Role of man in the development of Holocene vegetation in Central Bohemia

Vliv činnosti člověka na lokální vývoj vegetace holocénu středních Čech

Petr P o k o r n ý

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In the subcontinental, semiarid lowland region of Central Bohemia (Czech Republic), continuous human impact acting together with diverse natural environmental conditions resulted in the present extraordinarily complex pattern of vegetation. Three radiocarbon-dated pollen diagrams for the area indicate that this complexity results from past vegetation development. During prehistory, places suitable for settlement (with respect to climate, geology, hydrology, etc.) were colonized and transformed first. This resulted in a diachrony in vegetation development due to human activity starting in the first half of the Holocene. This caused an increase in diversity in the region as plant species persisting from previous periods, along with those associated with different agricultural practices, increased. Local abiotic factors affected not only the chronology of human impact but also its specific effects on the ecosystem. Anthropogenic pressure may have had different effects under different conditions. Human population pressure was the mediator between the abiotic diversity and selectively transformed vegetation suitable for the respective habitats. Differences in the chronology of human impact, mixed oak woodland degradation, and the chronology of beech, silver fir and hornbeam expansion are documented for the different ecological zones of the study area. These differences shed light on the mechanisms resulting in some of the important changes in Holocene vegetation. In the absence of man, the decline in mixed oak woodlands, typical of the Middle Holocene in Central Bohemia, would have been probably much slower and less extensive. Unlike in the uplands and mountains, the expansion in the area of beech, silver fir and hornbeam would have been insignificant. The present vegetation resulted to a large extent from management during High Middle Ages. There is almost no continuity in vegetation from the late prehistory to the present.

K e y w o r d s : Central Europe, the Holocene, deforestation, forest composition changes, human impact, pollen analysis

Introduction

Central Bohemia is the lowland part of the Czech Republic, with the capital Prague at its southern edge. This region is specific in terms of Central European environment. Diverse geology and soil conditions, a long history of human impact and its geographical position at the transition between continental and oceanic Europe have resulted in a characteristic pattern of contrasting biotopes and high biological diversity. This is without doubt a result of complicated developments during the Holocene. Unfortunately, due to the absence of an adequate fossil record in the form of peat deposits (the region is too dry for peat formation), our knowledge of the history of the regional vegetation is very incomplete and, as a consequence our understanding of the development of present day vegetation and landscape diversity is poor.

The first palaeobotanical data for Central Bohemia is that of Losert (1940a,b) who described the development of Late-Glacial and Early Holocene vegetation at two adjacent sites in the middle course of the Labe (Elbe) river. Later research of Pacltová & Hubená (1994) and Břízová (1995, 1999a) concentrated on the middle Labe valley, a specific ecological zone, and resulted in a relatively complete picture of the vegetational history of the floodplain during Early and Late Holocene. In N Bohemia, a large lowland lake Komořanské jezero was studied using pollen analyses (Rudolph 1926, Losert 1940c, Jankovská 1983, 1984, 1998, 2000). Břízová (1999b) investigated the Late-Glacial and Early Holocene sediments in the peat deposit at Rynholec, a site that is also covered by the present paper. Rybníčková & Rybníček (1999) analysed two sequences from several kilometers W of Rynholec. Earlier investigations done in the same area were published by Puchmajerová (1948). Only a short, rather preliminary study by Buttler (1993) of the loess plateau exists for the central part of the area. Although much more is known about the vegetation history of other parts of Central Bohemia, most of its loess plateau remained almost unknown to palaeobotanists. On the other hand, quaternary geological, geomorphological, malacostratigraphical and archaeological data for the same area are plentiful. This information, although scattered in regional literature, is in many cases relevant to discussions about the development of vegetation in the past.

In recent field investigations, several peat deposits situated at key locations were found, which were appropriate for further pollen-analyses. In the present paper, results for three contrasting sites are used to illustrate the surprising differences in the development of local vegetation and draw conclusions about what determined them. It must be stressed that this information is too fragmentary to determine the development of vegetation in Central Bohemia, an area of high environmental complexity, now and also in the past.

The aim of the present paper is to compare past developmental trends and evaluate how a combination of environmental and human-impact factors affected changes in vegetation composition.

Study area and description of the sites

Due to its position between important European biogeographical units, Central Bohemia may be regarded as an area where various phytogeographic elements present in Central Europe occur together: Boreo-continental (represented by e.g. *Astragalus arenarius*, *Pulsatilla patens*, *Hierochloë odorata*, *Carex humilis*, *Lilium martagon*, *Veratrum nigrum*, *Ligularia sibirica*, *Geum rivale*), Submediterannean (*Quercus pubescens*, *Festuca valesiaca*, *Ranunculus illyricus*, *Stipa pennata*, *S. capillata*, *Alyssum saxatile*), Alpine-Carpathian (*Soldanella montana*, *Polygala chamaebuxus*, *Phyteuma nigrum*, *Melica uniflora*, *Euphorbia amygdaloides*, *Carex davaliana*) and Central-European (*Euphorbia dulcis*, *Potentilla neumanniana*, *Galium sylvaticum*, *Corydalis cava*, *Lysimachia nemorum*, *Asarum europaeum*, *Lunaria rediviva*). Central Bohemia also harbours some endemic species, such as *Dianthus bohemicus, Pinguicula bohemica, Melampyrum bohemicum* and several other endemic infraspecific taxa (Slavík 1980). The presence of species from very different climates and habitats (most of them at the limit of their geographic distribution) results from a high microhabitat diversity, caused mainly by the many contrasting geological substrates present within a relatively small area. They vary from ultramafic serpentinite to acidic sandstone and from erosion-resistant quartzite to easily eroded calcareous marl. This not only makes soil chemistry and structure diverse but also determines the

