Palaeogeography of forest trees in the Czech Republic around 2000 BP: Methodical approach and selected results

Paleogeografie hlavních dřevin na území České republiky před 2000 lety: Metodický přístup a vybrané výsledky

Petr P o k o r n ý

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Spatial variations in regional forest composition are analyzed for the period around 2 000 years before present in the territory of the Czech Republic. The results of pollen analyses at 16 different sites (original data and those published by other authors) form the basis of this study. The results are preliminary because of the small number of sites sampled. This article demonstrates the possibilities of the approach and is the first step to a wider application in the future. The conclusions indicate that pollen analysis is accurate enough in most cases for the reconstruction of past forest composition on a regional scale, and different deposits reflect spatial heterogeneity. Altitude, intensity of human impact, and soil type were the major factors affecting past distribution of forest trees. Oak and hornbeam woodlands, although widely affected by human activity, dominated the lowlands. Beech and silver fir were an important admixture in these communities. Although oak was present at higher altitudes, the occurrence of upland oak woodlands was limited more than indicated by recent geobotanical reconstructions. Instead, mixed forests existed at middle altitudes, often dominated by silver fir and beech. In less favourable habitats, spruce was common. Such upland forests extended high into the mountains, where because of the more severe climatic conditions beech and spruce started to dominate over silver fir.

K e y w o r d s : Pollen analysis, palaeoecology, palaeogeography, natural forest composition, forest trees, human impact, Late Holocene

Introduction

From the beginning of pollen analysis, more than one century ago, the method was used to reconstruct the changes in regional forest composition that occurred in the Late-glacial and Holocene periods. On the basis of such data, individual "forest provinces" were designated for Europe (for Central Europe by Firbas 1949, 1952) and more recently, the main migration routes of individual forest species were identified using isopollen maps (Ralska-Jasiewiczowa 1983, Huntley & Birks 1983, Rybníčková & Rybníček 1988). In this short study, the pollen analysis is used to reveal fine scale differences in regional forest composition for the period around 2 000 years BP (BP = before the present). This period was chosen because it provides information on the original composition of the forests in this area, which can be related to the present situation and, last but not least, due to the scarcity of such data for older periods of the Holocene in the Czech territory.

The following questions are asked: (a) Is pollen analysis able to detect regional forest composition with sufficient spatial accuracy? (b) To what degree did the past forest composition reflect regional climatic and edaphic conditions? Was the distribution of forest trees directly affected by human activity? (c) Do the observed patterns agree with the results of potential vegetation mapping and the present geobotanical view of the problem?

The first question asked is a methodical one. Pollen spectra are traditionally regarded as representatives of relatively wide areas, and unlikely to give an insight into the spatial heterogeneity in past vegetation. Especially in the territory of the Czech Republic with its relatively fine grain mosaic of contrasting landscapes, this may be why the method of pollen analysis is not sensitive enough for medium-scale (in the order of kilometer) vegetation patterns – at least in theory. However, the results of recent studies on pollen deposition contradict this opinion. For example, Sugita et al. (1999) demonstrated that the majority of pollen rain in an average European landscape comes from the distances of 800–1000 meters. Earlier studies by Jansen (1986) and Régnell (1989) resulted in the same conclusion. Andersen (1992) and Andersen et al. (1983) described local pollen spectra from small forest hollows, with the majority of pollen grains coming from distances no greater than 50 meters. On the other hand, the pollen spectra from large water bodies is more likely to be from vegetation several kilometers ways than from local sources (Bradshaw & Webb 1985, Prentice 1985).

The second question is more difficult to answer. Although all the main forest tree taxa were present here around 2 000 BP (e.g. Firbas 1949, 1952, Rybníčková & Rybníček 1996, Huntley & Birks 1983), obstacles to migration could have affected the distribution of some species, especially that of the latest immigrant, *Carpinus betulus*. Even more serious is the influence of human management, which seriously affected the lowlands, while the upland and especially mountainous landscapes were left largely in a natural, or semi-natural condition (Rybníček & Rybníčková 1992, Pleiner & Rybová 1978, Ložek 1999). Past human impact can be estimated from pollen diagrams using the AP/NAP ratio (the ratio between arboreal and non-arboreal pollen) and the total percentage of primary anthropogenic indicators. These were used in the present contribution to assess the influence of management on forest composition.

