of the site by alder. Finally, a closed alder carr had developed.

During the next 900 years the alder carr declined and re-established repeatedly. In the pollen record four stages dominated by alder were associated with few heliophilous wetland herbs, mostly grasses and *Cyperaceae* (different *Carex* species according to the macrofossil data). A similar tendency is observed also in the macrofossil diagram, where three alder-dominated stages can be distinguished as well. Some chronological displacement between the pollen and the macrofossil records is probably caused by the fact that the core was subsampled contiguously for macrofossil analysis, whereas for pollen analysis a discontinuous subsampling was performed.

The uppermost two samples of the pollen diagram comprise approximately the last 70 years, for which direct botanical observations are available (MIKYŠKA 1926, MIKYŠKA 1964, KLIMEŠOVÁ & KLIMEŠ 1996, RYDLO, unpubl.). In the *Sphagnum* peat layer (16–27 cm), several mosses indicating mesotrophic to eutrophic habitats are recorded (*Sphagnum palustre*, *S. recurvum*, and *Calliergon cordifolium* were abundant, and *Sphagnum squarrosum* and *Rhizomnium punctatum* were infrequent). This layer, formed by species indicating an open vegetation, corresponds to the situation recorded by MIKYŠKA (1926) in the 1920s. The current situation of the locality, which is completely covered with alder carr, is reflected by the pollen and macrofossil sample taken from a surface moss polster.

DISCUSSION

Taphonomy of the pollen spectra

In the dynamic environment of a river floodplain where the position of the river bed is not fixed and where erosion and accumulation periods alternate, a long, well-preserved, and undisturbed palaeoecological record has rarely been studied. We have found a profile with a continuous sedimentation from about 160 BC up to recent. It is a pertinent question to what extent this profile was disturbed by the nearby river and influenced by accumulation of flood loams. The deposition of redeposed pollen and macrofossils may complicate the interpretation of the palaeoecological record. The lowermost one third of the profile was formed predominantly by finely granular clay material, which represents a flood deposit. One reason why such deposits were avoided in palaeoecological studies in the past was the fear that the pollen would be selectively transported by water either into or out of the site. The ecological coherence of floodplain diagrams suggest that this is not an insurmountable problem in most cases (Brown 1997). This seems to be true also in our case as there was no significant change in the regional pollen record at the transition from floodplain sedimentation to autochthonous organic sedimentation. In addition, direct observations showed (Brown 1985) that while flood waters often contain a high concentration of pollen, flood deposits contain very little due to the constant turbulence which does not allow pollen to settle out. Because of this, we consider our results comparable and equally reliable to those obtained from any peat-bog.

Zonation of the pollen and macrofossil diagrams

We used two approaches to evaluate the diagrams. Visual zonation is the commonly used one whereas multivariate analysis is less frequently used even though is an efficient and well-established approach (Prentice 1986). The advantage of multivariate analysis over subjective visual evaluation is its repeatability (using the same data and the type of analysis, the same results are obtained by any researcher). However, the process of multivariate analysis does not include any information outside the analyzed data set. Thus, no experience of the researcher is used in the interpretation of primary data. As a result, the zonation based on a multivariate analysis reflects well the pattern in the data-set, but its predictive power is usually lower than that of the traditional visual zonation.

Visual evaluation of our diagrams resulted in four zones differing in species composition and abundance. To establish individual zones more weight was given either to species composition (transition of zones NBL-1/2) or to the dominance of selected taxa (transition of zones NBL-2/3 and NBL-3/4). Using the ordination axes I and II, DCA procedure separated individual pollen and macrofossil samples quite well. Further separation of any group consisting of a minimum of 3 samples based on both pollen and macrofossils was possible in one way only, with a zone boundary placed between sample Nos. 17 and 18. Any other division would result in an overlap between envelopes enclosing groups of samples based on pollen, macrofossil data, or both.