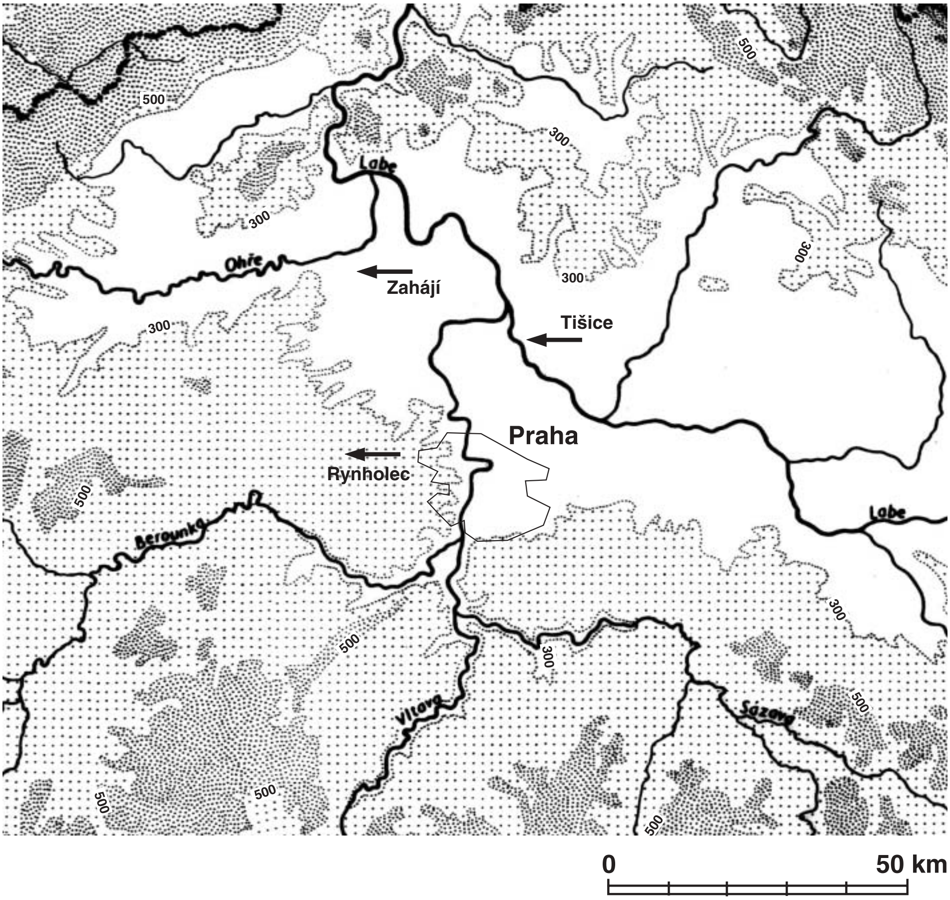

Fig 1. – Study area and position of the sample sites.

nature of micro- and mesorelief, and predisposes individual sites to different kinds of human management. The effects of bedrock quality are usually complicated by superposition of unconsolidated Quaternary sediments, most important of which are gravelly river terraces and extensive loess deposits of variable thickness (Ložek 1980, Kunský 1968). In mountainous regions, e.g. the Alps, extreme diversity is caused mainly by altitude and exposure. The Central-Bohemian landscape is a slightly undulating plain, sculptured by geomorphic processes during the Quaternary. The explanation of regional diversity is thus complicated and historical factors must be taken into account.

The overall climate of the study area is relatively hot, semiarid and subcontinental, with average July temperature 18–19°C, January temperature from –2 to –4°C, and average annual rainfall 450–600 mm. The effect of macroclimate is rather uniform, and local anomalies, like slope exposure, position on plateau or valley bottom, or in valley with respect to prevailing wind, are more important.

As for human occupation, the study area (especially its central part) is one of the principal old settlement areas of Central Europe. Human influence in Central-Bohemian land-

Table 1. – Characteristics of study sites. Climatic stations are indicated for climatic data.

Site	Type of deposit studied	Basic sediment description	Mean annual rainfall (mm)	Mean annual temperature (°C)	Bedrock	Soils (FAO-UNESCO 1988 classification)	History of human settlement
Zahájí	medium-size spring mire in a brook valley	570–160 cm: eutrophic *Carex-Phragmites* peat containing Al-Fe alumns; 160–1 cm: eutrophic peat with silt admixture, in upper part with wood fragments	496 (Doksany)	8.3	loess, marl, small exposures of sandstone	chernozem and calcaric regosol	continuous and dense occupation since the middle Holocene
Tišice	oxbow lake in the river floodplain	315–250 cm: lake sediment (gyttja); 250–60 cm: eutrophic peat with *Carex*, *Phragmites* and small twigs; 60–0 cm: cultivated soil (not analysed)	542 (Tuháň)	8.6	flood loam, terrace gravel, aeolian sand	eutric fluvisol, eutric cambisol and ferro-humic podzol	continuous and dense occupation since the middle Holocene
Rynholec	medium-size spring mire in the brook valley	520–30 cm: eutrophic peat containing remains of mosses and *Carex*; 30–0 cm: cultivated soil (not analysed)	522 (Lány)	6.9	sandstone and marl	eutric cambisol	sparse occupation since the Mesolithic, significantly denser from the La-Téne period

Table 2. – Radiocarbon dates for studied profiles.