At the beginning of the High Medieval period, i.e. the one following that under study, human impact accelerated enormously. This is easily seen in all the pollen diagrams analyzed in this paper. It resulted in complete structural and functional rebuilding of most natural ecosystems through processes such as soil degradation, slope erosion, silting of floodplains, changes in local hydrology, micro-, and even mesoclimatic changes, etc. (for details see Roberts 1989, Rybníček & Rybníčková 1992, Pokorný 1999). Some of the changes were reversible, but not all. Up to now, eight centuries of intense human activity have affected not only the abiotic characteristics of individual habitats, but also their biotic composition. Active woodland destruction and management, sometimes combined with the influence of pathogens, has led in some cases to the rapid decline of certain tree taxa (e.g., *Abies alba* since the start of Modern period – Málek 1983). On the other hand, it led to the spread (or even intentional introduction) of invasive species. By taking into account all these changes, it is likely that the potential natural vegetation is somewhat different from that existing 2 000 years ago, even if the climate has not changed significantly. This is a good reason for using vegetation-historical data (such as pollen data) for vegetation reconstruction, rather than analogies derived from field experience of modern vegetation. On the other hand, by combining these two approaches (historical data and modern analogies), we have a tool for assessing of the effect of human activity on these ecosystems in the past.

Material and methods

Appropriate data selection is the key to the approach used in this paper. I selected the period around 2 000 years BP, i.e. the second half of the Older Subatlantic Period (sensu Firbas 1949, 1952). In addition to the above reasons, the aim was to select a period, which could be easily differentiated without radiocarbon dating the pollen diagrams (most diagrams from the territory of the Czech Republic are not dated). The following was the best technique for this and was applied to each diagram: The period between *Abies* rational limit (term used according to Watts 1973) and the abrupt start of the Younger Subatlantic (SA2, indicated by a sudden rise in anthropogenic indicators during the High Medieval colonization) was determined. In the upper 1/4 of this section, a biostratigraphic zone was delimited. All the samples that fell in this zone were used as input data for further analysis. In some cases, the age of the selected period was confirmed by radiocarbon dating. Only those pollen profiles where the representation of the period of interest is excellent and pollen counts are large enough were evaluated. Besides the three original suitable unpublished diagrams, another 13 were selected from the literature (Table 1). Fortunately, the sites are more or less evenly distributed in the territory (Fig. 1), although there are some serious gaps in the spatial data, reflecting the present state of this pollen-analytical investigation.

Climatic data is the 50-yr average (1901–1950, Vesecký et al. 1960) from the weather stations nearest to the study sites. Soil types prevailing in the area (5 km radius around each site) were derived from the pedological maps 1 : 50 000 (Tomášek et al. 1986–1994). Soil nomenclature follows the recommendations of FAO (Tomášek 2000).

Data were analysed to study the relationship (a) between environmental parameters (Table 1) and the percentage of selected tree taxa in each data set, and (b) representation of individual forest tree taxa in the total spectra. Data were analysed by using the simple