Local vegetation succession

It has been shown in numerous palaeoecological studies that vegetation succession during the terrestrialization of freshwater lakes is rarely determined by a single factor. Numerous autogenic as well as allogenic factors cause the probabilistic character of the transition between individual succession stages (Walker 1970, Tallis 1983, Singer et al. 1996, Yu et al. 1996). The main factors responsible for successive vegetation development in the site under the present study seem to be the changing hydrological regime of the locality (effects of the river and artesic springs), and changes in nutrient availability (competition for nutrients between *Sphagnum* mosses, herbs, and seedlings of woody plants). The fast transition between individual successional stages has been promoted by a high accumulation rate of peat (2.4 mm/year, on average). The effect of allogenic factors prevailed at the beginning of succession, and later autogenic factors became dominant. Over the last nine centuries autogenic factors contributed significantly to the characteristic successional pattern in the alder carr community as described below.

The dynamics of the alder carr

Forests dominated by alder have been present in Central Europe since the Early Holocene (Huntley & Birks 1983, Lang 1994, Berglund et al. 1996). They represent an important successional stage of terrestrialization of freshwater bodies. In wet, oceanic climates they are a characteristic transient vegetational stage in eutrophic lake basins that have filled up. Later, they often develop into oligotrophic *Sphagnum* mires (Walker 1970, Tallis 1983). According to some authors (e.g. Marek 1965), alder-dominated forests may persist continuously at one site over thousands of years. However, the character of the alder life cycle (McVean 1953, 1956a) makes this idea uncertain. Long-term persistence of alder-dominated stands require continuous alder regeneration. Alder carrs require nearly full light conditions for their establishment. Most alder-dominated stands with a canopy cover of 30–50% are not suitable for alder seedlings to survive (Korpeľ 1995, Tucker & Fitter 1981). The light regime in a closed alder carr is insufficient even for regeneration from the bases of dead mother trunks, so daughter trees have a low vitality and soon die. Seedlings and basal shoots can develop and contribute to the canopy only in a swamp carr on a floating mat where trees are short (2 to 3 m tall, with little foliage) and sparse (McVean 1956b).

Another factor adversely affecting the establishment of alder seedlings in alder-dominated stands is often the too high soil moisture (McVean 1956a). In an alder carr, mineralization of the peat results in increased soil moisture and waterlogging. The age structure of most alder stands also raises doubts about their long-term persistence. Even-aged alder populations, indicating a short single period of alder establishment, are usually found (Pigott & Wilson 1978, Tucker & Fitter 1981). Therefore, the natural regeneration of alder in an alder carr seems to be unlikely.

In the case of the "Na bahně" site, we have found alder carr persisting over several centuries. However, it was found in the palaeoecological record to be a dynamic system with a tendency towards cyclic development. Closed-canopy alder carr alternated several times with open vegetation dominated by sedges and *Sphagnum*. It resembles the hypothesis of cyclic development made for various types of forests (Míchal 1983, Delcourt & Delcourt 1991, Korpeľ 1995, Schmidt 1998).

The second half of the last alder carr cycle has been recorded on the site by several botanists and documented since the 1920s. In the centre of the locality, Mikyška (1926) described a mire surrounded by young alder carr forming a belt close to the terrace edges. In his second paper (Mikyška 1964), he described the vegetation of the same locality after 38 years. The central part of the mire was already overgrown by young alder forests. At present alder forms a homogeneous stand on the whole surface of the site (Klimešová & Klimeš 1996), differing only in the age of the trees between the centre and the margin (Klimešová et al. 1997). The results of the botanical studies carried out over the last 75 years accord well with the pollen and macrofossil analyses. The observed pattern of long-term cyclic development can be explained using one of the following models:

(a) Allogenic model – direct human disturbance

The decline of the tree canopy could be associated with cutting. Decomposition of alder trunks and stumps is relatively fast, so their absence in the peat noted by us during the pilot study cannot serve as evidence against cutting. However, the timing of the individual successional cycles of the alder carr does not correlate with that of anthropogenic impact, as evidenced by pollen analysis (POKORNÝ & BENEŠ, in prep.). Therefore the hypothesis of direct human disturbance is not supported by any evidence.

