Proceedings IAVS Symposium, pp. 316-320, 2000
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Structure and dynamics of a floodplain alder carr during the late Holocene

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Abstract. The late Holocene history of an alluvial alder carr in E. Bohemia, Czech Republic and its vegetation dynamics were studied using pollen, macrofossil and tree-ring analyses together with vegetation analysis. Due to high accumulation rates and good preservation of the palaeo-ecological record, a detailed reconstruction of vegetation changes during the last 2160 yr was possible. After an oxbow had filled up, a peat bog and later an alder carr developed. Pollen and macrofossil analyses indicated cyclic succession in the course of the past 900 yr, with several alder carr and open wetland stages. The last cycle was documented by vegetation analysis and confirmed by tree ring analysis. In the 1880s the current forest margin was established. The centre of the locality was overgrown by the alder carr between 1940 and 1950. Since that time hardly any alder established in the study site. The present dynamics of the tree layer are characterised by a high mortality of suppressed *Alnus* trees, and of *Betula pubescens*, irrespective of tree age.

Keywords: *Alnus glutinosa; Betula pubescens;* Cyclic succession; Late Holocene; Pollen analysis; Population dynamics.

Nomenclature: Ehrendorfer & Gutermann (1973).

Introduction

Alder carrs belong to the most naturally heterogeneous and dynamic ecosystems in temperate Europe (Ellenberg 1986; Prieditis 1997). They are basically formed by hummocks and hollows with permanent standing water. Temporally flooded habitats also occur. Uprooting of mature trees results in gaps where light regime, nutrient availability and competition differ from the closed-canopy forest (Carlton & Bazzaz 1998). Gap centres, usually at slightly lower elevations than their surroundings represent another habitat – small water bodies which persist for many years, until they are terrestrialized (Jeník 1980). The small-scale habitat heterogeneity is reflected in a remarkable mixture of plant species with different soil moisture requirements and tolerance of anaerobic conditions (Döring-Mederake 1991). The long-term dynamics of alder carrs has received insufficient attention (but see Marek 1965; Brock et al. 1989). However, it has been suggested that the alder carrs may persist at a site over more than 800 yr (Marek 1965). The *Alnus glutinosa* stands are usually more or less even-aged in alder carrs (Pigott & Wilson 1978; Tucker & Fitter 1981). Trees belonging to younger age classes are markedly under-represented and establishment of alder seedlings is rare (McVean 1956; Tucker & Fitter 198; Klimešová & Klimeš 1996; Prieditis 1997). It has been speculated that alder carrs follow a cyclic development (Faliński 1986; Remmert 1991) and that the establishment of *Alnus* is restricted to the peat bog stage of this development (Jeník 1980). A similar cyclic development has been reported from several other forested ecosystems (Míchal 1983; Delcourt & Delcourt 1991; Korpel' 1995; Schmidt 1998). Unfortunately, there is little evidence to support or reject this hypothesis in any of the habitats. In alder carrs the peat, containing pollen and macrofossils, is usually mineralised due to its aeration by alder roots so that only a thin layer of it is preserved (Jeník 1980; Rybníček & Rybníčková 1987; Döring-Mederake 1991). Therefore, in most cases the long-term history of alder carrs cannot be studied by using a standard pollen analysis. Data based on other approaches (direct historical observations, archaeological studies, etc.) are also scarce so that little is known about the long-term dynamics of alder carrs in temperate Europe.