Site	Profile depth (cm)	Laboratory No.	Age determination method	Type of material	Measured ^{14}C date
Zahájí	98	Erl-3007	AMS	piece of *Alnus* wood	665±38 B.P.
Zahájí	185	Erl-3008	AMS	piece of wood	1005±39 B.P.
Zahájí	298	Erl-3012	AMS	aboveground parts of cf. *Molinia coerulea*	2830±44 B.P.
Zahájí	498	Erl-3013	AMS	aboveground parts of cf. *Molinia coerulea*	4134±50 B.P.
Zahájí	555	Erl-3011	AMS	wood (twigs)	4788±49 B.P.
Tišice	155	CU-1532	Conventional	peat – bulk material	2671±135 B.P.
Tišice	245	CU-1543	Conventional	peat – bulk material	4241±171 B.P.
Rynholec	88	Erl-4511	AMS	piece of wood	1273±37 B.P.
Rynholec	285	Erl-4626	AMS	aboveground parts of *Carex* sp.	7161±57 B.P.
Rynholec	410	Erl-4513	AMS	piece of wood	8921±64 B.P.
Rynholec	510	Erl-4514	AMS	piece of wood	10271±76 B.P.

scape has a long history and was so intensive, that the separation of "natural" from "artificial" in the present and past ecosystems is highly problematic, sometimes even impossible. We must count with the fact that over the entire period studied, human populations deeply affected vegetation and other constituents of past ecosystems. According to the results of archaeological investigations, the settlement was continuous in many sites for at least the past 7 000 years, i.e. since the Early Neolithic (Kuna 1998a).

For the purpose of this article, three contrasting sites were selected, each situated at one of the three basic ecological zones of Central Bohemia (Fig. 1, Table 1): (a) Loess plateau. A large loess plain sculptured by parallel valleys (Zahájí site). (b) Main river valley. Valley of the river Labe with extensive gravel terraces (Tišice site). (c) Uplands. The Džbán uplands are an example of an undulating landscape representing the W boundary of the Central-Bohemian Plateau (Rynholec site). These sites were selected because they had a palaeoecological record that covered at least the period from the Middle Holocene to the present without any apparent hiatuses.

Methods

The present study is based on the pollen analyses of three profiles through autochthonous organic sediments. Sampling was performed using a modified 5 cm-diameter piston corer (Wright et al. 1984, Wright 1991).

Samples for pollen analyses were treated by acetolysis. As most sediments contained some mineral particles, the samples were pre-treated with concentrated (35%) cold hydrofluoric acid (HF) for 24 hours (Moore et al. 1991). Extracted microfossils were stained with 0.3% safranin and mounted in a glycerol-water (1:1) mixture. In each sample at least 700 pollen grains were counted. For pollen identification a reference collection and the following keys were used: Faegri & Iversen (1989), Moore et al. (1991) and Punt (1976–1996). Pollen nomenclature follows ALPADABA (Alpine Palynological DataBase), located at the Institute of Plant Sciences, Bern. According to this nomenclature, pollen grains of *Triticum* are included in *Avena*-type. In theory, separation of both taxa is possible, but was difficult with the available instruments.

Pollen types included in the total sum affect the interpretation of pollen diagrams. In the present study, pollen grains potentially produced by local aquatic and marsh vegetation are excluded. Sometimes, however, it was difficult to evaluate the role of certain taxonomically broad taxa (e.g. those of higher taxonomic level like *Cyperaceae*, *Gramineae*) in the regional vegetation cover. The percentage values were thus calculated on the basis of arboreal and non-arboreal pollen sum (AP+NAP), excluding only demonstrably aquatic taxa. On the other hand, *Pteridium*, *Equisetum* and all monolete spores are included in the total sum. (In many plant communities these taxa have an ecological role equivalent to that of spermatophytes.) Concealed, corroded, degraded and indeterminable pollen grains are classed as "varia". To facilitate the comparison of pollen diagrams, taxa and order in which they are presented in the diagrams are identical. Diagrams were prepared using POLPAL computer program (A. Walanus & D. Nalepka, Kraków). They were zoned visually on the basis of both presence and abundance of ecologically important taxa. Considering the purpose of the zonation, the number of zones was limited. In addition, samples were compared using Constrained Single Link Cluster Analysis (CONSLINK) in the POLPAL program.

In order to estimate past species diversity, palynological richness was calculated using rarefaction analysis (Berglund 1986, Birks & Line 1992). The results are presented in the pollen diagrams.

Microscopic charcoal particles amongst the pollen were counted using the point-count method (Tolonen 1986). Microscopic charcoal curves were compiled using the ratio between total pollen sum and number of particles.

Radiocarbon dates used in the present study were derived from bulk sediments and macrofossils measured by AMS as well as by conventional ^{14}C methods. For compatibility, the dates are all expressed in uncalibrated form. Radiocarbon analyses were done at the Physikalisches Institut der Universität Erlangen-Nürnberg (Erl-) and Faculty of Natural Sciences, Charles University, Prague (CU-). For description of ^{14}C sample see Table 2. Age calculations are based on a ^{14}C half-life of 5730 years.

Results

Zahájí site (Fig. 2)

The pollen record for this site covers the last 5 000 years (uncalibrated) without any apparent hiatuses. Its position in the valley of a stream surrounded by a loess-covered plateau makes this site representative of that part of the Central Bohemian landscape not situated in the big rivers' alluvia. The dominance of carbonaceous chernozem soils, continuously and comparatively densely occupied by man since at least the Middle Holocene (according to archaeological investigations, Kuna 1998a), is the main feature of this type of landscape. A dry, subcontinental climate makes the region sensitive to deforestation and hence the persistence of open vegetation.