(b) Other allogenic impacts

Changes in water level and nutrient availability, either human- or climatically-induced, may also stimulate or prevent the establishment of alder and eventually cause a dieback of the fully matured stand. Human-induced changes of hydrological conditions resulting in the dieback of alder-dominated forest have been described by BROCK et al. (1989). JANSSEN et al. (1995) explained the dieback and new establishment of an alder stand by fluctuations in water level caused by long-term changes in river discharge. It is difficult to reject any of these hypotheses in our case. However, the results of the pollen and macrofossil analyses and the continuous character of the sedimentation indicate that abrupt hydrological changes did not occur during critical periods in the development. The same holds true for nutrient availability.

(c) Autogenic model

As alder cannot regenerate in closed-canopy stands, a massive dieback of even-aged alder trees can be expected at an age of 100–150 years, depending on their vitality. Increased light availability may stimulate the development of an open mire covered with light-demanding plants and intensively accumulating peat. The more the substrate has been mineralized during the previous alder phase, the longer the stage of open vegetation is, because the mineralization resulted in an increased soil moisture. Therefore, the evapotranspiration rate decreases as the result of tree layer dieback, thus contributing to the general waterlogging of the site. Only when the newly formed peat layer starts doming over the groundwater table again (as a whole or by forming tussocks), alder seedlings may establish on the site and the cycle is completed. A newly-established alder stand is even-aged because the establishment took place during a short time. This development can be further complicated by the fluctuation of the water level.

If the peat layer is repeatedly mineralized during the alder carr phase, the cycle can hardly be inferred from palaeoecological data. In the case of larger alder stands the cyclic development may take place in a mosaic of patches. Even in this case pollen analysis does not represent a suitable approach for studying the long-term cyclic development, because of the noise caused by the dispersal of pollen between individual patches. WIEGERS (1985) proposed a similar pattern of cyclic succession for floating fen woodlands albeit with one more factor: vertical movement of the whole surface below the water table caused by the weight of the trees. In the central part of the "Na bahně" site, where the core has been taken, peat mineralization is a slow process due to the high and stable water level resulting from the local springs. Thus the exceptional hydrological conditions resulted in a well-preserved palaeoecological record. Cyclic development directed by autogenic factors was still possible here: the high water-level further increased after a dieback of the tree layer, and later on, when the mire vegetation formed relatively dry hummocks, establishment of alder was again made possible.

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REFERENCES

ABBY B. & BERGLUND B.E. (1986): Characterization of peat and lake deposits. In: BERGLUND B.E. (ed.), *Handbook of Holocene palaeoecology and palaeohydrology*, J. Wiley, Chichester, pp. 231–246.

BENNETT K.D. & BIRKS H.J.B. (1990): Postglacial history of alder (*Alnus glutinosa* (L.) GAERTN.) in the British Isles. *J. Quaternary Sci.* 5: 123–133.

BERGLUND B.E., BIRKS H.J.B., RALSKA-JASIEWICZOWA M. & WRIGHT H.E. (1996) (eds.): *Palaeoecological events during the last 15 000 years*. J. Wiley, Chichester.

BROCK T.C.M., JONGERHUIS R., VAN DER MOLEN P.C. & RAN E.T.H. (1989): A comparison of the history and present state of an *Alnus glutinosa* and *Betula pubescens* dominated patch of wetland forest in the nature reserve "Het Molenven", The Netherlands. *Acta Bot. Neerl.* 38: 425–437.

BROWN A.G. (1985): The potential of pollen in the identification of suspended sediment sources. *Earth Surface Processes & Landform* 10: 27–32.

BROWN A.G. (1997): *Alluvial geoarchaeology (Floodplain archaeology and environmental change)*. Cambridge University Press, Cambridge.

DELCOURT H.R. & DELCOURT P.A. (1991): *Quaternary ecology. A paleoecological perspective*. Chapman & Hall, London.

DÖRING-MEDERAKE U. (1991): Feuchtwälder im nordwestdeutschen Tiefland. *Scripta Geobot.* 19: 1–22.

ELLENBERG H. (1996): *Vegetation Mitteleuropas mit den Alpen*. Ed. 5. Verlag Eugen Ulmer, Stuttgart.

ERDTMAN G. (1943): *An introduction to pollen analysis*. Chronica Botanica, Waltham.