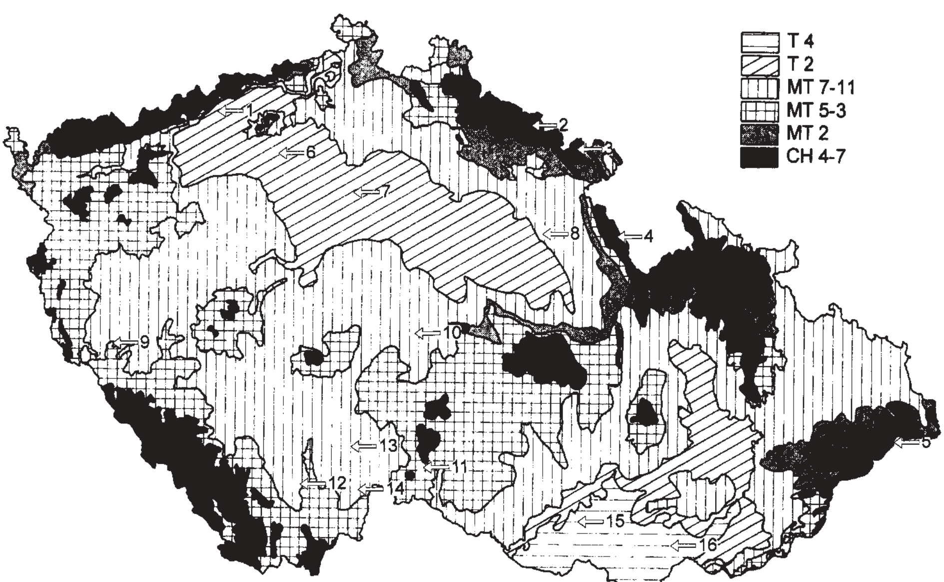

Fig 1. – Location of the study sites on the climatic map of the Czech republic (adapted from Quitt 1971). Abbreviations for the climatic regions: T4 – warm and dry, T2 – warm and less dry, MT – cool, CH – cold.

Table 1. – Reference table for the sixteen sites. Percentages for selected taxa is given for each genus/pollen group. Aboreal pollen is expressed as % of total terrestrial pollen. Temperature = mean annual temperature (°C). Precipitation = mean annual sum of precipitation (mm). Characteristic of site and soils in the area is given.

	1 Komořanské jezero	2 Černá hora	3 Čáp	4 Kunštátská kaple
Corylus	7.8	6.6	2.6	6.5
Quercus	12.5	7.9	6.4	3.9
Pinus	15.6	13.2	15.4	9.1
Picea	15.6	17.1	12.8	23.4
Fagus	23.4	22.4	32.0	29.9
Abies	23.4	26.3	25.6	23.4
Carpinus	1.6	6.6	5.1	3.2
Cerealia	0.0	0.0	0.0	0.6
Arboreal pollen	90	95	96	80
Type of data	counting sheet	pollen diagram	counting sheet	counting sheet
Source of data	Jankovská 2000	Speranza et al. 2000	Kuneš & Jankovská 2000	Rybníčková, 1966
Altitude (m a.s.l.)	230	1190	670	1030
Temperature	8.4	3.9	6.8	5.4
Precipitation	474	1223	778	1116
Latitude	50°32'	50°39'	50°35'	50°15'
Longitude	13°32'	15°45'	16°07'	16°27'
Site	Large lake in foothills of mountain	Small mountain bog	Small oligotrophic mire in sandstone gorge	Small mountain bog
Soils	Pellic Vertisol and Stagno-gleyic Luvisol, Acidic Cambisol on mountain slopes	Cambic podzol, Ferro-humic Podzol and alpine Lithosol.	Acidic Cambisol and Ferro-humic Podzol on sandstone bedrock	Cambic Podzol and Ferro-humic Podzol, highly acidic Cambisol

	5 Súlov	6 Zahájí	7 Tišice	8 Na bahně
Corylus	11.3	12.5	2.0	8.9
Quercus	1.6	21.4	4.1	16.6
Pinus	8.1	26.8	81.6	33.3
Picea	16.1	1.8	2.7	2.2
Fagus	24.2	17.9	1.0	11.1
Abies	35.5	12.5	6.8	11.1
Carpinus	3.2	5.4	0.4	16.6
Cerealia	0.0	1.8	1.4	0.2
Arboreal pollen	85	40	80	90
Type of data	pollen diagram	counting sheet	counting sheet	counting sheet
Source of data	Rybníček & Rybníčková 1995	Pokorný, original data	Pokorný, original data	Pokorný, original data
Altitude (m a.s.l.)	825	190	165	240
Temperature	6.1	8.3	8.6	7.8
Precipitation	1267	496	542	602
Latitude	49°29'	50°22'	50°17'	50°12'
Longitude	18°34'	14°08'	14°32'	15°56'
Site	Small upland mire	Medium size, lowland mire in the brook valley surrounded by loess plateau	Small lake in large river floodplain, fringed by terraces	Small mire at the edge of medium-sized river terrace
Soils	Cambic Podzol and Ferro-humic Podzol, highly acidic Cambisol	Chernozem and Calcaric Regosol on loess and calcareous marl	Eutric Fluvisol in the river floodplain, Eutric Cambisol and Ferro-humic Podzol	Eutric Fluvisol in the river floodplain, Eutric Cambisol, Ferro-humic Podzol and Pellosol