The oldest part of the record (zone Z1; between ca 5 000 and 4 300 yr B.P.) represents the period that precedes the expansion of silver fir and hornbeam into the area. On the loess substrata there was mixed oak woodland with important admixture of *Ulmus* and *Tilia*, and probably also other tree species like *Corylus*, *Fraxinus*, *Fagus* and *Picea*. Abundance of *Picea abies* and *Fagus sylvatica* pollen is rather surprising considering the ecological requirements of these trees and low altitude of the site. High percentages of these taxa point to local occurrence rather than long distance transport. Beech and spruce must have occurred on slopes and bottom of the valley (supposedly as an admixture in oak-dominated woodland). The pollen record indicates that beech started to become more abundant shortly before 5 000 B.P. Pine was relatively rare in the area. The abundance of *Betula* pollen is probably the result of its local high representation. The same may be true for *Alnus*, but its percentages are so low that the presence of an alder carr in the local marsh is unlikely. Regional woodlands, though abundant, were definitely not completely natural. Continuous presence of anthropogenic indicators (primary and secondary) indicate that Neolithic man greatly influenced the vegetation. The high abundance of *Plantago lanceolata* and *Calluna vulgaris* pollen probably reflects the expansion of pastures early in this period. Such grazing activity must have played an important role in the changes in forest composition that started at the transition between zones Z1 and Z2. The reduction in forest cover enabled the xerothermic species, which form an anthropogenic steppe-like vegetation, to expand their range. Due to human activity, species diversity is very high. This is illustrated by the results of rarefaction analysis, which continuously shows very high palynological richness.

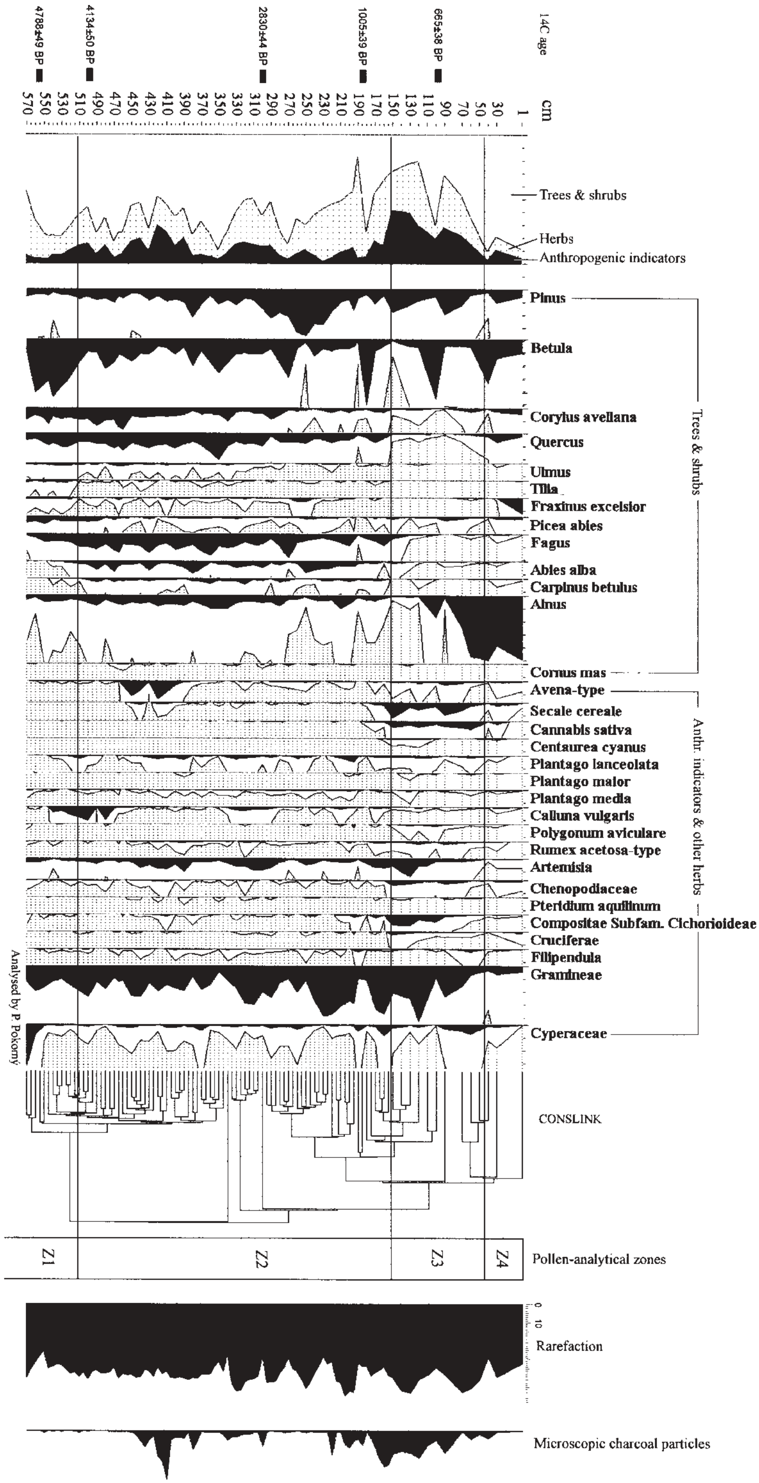

Fig 2. – Pollen diagram for the Zahájí site. 50°22'N, 14°08'E, 190 m a.s.l.

Pollen zone Z2 covers a long period between ca 4 300 and 850 yr B.P, a period of numerous and complicated changes in vegetation. Zone Z2 starts with an expansion of *Abies alba* and *Carpinus betulus* into regional woodland communities and decline in *Tilia* and *Fraxinus excelsior*. The decline in *Ulmus* was insignificant at this time but more marked at about 2 800 B.P. Pine expanded in secondary biotopes. Changes in woodland composition must have been marked and rather complex due to immigration of species, felling of trees, grazing and burning (microscopic charcoal particles show a positive correlation with human impact). The anthropogenic indicators oscillate, which probably reflect phases of settlement expansion and regression. The strongest occurred between ca 4 000 and 3 500 yr B.P., i.e. during the Bronze Age. During the periods of expansion, arboreal pollen percentages declined to less than 50%. The landscape at this time was largely deforested and a cultural one.