The locality 'Na bahně' in E. Bohemia (Czech Republic) is situated at the foot of a pleistocene terrace. Many powerful and persisting springs supply the alder carr with water. Its drying-out is prevented and the water regime is remarkably stable both within a year and between years (Klimešová & Klimeš 1996). Consequently, mineralization of the peat is slowed so that the entire history of the present alder carr could be recorded in the peat. Recent history of the locality has been recorded by several botanists. Rare peat bog plants were reported from the locality at the end of the last century (Hansgirg 1881; Sitenský 1891). In 1924 Mikyška studied the vegetation of the locality. The centre was formed by a peat bog with herbaceous vegetation dominated by *Menyanthes trifoliata, Carex nigra, Potentilla palustris*, large carpets of *Sphagnum recurvum* and *S. flexuosum*, and other heliophilous species (Mikyška 1926), indicating low pH and low nutrient availability (Klimešová & Klimeš 1996). The peat bog was surrounded by an alder carr, locally with abundant *Calla palustris* (Mikyška 1926). In the 1940s the peat bog in the centre of the locality was overgrown with young *Alnus* trees (Mikyška 1964). In the 1980s the vegetation consisted of a homogeneous *Alnus* stand (Rydlo 1981; Klimešová & Klimeš 1996). In 1988 we marked more than 500 trees of *A. glutinosa* and *Betula pendula*, and repeatedly measured their growth until 1998 to evaluate the dynamics of individual tree populations (Klimešová & Klimeš 1996; Klimešová et al. 1997). The stand has also been studied using dendrochronological methods which provided details on the development of the stand during the last cycle (Klimešová et al. 1997).

The aim of this paper is to bring together the available information based on different methods and to reconstruct the development and dynamics of the locality 'Na bahně' during the late Holocene.

The locality

The alder carr 'Na bahně' is situated in the Orlice River floodplain (240 m a.s.l., 50°12'N, 15°58' E), E Bohemia, Czech Republic, at the foot of the youngest (Würm) terrace. The terrace, ca. 5 m in height, surrounding the alder carr from three sides, is covered by a deciduous forest dominated by *Quercus robur.* Towards the Orlice River wet unmanaged meadows invaded by *Alnus* saplings are found. The shortest distance to the river is ca. 150 m. Mean annual air temperature is 7.8 °C, mean annual precipitation is 602 mm (Nově Hradec Králové Meteorological Station, 8.5 km W of the locality; Vesecký et al. 1961).

Data collection

Palaeobotany

A series of exploratory borings was performed in the centre of the locality in spring 1997. The layer of organogenic deposits was up to 0.5 - 5 m deep. A 5-m long core was taken with a 5-cm diameter Russian-type corer (Jowsey 1966). The sediments were analysed for their components according to methods by Troels-Smith (1955), modified by Aaby & Berglund (1986).

Three samples consisting of pieces of wood were taken for ^{14}C dating. The samples were AMS-dated at the Radiocarbon Dating Laboratory, Department of Quaternary Geology, Lund, Sweden. Age calculations were based on a ^{14}C half-life of 5568 yr. The results were calibrated (Stuiver & Reimer 1993) and are reported in calendar time scale.

The samples used for pollen and other microfossil analyses were prepared by the modified acetolysis method (Erdtman 1943). As the lower part of the core had a more or less mineral character, the samples were pre-treated with concentrated hydrofluoric acid for 24 h (Faegri & Iversen 1989; Moore et al. 1991). The extracted microfossils were lightly stained with 0.3 % safranin and mounted in a glycerol-water mixture. In each sample an average of 1500 pollen grains were counted. The percentage values were calculated on the basis of the total sum, including all pollen types.

A macrofossil analysis was performed using the same core as for pollen analysis. The core was cut into 20-cm contiguous samples and their volume was determined. Macrofossils were extracted by heating the sample in a 5% sodium hydroxide solution for 5 min and then sieved under running water. Sieves with mesh sizes of 200 µm, 300 µm and 700 µm were used. The residues were examined under a stereomicroscope and the total amount of macrofossils was counted. In the macrofossil analysis the absolute number of items of each taxon was recalculated to a standard volume of 500 cm^3.

Zones in the pollen and macrofossil data were delimited using Detrended Canonical Analysis (DCA; Hill 1979). Samples were grouped into 'zones' using a simple iterative procedure linking simultaneously pollen and macrofossil samples into groups whose envelopes did not overlap.