	9 Lštění	10 Malčín	11 Suchdol	12 České Budějovice
Corylus	6.2	7.8	7.1	3.7
Quercus	2.5	2.2	2.8	9.2
Pinus	4.9	5.6	4.3	11.0
Picea	49.4	11.2	17.1	18.4
Fagus	16.0	16.8	28.5	18.4
Abies	21.0	55.9	38.5	36.8
Carpinus	0.0	0.6	1.4	0.7
Cerealia	0.0	0.0	0.3	1.8
Arboreal pollen	85	95	90	75
Type of data	pollen diagram	counting sheet	counting sheet	counting sheet
Source of data	Moravec & Rybníčková 1964	Jankovská 1990	Rybníčková 1974	Pokorný et al. 2002
Altitude (m a.s.l.)	840	520	650	380
Temperature	7.6	6.9	6.4	7.8
Precipitation	662	661	712	620
Latitude	49°29'	49°41'	49°07'	48°58'
Longitude	13°02'	15°28'	15°15'	14°28'
Site	Small upland mire	Small mire in a brook valley cut to the granitic bedrock	Medium sized mire on granitic bedrock	Small oxbow lake in flat basin
Soils	Acidic Cambisol	Acidic Cambisol, Stagno-gleyic Cambisol	Highly acidic Cambisol	Eutric Fluvisol in the river floodplain, Stagno-gleyic Cambisol, Eutric Cambisol and Ferro-humic Podzol

	13 Borkovická blata	14 Branná	15 Olbramovice	16 Vracov
Corylus	2.8	3.9	1.2	6.7
Quercus	2.8	6.2	12.1	27.0
Pinus	23.7	26.5	28.2	15.7
Picea	13.9	18.7	20.2	4.5
Fagus	16.7	20.2	8.1	22.5
Abies	39.0	23.4	12.1	11.2
Carpinus	1.0	1.1	6.0	9.0
Cerealia	0.0	0.0	12.1	3.4
Arboreal pollen	90	87	55	57
Type of data	counting sheet	counting sheet	pollen diagram	counting sheet
Source of data	Jankovská 1980	Jankovská 1980	Svobodová 1997	Rybníčková & Rybníček 1972
Altitude (m a.s.l.)	420	435	205	193
Temperature	7.8	7.8	8.9	9.2
Precipitation	627	627	661	540
Latitude	49°13'	48°58'	49°00'	48°58'
Longitude	14°38'	14°48'	16°34'	17°12'
Site	Large oligotrophic mire in flat basin	Large mire in flat basin	Small lowland lake	Smaller lowland lake in the flat basin
Soils	Stagno-gleyic Cambisol and Fibric Histosol (peat)	Stagno-gleyic Cambisol and Fibric Histosol (peat)	Chernozem, Orthic Luvisol and Eutric Cambisol	Chernozem, Arenosol, Eutric Cambisol

regression function in Statistica™ software (StatSoft 1998) . The significance level of 5% ($P < 0.05$) was taken as the minimum confidence limit.

Overall pollen spectra of individual sites were compared by multivariate analysis. Pollen percentages of individual tree taxa were used as input data for CANOCO 3.10 program (ter Braak 1990), and a Canonical correspondence analysis (CCA) was performed.