Pollen zone Z3, dated between ca 850 and 300 yr B.P., i.e. the High and Late Medieval, indicates marked initial changes in vegetation. Strong human activity reduced forest cover to a minimum and the landscape became open. Sharp, temporary peeks in the *Betula* curve (which also occurred earlier) correspond to minima in *Cyperaceae* and *Gramineae* curves. This probably reflects a cyclic behaviour in local wetland vegetation – alterations between swamp forest and open fen communities. It is unknown whether this was natural (analogous to autogenous cyclic succession in alder carr communities – see Pokorný et al. 2000) or human-induced (felling of full-grown birch trees).

Pollen zone Z4. This is the youngest pollen zone and can be dated to the past ca 300 years. It shows a reduction in human impact in the partial reforestation of the area. This is also the case for the mire itself, where *Alnus* and later also *Fraxinus* formed a closed canopy. Their local presence (in case of *Alnus* confirmed by the occurrence of wood fragments, seeds, and fruits) results in pollen over-representation.

Tišice site (Fig. 3)

The pollen record for this site covers the period from about 5 500 B.P. to High Middle Ages. The site is located in the alluvium of a large river surrounded by gravel terraces and sand dunes, i.e. in an environment of markedly different geological and soil conditions compared to the previous site. As in the case of the Zahájí site, extensive archaeological investigations revealed evidence of dense and continuous human occupation since at least the Early Neolithic (Kuna 1998b).

The lowermost pollen zone T1, dated between ca 5 500 and 3 100 yr B.P., reflects vegetation development under weak but more or less continuous human impact. Regional woodlands, which still had a semi-natural character, were dominated by oak. Other tree species (*Ulmus*, *Tilia*, *Fraxinus*, *Corylus*, and *Picea*) probably grew in these woods as an admixture. Beech was also present, but not important. Vegetation around edges of the oxbow lake was dominated by *Alnus glutinosa*. Pine stands must have been present in dry habitats such as sand dunes. It is likely that there were no significant differences in vegetation between the river floodplain and the surrounding landscape. This was due to the diverse geomorphology of the floodplain before massive sedimentation of flood loams, which first occurred at the beginning of High Medieval Period (Dreslerová 1995, Opravil 1983).

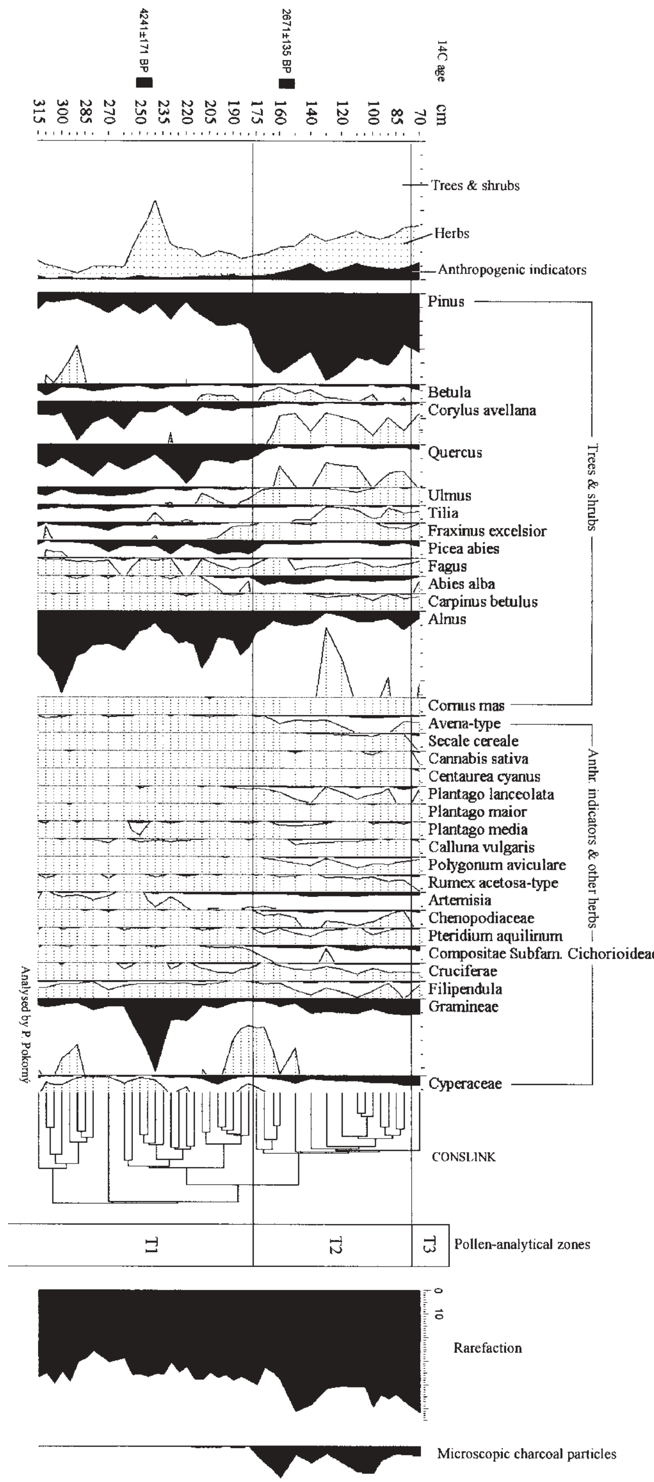

Fig 3. – Pollen diagram for the Tišice site. 50°16'N, 14°32'E, 165 m a.s.l.