FAEGRI K. & IVERSEN J. (1989): *Textbook of pollen analysis*. J. Wiley, Chichester.

FOSTER D.R., ORWIG D.A. & MCLACHLAN J.S. (1996): Ecological and conservation insights from reconstructive studies of temperate old-growth forests. *Trends Ecol. Evol.* 11: 419–424.

FREY W., FRAHM J.P., FISCHER E. & LOBIN W. (1995): *Die Moss- und Farnpflanzen Europas*. G. Fischer Verlag, Stuttgart.

HILL M.O. (1979): *DECORANA, a FORTRAN program for detrended correspondence analysis and reciprocal averaging*. Cornell University Press, Ithaca.

HULME P.D. & SHIRRIFFS J. (1994): The Late-glacial and Holocene vegetation of the Lang Lochs Mire area, Gulberwick, Shetland: a pollen and macrofossil investigation. *New Phytol.* 128: 793–806.

HUNTLEY B. & BIRKS H.J.B. (1983): *An atlas of past and present pollen maps for Europe 0-13,000 years ago*. Cambridge University Press, Cambridge.

JANKOVSKÁ V. (1980): *Paläogeobotanische Rekonstruktion der Vegetationsentwicklung im Becken Třeboňská pánev während des Spätglazials und Holozäns*. Vegetace ČSSR A11, Academia, Praha.

JANKOVSKÁ V. & KOMÁREK J. (1982): Das Vorkommen einiger Chlorokokkalalgen im böhmischen Spätglazials und Postglazial. *Folia Geobot. Phytotax.* 17: 165–195.

JANSSEN C.R., BERENDSEN H.J.A. & VAN BROEKHUIZEN A.J.D. (1995): Fluvial activity and vegetation development 4000–2000 BP in southwestern Utrecht, The Netherlands. *Meded. Rijks Geol. Dienst* 52: 357–367.

JENÍK J. (1980): Struktura slatinné olšiny (*Carici elongatae-Alnetum*) v regresivní fázi (Structure of alder carr (*Carici elongatae-Alnetum*) in the regressive stage). In: HINDÁK F. (ed.), *Zborník referátov z 3. zjazdu Slovenskej botanickej spoločnosti pri SAV vo Zvolene (Proceedings of the 3rd congress of the Slovak Botanical Society of S.A.S., Zvolen)*, SBS pri SAV & VŠLD, Bratislava & Zvolen, pp. 53–57.

JOWSEY P.C. (1966): An improved peat sampler. *New Phytol.* 65: 245-248.

KLIMEŠOVÁ J. & KLIMEŠ L. (1996): Vegetace přírodní památky "Na bahně" po 70 letech (Vegetation of the Natural Reserve "Na bahně" (E. Bohemia, Czech Republic) after 70 years). *Příroda* 5: 147–157.

KLIMEŠOVÁ J., KLIMEŠ L. & KYNCL J. (1997): Věková struktura olše a břízy v olšině "Na bahně" (Age structure of *Alnus glutinosa* and *Betula pubescens* in the alder carr "Na bahně" (E Bohemia, Czech Republic)). *Příroda* 11: 85–93.

KORPEĽ Š. (1995): *Die Urwälder der Westkarpaten*. Gustav Fischer Verlag, Stuttgart.

KUHRY P. (1997): The palaeoecology of a treed bog in western boreal Canada: a study based on microfossils, macrofossils and physico-chemical properties. *Rev. Palaeobot. Palynol.* 96: 183–224.

LANG G. (1994): *Quartäre Vegetationsgeschichte Europas*. Gustav Fisher Verlag, Jena.

MAREK S. (1965): Biologia i stratygrafia torfowisk olszynowych w Polsce (Biology and stratigraphy of the alder bogs in Poland). *Zesz. Problemove Postepów Nauk Roln.* 57: 5–158.

MCVEAN D.N. (1953): Biological flora of the British Isles. *Alnus glutinosa* (L.) GAERTN. *J. Ecol.* 41: 447–466.

MCVEAN D.N. (1956a): Ecology of *Alnus glutinosa* (L.) GAERTN. III. Seedling establishment. *J. Ecol.* 44: 195–218.