Results and discussion

Pollen analysis as a tool for studying past regional forest composition

The general opinion is that a deposit used for pollen analysis is influenced by the radius of the area from which the pollen is derived (Andersen et al. 1983, Jansen 1986, Régnell 1989, Andersen 1992, Sugita et al. 1999). In this study, the site Komořanské jezero lake (no. 1 in Table 1) is a good example of this. The composition of pollen from this large lowland lake, situated in the Mostecká pánev basin in the foothills of the Krušné hory Mts, is obviously strongly affected by extra-regional pollen rain. If compared with pollen spectra from mountainous and lowland regions, the Komořanské jezero record is strikingly similar to upland and highland sites (Fig 2). This means that the Komořanské jezero pollen spectra better reflect the vegetation composition of the slopes of the Krušné hory Mts than the vegetation of the Mostecká pánev basin. Similar observation were made by Bradshaw & Webb (1985) and Prentice (1985), who concluded that the larger the lake surface, the more extra-regional pollen it collects.

On the other hand, the results from peat deposits demonstrate that the pollen is generally of much more local origin. In most cases, the method appears to be sensitive enough to trace regional differences even within the territory of the Czech Republic, where the mosaic of contrasting landscapes can be relatively fine. Only in mountainous sites situated above 1000 meters a.s.l. (sites no. 2 and 4), is a certain portion of the pollen spectra likely to be of extra-regional in origin, as the occurrence of hornbeam (*Carpinus betulus*) is very doubtful at these elevations and must be reconstructed only on mountain slopes below ca 700 meters. This is a warning against interpreting single pollen spectra from mountainous sites solely in qualitative terms (see Speranza et al. 2000 and recent discussion on their paper). Air masses rising up mountain slopes, usually in the direction of the prevailing wind (from the NW in our case), carry pollen grains to higher altitudes, as observed in the Alps during studies using pollen traps (van der Knaap, pers. comm.).

Factors affecting forest composition at 2 000 BP

Although only a limited number of sites were included in this study (due to the lack of pollen spectra for this period for this area), statistical analyses yielded some results (Table 2). The occurrence of *Quercus* and *Pinus* is negatively correlated with altitude, while that of *Picea* and *Fagus* is positively correlated with this factor. The higher the mean annual temperature, the more *Quercus* pollen there is, and the opposite is true for *Fagus.* It should be noted, however, that mean annual temperature is a function of altitude. The amount of tree pollen was negatively correlated with temperature; lowland sites had a more open landscape in the most favourable regions due to the effect of man, illustrated by the negative correlation between the AP value and the amount of cereal pollen. In regions of open landscape, *Quercus* was most common, and a high presence of *Abies* pollen is found only in forested regions. This points to the fact that the vegetation changed not only along altitudinal or temperature gradients, but also along gradients of human impact. Evaluation of the interactions between these factors is difficult and is a task for future research.

Qualitative conclusions can be reached, based on the characteristics of pollen spectra from different sites (see the pollen percentage values in Table 1). The highest values for *Carpinus* are from the more eastern sites (especially lowland sites no. 8 and 16), while in the south and southwest, the values for this species are low, and at site no. 9, it is absent. This can be explained by the acidic substrata of these sites, where hornbeam was a rare component of acidophilous oak woodlands (as in present woodlands of this type – Neuhäuslová et al. 1998). Since *Carpinus betulus* is the latest species of forest tree to reach the territory, coming from the north-east around 4 000 BP (Rybníčková 1985), it can be hypothesized that its rare occurrence in the southwest is a result of its late arrival. Nevertheless, the picture is even more complicated if consider the possibility that man affected the hornbeam expansion to natural forest communities (Ralska-Jasiewiczowa 1964). Human impact was relatively low in south and southwestern Bohemia, but high in lowland central and eastern Bohemia, and lowland Moravia. More factors may have played role in the expansion of *Carpinus betulus*, but edaphic conditions were probably the most important.