The beginning of zone T2 (about 3 100 yr B.P.) is the period of great changes in vegetation. *Quercus, Ulmus, Fraxinus*, *Picea* and *Corylus* declined rapidly, and *Pinus* and *Abies alba* increased. The expansion of *Carpinus betulus* occurred later and was rather weak. Based on anthropogenic indicators, charcoal particles and absolute dating, this rapid change in vegetation was triggered by Late Bronze Age human populations. Since then discontinuous secondary woods were present in the landscape, in which pine started to dominate. The transition from mesophilous mixed oak woodland to poor pine stands must have been accompanied (or even caused) by changes in soil chemistry. Human activity (possibly grazing) probably not only affected the vegetation but also increased soil leaching and erosion. This led to the formation of nutrient-poor acidic sand and gravel substrata.

The youngest layer of the profile belongs to pollen zone T3, and because of the presence of *Centaurea cyanus* and the dominance of *Secale cereale* among cereal pollen is dated biostratigraphically to the High Medieval Period. As at the other sites, this was a period of significantly increasing anthropogenic pressure.

Rynholec site (Fig. 4)

The pollen record from the Rynholec site is the longest recently studied in the area: it covers the entire Holocene. Unlike the other two sites, which are situated in the flat central part of the region, Rynholec is located at the bottom of a valley in the transitional zone between the central lowland and western marginal uplands. As the prevailing wind is from NW, and as the air masses come from higher altitudes (above 500 m a.s.l.) they can sometimes be cold. Cool air is trapped in the valley bottom and affects the vegetation. This is probably responsible for the light settlement of the area by man throughout most of prehistory (Venclová 2001).

At the end of the Late-Glacial and beginning of the Holocene (pollen zone R1, between about 10 300 and 9 100 yr B.P.) forests consisted of pine and birch. Other trees (*Corylus avellana, Quercus, Ulmus, Tilia, Picea abies* and *Alnus*) appear in the record at the beginning of zone R2 (ca 9 100 yr B.P.) or shortly after. At the start of zone R3 (ca 8 000 B.P.), these trees became important component of the regional vegetation. Considering the low altitude and dryness of the area the abundance of *Picea* pollen is interesting. It is likely that spruce grew in the waterlogged bottom of the valley or on the mire. It is difficult to account for several prominent oscillations in tree pollen in this period. They may be the result of fires (natural rather than human-induced). This accords with high amounts of microscopic charcoal in the sediment. It is likely that regular fires are responsible for the dominance of pine in the area (in that case, this type of vegetation is called a "fire climax"). A similar interpretation was proposed by Rybníčková & Rybníček (1999) for two profiles situated 8 and 17 km from Rynholec. In the R3 zone, primary anthropogenic indicators are missing, or negligible. The surroundings of the site were evidently unattractive for Neolithic, Eneolithic and Bronze Age man, most probably due to unfavorable local climatic and soil conditions. Archaeological investigations carried out in the area by Venclová (2001) arrived at the same conclusion, as there is little evidence of human occupation up until the Iron Age.

At the onset of zone R4 (ca 2300 yr B.P.) there is a slight increase in the percentages of anthropogenic indicators. The area was attractive for Iron Age populations because of the occurrence there of iron ore. At this time, *Fagus* and *Abies* increased in abundance. This is