Other methods

We made phytosociological relevés in the summer and autumn of 1987, using standard methods described by Mueller-Dombois & Ellenberg (1974). In a belt, 70 m in width and 140 m in length situated across the alder carr we labelled all 830 trees in the autumn of 1987. Trunk girth at the standard 1.3 m height was measured in the autumn of 1987 and in 1998. A comparison between relevés by particular authors was made using DCA. In randomly selected 72 *Alnus* and 14 *Betula* trees growing in the above belt two cores were taken from with a Pressler increment borer at 1.3 m height to count the number of tree rings.

Results

Palaeobotanical reconstruction

Three zones were distinguished by DCA ordination in the core both for pollen and macrofossil data (Fig. 1). The lower zone (160 BC - 680 AD) represented a small oxbow lake, ca. 1.5 m deep, dominated by wetland plants, such as *Myriophyllum spicatum, Batrachium* spec., *Potamogeton* spec. and *Nuphar lutea*. The occurrence of some taxa was proved by trichosclereids (*Nymphaeaceae*) and leaf spines (*Ceratophyllum*). The presence of zygospores of the chlorococcal alga *Mougeotia* indicates permanent water. Amphibious plants, such as *Alisma plantago-aquatica, Polygonum amphibium* and *Sagittaria sagittifolia* were abundant in the littoral. An adjacent belt of wetland vegetation was formed by sedges (predominantly *Carex rostrata*) and other common wetland plants (*Lycopus europaeus, Lythrum salicaria, Cicuta virosa, Ranunculus flammula, Solanum dulcamara*). An alder stand was apparently situated closely to the oxbow lake, because *Alnus* was well represented in the pollen spectrum. *Pinus*, *Carpinus betulus* and *Tilia cordata* grew probably on the adjacent terrace slope.

After the oxbow had filled up a wetland dominated by *Filipendula ulmaria* and *Caltha palustris* was developed (middle zone, 680 - 970 AD). Sedges (*Carex vesicaria, C. pseudocyperus* and *C. echinata*) were relatively infrequent there. Although *Alnus glutinosa* pollen were abundant, the number of macrofossils slowly decreased, indicating that

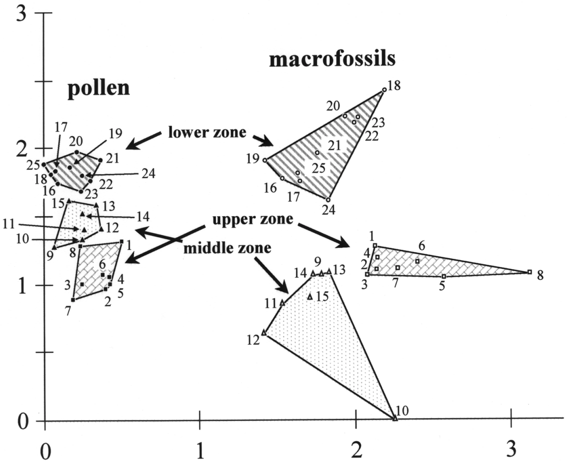

Fig. 1. DCA ordination diagram of the pollen and macrofossil data from a 5-m core. The 20-cm contiguous samples are labelled with numbers; samples belonging to the three zones are in envelopes.

the alder locally declined. Later on a *Sphagnum* dominated fen developed, with *Equisetum, Ericaceae* and *Calla palustris.* Since this time the river sediments contributed only little to the sedimentation process and the effect of local springs at the foot of the terrace became dominant. The alluvial wetland changed to a spring type wetland.

The upper zone (970 AD - present) began with a marked vegetation shift. *Sphagnum* decreased and *Potentilla palustris, Lycopus europaeus, Cicuta virosa, Caltha palustris, Carex echinata* and *Sparganium minimum* became more abundant in the peat bog. After that the wetland became overgrown with *Alnus* and *Betula*, and a closed forested wetland was established.