At the lowland site Tišice (no. 7), situated in the floodplain of the river Labe, there is a high percentage of *Pinus* pollen. In this case, edaphic conditions were also most probably responsible, as extensive sandy and gravel river terraces with aeolian dunes of Late-glacial age surround the site. Moreover, the site is not far from the extensive sandstone region of Kokořínsko, where pine must have grown naturally on acidic sandstone substrata, and where a large pool of diaspores was present. It is likely, though not yet proven, that *Pinus* was an important element in natural and semi-natural woodlands of the middle region of the Labe river (see also Břízová 1997, 1999).

Table 2. – The results of simple regression analyses. Values that reach minimum significance level of 5% (P < 0.05) are in bold.

	altitude	temperature	precipitation	latitude	longitude	CORYLUS	QUERCUS	PINUS	PICEA	FAGUS	ABIES	CARPINUS	CEREALIA
temperature	**–0.922**												
precipitation	**0.858**	**–0.864**											
latitude	0.205	–0.345	0.196										
longitude	0.222	–0.263	**0.589**	–0.123									
CORYLUS	0.125	–0.216	0.196	0.248	0.148								
QUERCUS	**–0.560**	**0.504**	–0.434	–0.004	0.092	0.272							
PINUS	**–0.534**	0.436	–0.362	0.248	–0.177	–0.351	0.109						
PICEA	**0.547**	–0.242	0.248	–0.229	–0.268	–0.177	–0.496	–0.485					
FAGUS	**0.557**	**–0.530**	0.439	0.059	0.281	0.270	–0.094	**–0.741**	0.185				
ABIES	0.378	–0.433	0.262	–0.261	0.030	0.084	**–0.592**	**–0.593**	0.192	0.384			
CARPINUS	–0.172	0.046	0.025	0.242	0.411	0.264	0.644	0.087	–0.449	–0.077	–0.490		
CEREALIA	–0.390	0.438	–0.179	–0.290	0.249	–0.370	0.343	0.179	–0.021	–0.401	–0.384	0.191	
AP	0.491	**–0.533**	0.323	0.193	–0.084	–0.160	**–0.681**	–0.186	0.235	0.265	**0.528**	–0.185	**–0.634**

Forest composition in 2 000 BP and currently: comments on geobotanical reconstructions

Three groups of sites (and outlying site no. 7) can be recognized (Fig. 2) on the basis of pollen percentages of the main forest trees (Table 1).

Group 1 (sites no. 6, 8, 15, 16) consists exclusively of lowland sites; other lowland sites (nos. 1, 7) belong to other groups for reasons described above. Low percentages of *Picea* pollen and a somewhat higher percentage of *Pinus* and other forest tree pollen (the complete species spectra) characterize pollen spectra of sites in this group. The low occurrence of spruce is best explained by the past conditions at these sites being warm and dry. However, spruce was not completely absent from the lowlands, and grew probably in extreme habitats in valley bottoms, where there were wet soils or peat. This supports the view of Nožička (1972) who came to the same conclusion after analysing historical documents. Pine could have been favoured in disturbed habitats, as human impact was relatively intense at these sites. Both *Quercus* and *Carpinus* are common. Hornbeam can reproduce when shaded – which is why it grows with oak (Opravil 1982). In our case, this is revealed by the positive correlation between these two species (Table 2). The high percentage of *Abies* and *Fagus* at warm lowland sites is more surprising. Firbas (1949, 1952) has demonstrated that *Fagus* naturally occurs commonly in central-European lowlands. Silver fir and beech must have been important in the lowland mixed oak woodlands in general. This fact is not reflected in geobotanical reconstructions (Mikyška et al. 1968, Moravec et al. 1969, Neuhäuslová et al. 1998). Recent pollen analyses from Central Bohemian lowlands (including also the sites no. 6 and 7) show that human management was an important determinant of forest tree composition in Prehistory. The periods of maximum expansion of *Pinus*, *Carpinus,* and *Abies* occured synchronously with periods of the most intense human impact. It is likely, that forest grazing, cutting, or coppicing favoured these trees over other species. In the most controversial case, *Abies*, this is supported by historical data collected by Málek (1983), which indicates that silver fir expansion was usually favoured by forest disturbance. Such ecological behaviour is not observed currently because of the absence of *Abies* diaspores (after a massive dieback).