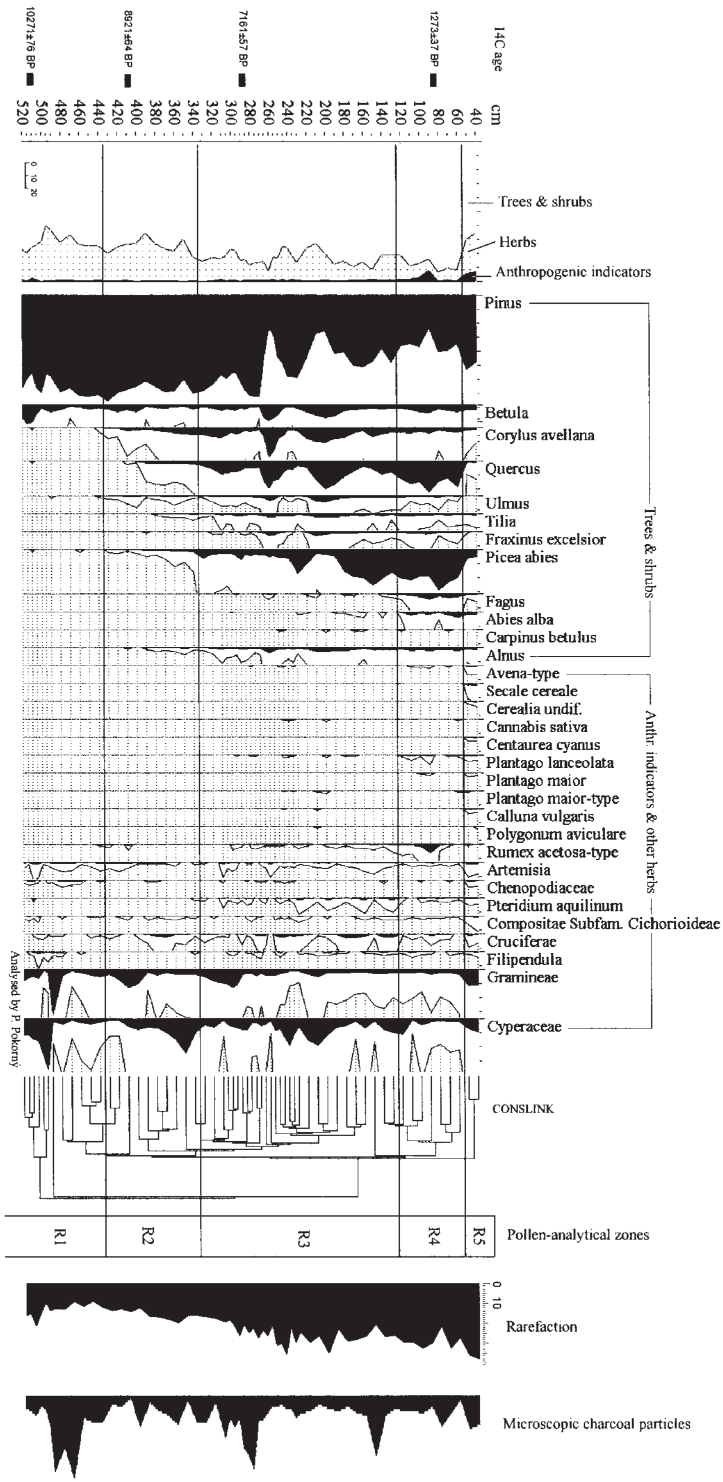

Fig 4. – Pollen diagram for the Rynholec site. 50°08'N, 13°58'E, 407 m a.s.l.

relatively very late compared to the other two studied sites. It can be correlated with human impact. Another important Late Holocene tree species, *Carpinus betulus*, is almost absent from the Rynholec site pollen record.

The youngest pollen zone R5 has a typical High Medieval pollen spectrum, which is sharply separated from the preceding one. Accelerated human impact completely altered the development of vegetation in the area, which was predominantly natural up until that time. This is different from what occurred at the two other sites, where the human-vegetation interactions lasted longer and were more continuous. This, together with a less favorable local climate, may account for the significantly lower palynological diversity at Rynholec, as revealed by comparing the rarefaction curves for the sites.

Discussion

History of local human impact and origin of present diversity of landscape and vegetation

An important result of the present study is the insight it has given into the processes by which humans have affected local environmental and biological diversity. At the Tišice site, the most marked prehistoric human impact dates back to the Late Bronze Age. It involved a significant vegetation change associated with the degradation of the landscape. This finding corresponds with the results of Ložek (1998). On the basis of a palaeomalacological investigations this author postulates that a Late Bronze Age environmental change occurred on the nearby sandstone areas, some 15 km to the north of the Tišice site. The present results indicate a similar process also occurred in the middle Labe area. Soil degradation and depauperization of the biota were triggered by human impact. It is possible, but difficult to demonstrate directly, that climatic deterioration amplified the effect of man's activity and made the environment more sensitive to his influence (Jäger & Ložek 1982). Only future research will demonstrate if the Late Bronze Age environmental degradation, with soil erosion, leaching and general depauperization, occurred in Central Bohemian acidic (sandstone and river terrace) areas in general. To prevent any misunderstanding, it must be stressed that the above environmental changes did not adversely affect all components of the ecosystem. They might have caused the decline of some of the more demanding trees, or extinction of local mollusc communities, but human populations would have adapted to these environmental changes and even proliferated, which is clearly demonstrated by the present results.

The pollen analysis at the Zahájí site indicates that the development discussed above did not occur generally throughout the region. In area with a nutrient-rich calcareous loess substrata, human impact had a different effect. Here, it caused an enrichment of biota through the formation of secondary open stands of vegetation as part of a mosaic of different biotopes (pastures, abandoned fields, ruderal habitats, woodlands in various stages of degradation, erosion slopes, wetlands on alluvia of streams and rivers etc.) As a result, landscape diversity (especially beta and gama diversity, according to the terminology of Whittaker 1972) increased enormously. In the Zahájí record, open vegetation occurred in the Neolithic, almost 5 000 years ago, as shown by continuous presence of *Artemisia*, *Chenopodiaceae*, *Calluna vulgaris* and *Plantago media*. This may indicate continuous human impact rather than a climatic influence. Unfortunately we do not have an older record to confirm that open grassland occurred throughout the entire Holocene in this the most continental part of Central Bohemia. Due to its dry climate, substrate diversity and the strong impact of Early Neolithic man (Linear Pottery Culture), this area is the most likely place where xerothermic vegetation was continually present, from Early Holocene steppes to open secondary vegetation (in the sense of Gradmann 1933).

If the rarefaction analysis results for Zahájí and Rynholec are compared, the former has a significantly higher palynological diversity. This is most probably the result of deforestation, which was lower at Rynholec than Zahájí. Human impact affected woodland vegetation both quantitatively (deforestation) and qualitatively. This is demonstrated by the present results, where the decline of the most demanding trees (*Ulmus*, *Tilia* and *Fraxinus*) is clearly a result of human influence. This decline is accompanied by the expansion of *Abies alba*, *Fagus sylvatica* and *Carpinus betulus*. An important fact is that these changes in forest composition occurred at different times at the different sites just as did human impact. The change in forest composition described above, together with the maximum settlement are dated at Zahájí to ca. 4 300 B.P., Tišice to ca. 3 100 B.P. and Rynholec after ca. 2 300 B.P. In the latter case, prehistoric human impact was so slight that *Ulmus*, *Tilia* and *Fraxinus* survived as relatively important forest trees up until the High Middle Ages.