The dynamics of *Alnus* and heliophilous wetland herbs showed opposite trends during the past ca. 900 yr, with four or three peaks of *Alnus*, based on pollen and macrofossils, respectively (Fig. 2). The results indicate a cyclic development of the alder carr during the last millennium.

The uppermost two samples of the pollen diagram (20 and 0 cm) included roughly the last 100 yr. In the *Sphagnum* peat layer (16-27 cm) mosses indicating mesotrophic to eutrophic habitats were abundant (*Sphagnum palustre, S. recurvum* and *Calliergon cordifolium). Sphagnum squarrosum* and *Rhizomnium punctatum* were infrequent. This layer with indicators of an open peat bog corresponds to the stage studied by Mikyška (1926). For more detailed palaeobotanical results see Pokorný et al. (2000).

Vegetation dynamics during the last 100 years

The oldest floristic records from the locality 'Na bahně' by Hansgirg (1881) and Sitenský (1891) include numerous species indicating an open peat bog environment. Some more floristic notes confirming these records were published at the verge of the century. Until the 1930s the centre of the locality was open, with a *Sphagnum* peat bog, whereas the foot of the terrace was covered with an alder stand (Mikyška 1926). The vegetation pattern changed remarkably between 1926 and 1964 (Mikyška 1964; Fig. 3). The central peat bog became overgrown by an alder carr and plants requiring an open canopy disappeared. The species composition of the alder carr surrounding the peat bog also changed markedly between 1924 and 1964. A comparison of the vegetation relevés of the alder carr recorded by Mikyška in the 1920s and 1960s indicates a major change in species composition reflected in a shift of x-coordinates of the sites in the DCA scatter diagram (Fig. 4). Later, the development slowed down. Hence, in the DCA, the envelopes encompassing relevés recorded by Mikyška (1964), Rydlo (1981) and Klimešová & Klimeš (1987) are situated close to each other (Fig. 4).

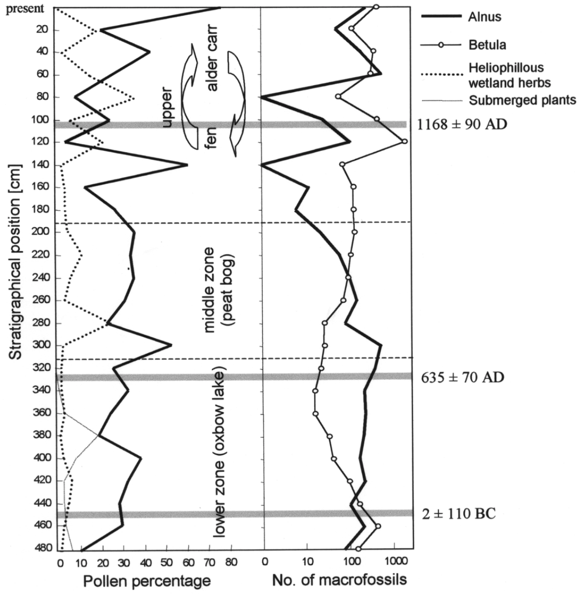

Fig. 2. Synthetic percentage pollen diagram and *Alnus* and *Betula* macrofossil diagram, illustrating local vegetation succession. The three zones were delimited using DCA multivariate analysis (see Fig. 1).