Group 2 (sites no. 1–5, 9–12). This group consists of upland and mountain sites, and lowland site no. 1, which deposited a record of mountain vegetation. Archaeological and palaeoecological studies indicate that during the period around 2 000 years BP, near-natural forests covered most of the uplands of the Czech Republic (Rybníček & Rybníčková 1992, Pleiner & Rybová 1978, Ložek 1999). Common features of the pollen spectra of these sites are: low percentages of *Quercus* and *Carpinus*, and high percentages of *Abies, Fagus* and *Picea* pollen. Spruce was especially important at site no. 9 (foothills of the Český les Mts). Silver fir was most important at sites no. 10–12, i.e. on the western slopes of the Českomoravská vrchovina uplands. For most upland and mountain regions, mixed forests with a high component of conifers can be reconstructed. Recently, this view was accepted by some geobotanists (Neuhäuslová et al. 1998). Nevertheless, according to the present results, the general role of *Abies* in upland forest composition (and also in the lowlands) remains undervalued in geobotanical reconstructions. Most of the upland woods must have been dominated by *Abies alba*. Extensive beech-silver fir forests must be reconstructed also in the areas of acidophilous oak woodlands on the present geobotanical map (Neuhäuslová et al. 1998). Jankovská (1988) came to a similar conclusion in a discussion

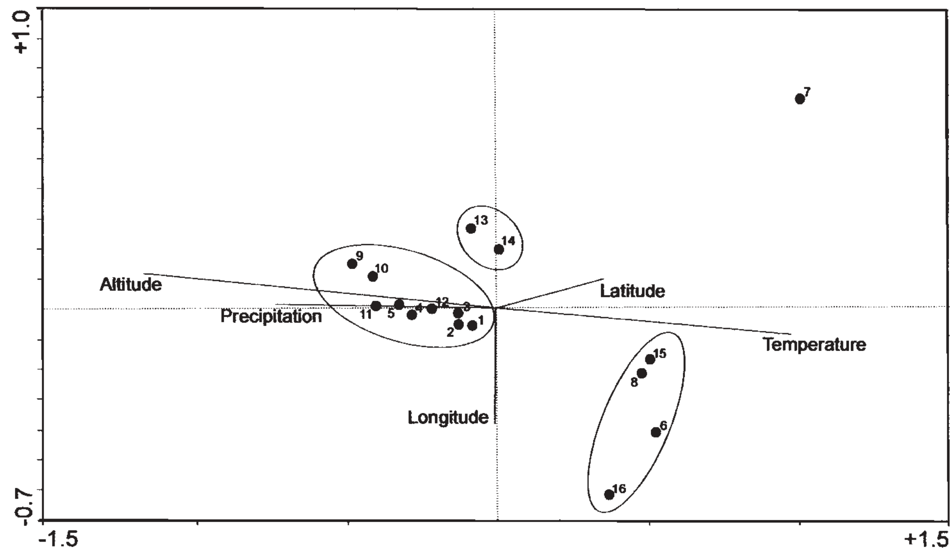

Fig 2. – CCA ordination diagram of individual sites (% of total tree pollen used as input data).

of the previous editions of the geobotanical map (Mikyška et al. 1968, Moravec et al. 1969).