MCVEAN D. N. (1956b): Ecology of *Alnus glutinosa* (L.) GAERTN. V. Notes on some British Alder populations. *J. Ecol.* 44: 321–330.

MÍCHAL I. (1983): Dynamika přírodního lesa (Dynamics of natural forest). *Živa* 31: 8–12, 48–51, 85–88, 128–133, 163–168, 233–238.

MIKYŠKA R. (1926): Reservace "Na bahně" u Bělče nad Orlicí na Královéhradecku ("Na bahně" natural reserve near Běleč nad Orlicí; Hradec Králové district). *Spisy Přír. Fak. Karlovy Univ.* 50: 1–19.

MIKYŠKA R. (1964): Naturschutzgebiet "Na bahně" bei Hradec Králové (Königgrätz) nach 38 Jahren. *Preslia* 36: 28–37.

MOORE P.D., WEBB J.A. & COLLINSON M.E. (1991): *Pollen analysis*. Blackwell, Oxford.

OPRAVIL E. (1983): Údolní niva v době hradištní (The river floodplain in Early Medieval period). *Stud. Archeol. Ústavu Českoslov. Akad. Věd, Brno* 11/2: 1–78.

PIGOTT C.D. & WILSON J.F. (1978): The vegetation of North Fen at Esthwaite in 1967–9. *Proc. Roy. Soc. London, Ser. B, Biol. Sci.* 200: 331–351.

PITHART D., ELSTER J., KOMÁREK O. & KLABOUCHOVÁ A. (1996): Microphyte vegetation. In: PRACH K., JENÍK J. & LARGE A.R.G. (eds.), *Floodplain ecology and management, The Lužnice River in the Třeboň Biosphere Reserve, Central Europe*, SPB Academic Publishing, Amsterdam, pp. 99–112.

PRACH K., HUSÁK Š., ČERNÝ R., KUČERA S., GUTH J., RYDLO J. & KLIMEŠOVÁ J. (1996): Species and vegetation diversity along the river. In: PRACH K., JENÍK J. & LARGE A.R.G. (eds.), *Floodplain ecology and management, The Lužnice River in the Třeboň Biosphere Reserve, Central Europe*, SPB Academic Publishing, Amsterdam, pp. 62–98.

PRENTICE I.C. (1986): Multivariate methods for data analysis. In: BERGLUND B.E. (ed.): *Handbook of Holocene palaeoecology and palaeohydrology*, J. Wiley, Chichester, pp. 775–797.

PRIEDITIS N. (1993): Black alder swamps in Latvia. *Folia Geobot. Phytotax.* 28: 261–277.

PRIEDITIS N. (1997): *Alnus glutionosa*-dominated wetland forests of the Baltic region: community structure, syntaxonomy and conservation. *Pl. Ecol.* 129: 49–94.

PUNT W. (1976-1995): *The northwest European pollen flora 1–7*. Elsevier, Amsterdam.

RŮŽIČKOVÁ E. & ZEMAN A. (1994): Paleogeographic development of the Labe river flood plain during the Holocene. In: RŮŽIČKOVÁ E. & ZEMAN A. (eds.), *Holocene flood plain of the Labe river, Contemporary state of research in the Czech Republic*, Geological Inst. AS CR, Prague, pp. 104–111.

RYBNÍČEK K. & RYBNÍČKOVÁ E. (1987): Palaeogeobotanical evidence of middle Holocene stratigraphic hiatuses in Czechoslovakia and their explanation. *Folia Geobot. Phytotax.* 22: 313–327.

RYBNÍČKOVÁ E. & RYBNÍČEK K. (1971): The determination and elimination of local elements in pollen spectra from different sediments. *Rev. Palaeobot. Palynol.* 11: 165–176.

SCHMIDT W. (1998): Dynamik mitteleuropäischer Buchenwälder. *Naturschutz Landschaftsplannung* 30: 242–249.

SINGER D.K., JACKSON S.T., MADSEN B.J. & WILCOX D.A. (1996): Differentiating climatic and successional influences on long-term development of a marsh. *Ecology* 77: 1765–1778.