Past changes in forest composition that resulted from human impact

The decline in certain broadleaved forest trees as a result of human impact is widely discussed in the literature (Faegri 1944, Iversen 1960, Aaby 1986, Lang 1994). The reverse process, the expansion of *Carpinus*, *Abies* and *Fagus*, will be discussed further here. A correlation between the increase in *Carpinus betulus* and human impact was postulated first by Ralska-Jasiewiczowa (1964) for Poland. The same phenomenon was later demonstrated for more western parts of Europe (Küster 1997). It is argued that hornbeam can withstand intensive utilization of woodlands by man, especially if managed by coppicing. This favours hornbeam over other trees (Pott 1981).

More controversial is the effect of man on expansion of *Abies alba*. This is supported by historical data (Málek 1983), which indicates that the expansion of silver fir was favoured by forest disturbance. This is unlikely to occur today, because there is almost no pool of *Abies* seed. The decline of silver fir in Central Europe over the last two centuries is attributed to pathogen attack. Silver fir declined as a result of felling trees for timber in the High Medieval and even Roman Periods (Küster 1994), but also possibly due to the expansion of disturbed woodlands due to man. It is important to realize that human-enhanced *Abies* expansion occurred at lowland sites, where conditions usually are not ideal for its growth. The situation might have been different in the upland and mountainous areas, where silver fir expanded naturally, especially during the Subboreal Period.

The role of man in the postglacial expansion of beech

The above mechanisms proposed for silver fir expansion may also apply to beech. Based on the pollen record, beech also appears to be benefited from man's activities in Central Bohemia. Similar observation was recorded by Küster (1997) for Germany, but his conclusions were rejected by Gardner & Willis (1999). According to the data presented here, it is very likely that *Fagus sylvatica* expansion was correlated with human impact, especially at Rynholec (Fig. 4). This suggestion is strengthened by comparing the Rynholec and Zahájí pollen diagrams. Although these sites are only 30 kilometers apart, the timing of beech expansion at the two sites differs by some 2500 years.

Fagus sylvatica started spreading into Central Europe around 6 000 years B.P. (Pott 1997). This expansion took the form of a migration that approached the Alps in two separate streams and continued slowly northwards. This process was associated with climatic development in the Holocene, and was similar to other postglacial migrations (Pott 1997, Gardner & Willis 1999). But different mechanisms might have operated at the regional and local levels.

Plant ecologists and foresters believe that *Fagus sylvatica* is the dominant tree in forests and form a continuous canopy, which strongly shades the whole community. Young beech seedlings are extremely tolerant of this shade (Newbold 1983, Ellenberg 1988) and can even survive on only 2% of the sunlight for a period of five years (Peters 1997). Therefore, beech is able to reproduce under the canopy of other forest trees and finally dominate over them. As soon as beech forest is established, the same mechanism assures its permanent regeneration. This could be the mechanism by which *Fagus sylvatica* expanded into large areas of western Europe and the mountains of Central Europe, i.e. regions with a relatively humid climate. This natural expansion of beech was probably restricted by the relatively dry climate in the subcontinental lowlands of Central Bohemia. The dry climate could have retarded the establishment and spread of beech, and reduced its ability to dominate the forest canopy (Ellenberg 1988, Pott 1997).

The present results indicate that the expansion of *Fagus sylvatica* in Central Bohemia was surprisingly asynchronous. It was not the result of a single migration. This, together with the observation that the expansion of beech is correlated with local human activity, lead to the theory that man influenced the establishment of beech in Central Bohemia. It is likely, that before its great increase in abundance, beech was locally present as an admixture in forest communities but unable to dominate the other forest trees. Its started to spread only after the natural forest structure was disturbed by forest management, e.g. tree felling, coppicing or forest grazing. As soon as beech formed compact stands within disturbed mixed oak forests, it was even able to spread without the help of man.

If the above is true, it is another example of how man can trigger a latent landscape/vegetation process. It is important to realize, that there is a marked difference between the proximate and ultimate cause of vegetation changes. It would be a mistake to state that Central Bohemian beech forests are of anthropogenic (or secondary) origin. Nevertheless, pollen record supports the idea that an anthropogenic trigger caused the initial spread.

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Souhrn

Střední Čechy jsou příkladem regionu s vysokou krajinnou a biologickou diverzitou. Jak ukazují výsledky pylových analýz, je tato diverzita mimo jiné výsledkem dlouhodobého lidského působení. Před totálním odlesněním a zkulturněním krajiny ve vrcholném středověku nebyla studovaná oblast zdaleka jednotným celkem. Radiokarbonově datované pylové diagramy odhalily překvapivé rozdíly ve vegetačním vývoji na poměrně omezeném geografickém prostoru. Rozdíly v intenzitě a chronologii lidského vlivu způsobily značnou diachronii vegetačních změn – tisícileté rozdíly zaznamenáváme v procesu degradace středoholocénních smíšených doubrav, v procesu expanze buku, jedle a habru. Kontinuální lidské působení na Podřipsku (lokalita Zahájí) mělo za následek zvýšení

mozaikovitosti krajiny a nárůst biologické diverzity. Nepřerušenou existenci sekundárního xerotermního bezlesí zde lze předpokládat minimálně po dobu uplynulých 5000 let. Naproti tomu ve středním Polabí (lokalita Tišice) měl zvýšený lidský vliv v mladší době bronzové za následek náhlou degradaci smíšených doubrav a jejich nahrazení druhově chudými společenstvy písčitých borů. Důvodem vzájemných rozdílů ve vegetačním vývoji jsou rozdílné edafické poměry. Zcela odlišný vegetační vývoj měl západní okraj Pražské plošiny na úpatí vrchoviny Džbánu (lokalita Rynholec). Z klimatických důvodů leží tento region již mimo tzv. starou sídelní oblast. První výraznější vlna osídlení zde nastala až v době laténské. Výsledkem je podstatně konzervativnější vegetační vývoj ve srovnání s předešlými dvěma zmíněnými lokalitami.

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