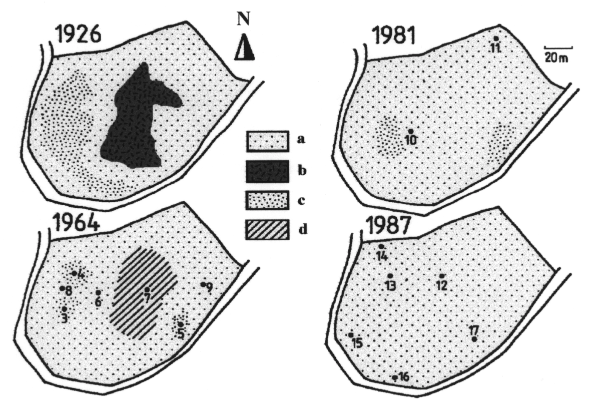

Fig. 3. Map of the locality 'Na bahně' according to Mikyška (1926, 1964), Rydlo (1981) and our research in 1987. Localisation of phytosociological relevés (3 - 17). Some important vegetation types are also given. Relevés 1 and 2 by Mikyška (1926) were recorded in the alder carr, their exact localization is unknown. a = alder carr; b = peat bog; c = alder carr with dominating *Calla palustris*; d = alder carr with dominaning *Lycopus europaeus*.

In 1998 the tree layer was dominated by *Alnus glutinosa*, (nearly 68% of the trees). Another important tree reaching the canopy was *Betula pubescens* (21 % of the trees). The remaining 10% included younger trees of *Ulmus minor, Tilia cordata, Sorbus aucuparia* and *Prunus padus*, which did not reach the canopy.

The relationship between tree age (*TE*) and trunk girth (*TG*) in 1998 was linear (regression analysis):

Betula: $TE = 0.93 * TG + 40.99$, $R^2 = 0.39$, $P < 0.001$;

Alnus: $TE = 0.94 * TG – 0.415$, $R^2 = 0.37$, $P < 0.05$.

The slope of the regression line was nearly the same for the two species ($P > 0.1$) but the increment differed between them ($P < 0.05$). In *Betula* the increment was close to 0, whereas in *Alnus* it was nearly 41. This difference can be explained by the fast growth of young *Alnus* trees and a stable increment in trunk girth in *Betula*. At present hardly any trees of either species younger than 40 yr can be found in the locality; most *Betula* trees are older than 70 yr. The distribution of the tree age of *Alnus* and *Betula* in the

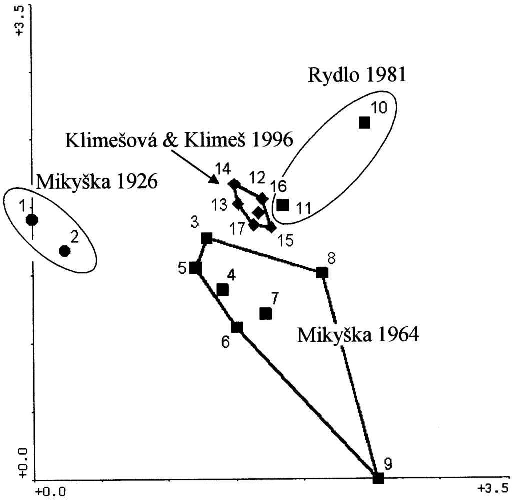

Fig. 4. DCA ordination of the presence/absence data based on relevés (1-17) recorded in the alder carr of the locality 'Na bahně' from 1926 to 1987.

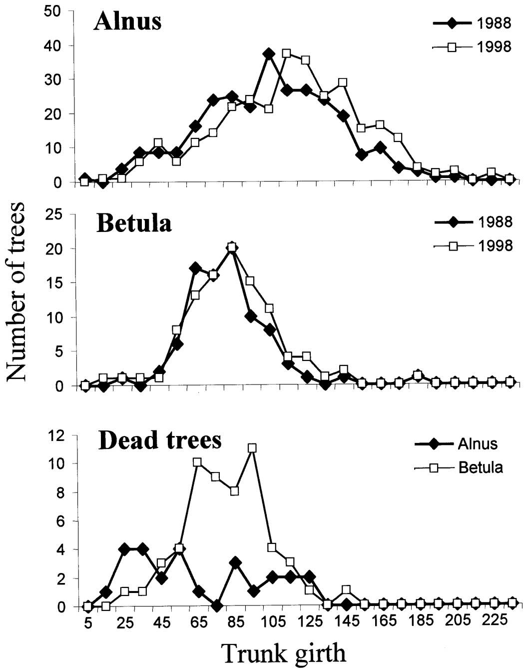

Fig. 5. Changes in size distribution of trunk girths in *Alnus glutinosa* and *Betula pubescens* in the locality 'Na bahně' from 1988 to 1998.

central and peripheral areas of the locality indicated that (1) the central part of the locality was colonized by *Alnus* in the 1950s and (2) the trees of the marginal belt of the locality established at the end of last century.