Group 3 (sites no. 13, 14). This small group consists of two sites situated in the Třeboňská pánev basin. They have similar qualitative characteristics to Group 2, but have a higher percentage of *Pinus* pollen in their spectra. The reasons are the acidic sandy substrata at these sites and the existence of extensive transitional mires, which were well developed and covered with pine forests (*Pinus sylvestris* and particularly *Pinus rotundata* – Jankovská 1980). In addition to pine, *Abies* must have been a dominant component of natural forests in the Třeboňská pánev basin. This is supported by the analyses of Jankovská (1976, 1980, 1988), who found macrofossils (complete cones) of silver fir, indicating that *Abies alba* was growing on top of several meters of peat during the Older Subatlantic Period. In the earlier version of the geobotanical map (Mikyška et al. 1968, Moravec et al. 1969), the important role of silver fir in the Třeboňská pánev region was not appreciated. Jeník (1974) and Březina (1975) assigned *Abies* a dominant position in their geobotanical reconstructions, and their suggestions are similar to the conclusions of the present paper. Recently, Neuhäuslová et al. (1998) used the term "silver fir-oak woodlands" (*Abieti-Quercetum*) to reflect the fact that *Abies* might have been an important component of natural acidophilous oak forests.

Conclusions

Due to the scarcity of pollen analyses for the Czech Republic, pollen data is usually not used for detailed reconstructions of past vegetation. Nevertheless, the results presented in this paper demonstrate that for carefully selected reference sites and after appropriate statistical analysis, such reconstruction is possible. This study indicates the most important forest tree species during the period around 2 000 years before present. Although the altitudinal zonation of forests corresponding to the present-day situation developed at that time, the species composition of those forests was much more diverse than indicated by a simple forest-zonation model. In many regions, there must have been a complete spectrum of forest tree species, forming a mosaic, with the dominant species dependent on local factors.

In the lowlands woods were affected by man to varying but generally an important degree. They were dominated by oak and hornbeam, but beech and silver fir were also common, or even important in less favourable microhabitats. The occurrence of hornbeam, silver fir, and pine in particular was favoured by forest management.

In the uplands, mixed forests existed, commonly dominated by silver fir and beech. Although oak was present in such regions, the extension of acidophilous oak woodlands was more limited than often postulated by geobotanists. Spruce was sometimes common as an admixture in such upland forests, reaching dominance in waterlogged locations or valley bottoms subject to severe frosts. This type of upland forest extended high into the mountains, where beech and spruce, favoured by more severe climatic conditions, started to dominate over silver fir.

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Souhrn

S použitím statistických metod je pro území České Republiky analyzována prostorová variabilita rozšíření hlavních lesních dřevin v době před 2000 lety. Základem této krátké studie jsou výsledky pylových analýz (originální data a publikované výsledky jiných autorů) na 16 lokalitách, přičemž hlavním důvodem jejich výběru je dobrá reprezentativnost pro vybrané období. Přes relativní nedostatek kvalitních dat, související se současným stavem bádání, výsledky ukazují, že použitá metoda je ve většině případů dostatečně citlivá k tomu, aby umožnila rekonstrukci složení lesních porostů v regionálním prostorovém měřítku. Hlavními faktory ovlivňujícími toto složení jsou výšková zonace, míra lidského působení a vliv rozdílných substrátů. Nížinné oblasti, v příslušnou dobu již do značné míry ovlivněné lidskou činností, byly kryté dubohabřinami, i když buk a jedle zde hrály úlohu místně významné příměsi. Přímý lidský vliv způsobil šíření borovice, habru a jedle. Přestože dub byl jistě přítomen také ve vyšších polohách pahorkatin, rozsah kyselých doubrav zde byl značně omezen. Rostly zde především smíšené jedlové lesy a bučiny. Na méně příznivých stanovištích hrál významnou roli také smrk. Tento typ lesů se rozkládal až do horských poloh, kde ovšem buk se smrkem převažovaly nad jedlí. Obecně vzato bylo složení lesů v době před 2000 lety podstatně pestřejší, než odpovídá představám odvozeným ze současného, člověkem již silně ovlivněného stavu. Ve většině oblastí bychom před dvěma tisíciletími nalezli téměř kompletní druhové spektrum dřevin. V podobě složité mozaiky zde pouze místně převládaly určité druhy, a to s ohledem na vliv lokálních stanovištních faktorů (významně se projevila např. přítomnost borovice na písčitých substrátech Třeboňska a středního Polabí).

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