SITENSKÝ F. (1891): *Über die Torfmoore Böhmens*. Archiv Naturw. Landesdurchforschung Böhmen, Prag.

STUIVER M. & REIMER P.J. (1993): Extended ^{14}C database and revised CALIB radiocarbon calibration program. *Radiocarbon* 35: 215–230.

TALLIS J.H. (1983): Changes in wetland communities. In: GORE A.J.P. (ed.), *Ecosystems of the word 4A, Mires: swamp, bog, fen and moor*, Elsevier, Amsterdam. pp. 311–347.

TER BRAAK C.J.F. & ŠMILAUER P. (1998): *CANOCO reference manual and user's guide to CANOCO for Windows Software for canonical community ordination (version 4)*. Microcomputer Power, Ithaca.

TUCKER J.J. & FITTER A.H. (1981): Ecological studies at Askham Bog Nature Reserve 2. The tree population of Far Wood. *Naturalist* 106: 3–14.

TUTIN T.G. et al. (eds.) (1964–1980): *Flora europaea 1–5*. Cambridge University Press, Cambridge.

VAN GEEL B. (1978): A palaeoecological study of Holocene peat bog sections in Germany and the Netherlands. *Rev. Palaeobot. Palynol.* 22: 337–344.

VESECKÝ A. (1961): *Podnebí Československé socialistické republiky, Tabulky (Climate of Czechoslovakia, Tables)*. ČHMÚ, Praha.

WALKER D. (1970): Direction and rate in some British postglacial hydroseres. In: WALKER D. & WEST R.G. (eds.), *Studies in the vegetational history of the British Isles*, Cambridge University Press, Cambridge, pp. 117–139.

WARTENBERG D., FERSON S. & ROHLF F.J. (1987): Putting things in order: a critique of detrended correspondence analysis. *Amer. Naturalist* 129: 434–448.

WIEGERS J. (1985): Succession in fen woodland ecosystems in the Dutch haf district. *Diss. Bot.* 86.

YU Z., MCANDREWS J.H. & SIDDIQI D. (1996): Influences of Holocene climate and water levels on vegetation dynamics of a lakeside wetland. *Canad. J. Bot.* 74: 1602–1615.

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APPENDIX

The list of pollen types not included in local pollen diagram (for separation criteria see methods)

Trees and shrubs: *Abies alba*, *Acer*, *Carpinus betulus*, *Cornus sanguinea*, *Corylus avellana*, *Euonymus europaeus*, *Fagus sylvatica*, *Fraxinus excelsior*, *Hedera helix*, *Juglans*, *Juniperus*, *Picea abies*, *Pinus sylvestris*, *Quercus*, *Sambucus nigra*, *Tilia*, *Ulmus*, *Viburnum opulus*, *Viscum album*.

Anthropogenic indicators: *Cannabis sativa*, *Centaurea cyanus*, *Chenopodiaceae*, *Convolvulus arvensis*, *Plantago lanceolata*, *Plantago major/media*, *Polygonum aviculare*, *Rumex acetosa*-type, *Rumex acetosella*-type, *Secale cereale*, *Triticum*-type, *Zea mays*.

Herbs: *Compositae* subfam. *Cichorioideae*, *Compositae* Subfam. *Asteroideae*, *Cruciferae*, *Galium*-type, *Umbelliferae*, *Caryophyllaceae*, *Gramineae*, *Calluna*, *Calystegia*, *Campanula*, *Centaurea jacea*-type, *Epilobium*, *Euphorbia*, *Helianthemum nummularium*-type, *Humulus lupulus*, *Impatiens*, *Labiatae*, *Lotus*-type, *Melampyrum*, *Mentha*-type, *Papilionaceae*, *Polygonum persicaria*-type, *Ranunculus*-type, *Rosaceae*, *Rubus*, *Sanguisorba officinalis*, *Stachys*-type, *Symphytum*, *Trifolium*, *Valeriana officinalis*-type, *Veronica*-type, *Viola palustris*-type.

Spores: *Anthoceros punctatus*, *Lycopodium annotinum*, *Polypodium*.