Current tree dynamics are characterized by ageing of the *Alnus* and *Betula* populations, and hardly any seedling establishment of either species. Trunk girth of *Alnus* trees increased significantly in the past 10 yr (Fig. 5), except for the smallest size classes. In *Betula* the increase was not so apparent because many big trees died during the last decade (Fig. 5). Mortality in *Alnus* was nearly the same in the middle and lower size classes, whereas no mortality has been recorded during the last 10 years in the higher size classes. From 1988 to 1998 8% of *Alnus* trees died, whereas in *Betula* 35% trees died and fell down.

Discussion

The development of the vegetation in the locality followed a classical alluvial successional series (Ellenberg 1986), starting with an oxbow, slowly filled up by sediments, later on developed into a wetland dominated by *Filipendula* and *Caltha*. At that time *Alnus glutinosa* was abundant in the pollen spectra but nearly missing among macrofossils, indicating its presence in the surroundings. Finally, before the second millennium, a *Sphagnum* bog developed and at about 1150 AD an alder carr established. It declined and re-established three times at least. The recent alder carr, situated along the foot of the terrace, established according to tree age, pollen and macrofossil data less than 130 yr ago. The centre of the locality was colonized by *Alnus* ca. 55 yr ago.

Our data show that an alder carr may persist in a locality over more than 800 yr. However, during the whole period the canopy of *Alnus* was not as dense as it is today. Its cover was repeatedly much reduced or even *Alnus* locally disappeared completely. The driving force of the cyclic development of the alder carr is unclear. The changes may be caused by the life history of *Alnus* itself. It cannot establish under a closed canopy and in small canopy gaps – a reduction of the tree layer cover to 30-50% is not sufficient for its establishment (Tucker & Fitter 1981; Korpel' 1995). Vegetative multiplication is also inefficient because the suppressed trees die soon. Therefore, the even-aged *Alnus* stands cannot persist for a time longer than the life-span of the alder, which is about 200 yr (Korpel' 1995), but in the study site usually less than 90 yr (Klimešová et al. 1997). The die-back of most *Alnus* trees in a stand may promote establishment of a peat bog with hollows and hummocks. The soil of the hummocks is relatively dry and therefore more appropriate for *Alnus* establishment than permanently wet sites (McVean 1956). Thus, an autogenous cycle in alder carrs may work, as suggested by Jeník (1980) and Faliński (1986). Alternatively, an allogenous cycle induced by cutting of adult alder trees by humans should be considered. However, the increased human activity indicated by a high incidence of pollen of synanthropic plants was not correlated with the decrease of *Alnus* pollen and macrofossils. Therefore, we do not have any additional evidence to support this explanation. Changes in hydrological regime of the locality could also explain the cyclic development of the alder carr. Human-induced changes in water table (Brock et al. 1989) and long-term fluctuations in water table caused by changes in river discharge (Janssen et al. 1995) have been described as factors enabling alder carr establishment. The pollen analysis, however, does not indicate any disrupt change in water regime of the locality.

The local source of spring water seems to buffer water level fluctuations caused by the river. The same holds for nutrients to some extent. Therefore, we conclude that the autogenous model of the cyclic development of the studied alder carr provides the most probable explanation of the observed pattern.

Acknowledgements. We thank J.W. Jongepier and Tomáš Kučera for constructive comments on an earlier version of this paper. This project was supported by grant M44 of the Agency for Nature Conservation and Landscape Protection of the Czech Republic (a part of the programme 'Environmental Management' of the Ministry of Environment no. 6110/2; 1991-1998).

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