Mires of the Šumava Mountains: 13,000-Years of Their Development and Present-Day Biodiversity

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ABSTRACT. In the Šumava Mountains, orography and geomorphology hand in hand with temperature gradient, distribution of precipitation and wind speed predisposed differentiated altitudinal development of numerous mountain mires. Comparison of vegetation development, based on the pollen analyses, during the last 13,000 years with the present-day biodiversity was carried out for reference sites of the Hůrecká Bog, the Rybárenská Mire, and the Velká Niva and Malá Niva Bogs. In the western part, the vegetation development, started in the Late Glacial, 11,000 years ago with the prevailing vegetation cover of steppe and tundra. The Holocene began with the open forests of Pinus *and* Corylus. *During the Holocene, the forests with composition of* Picea, Fagus *and* Abies *reached the climax stadium 2000 years ago. Earlier than the western mires, already 13,000 years ago witness the vegetation development of the Late Glacial (Velká Niva and the Malá Niva Bogs). The subsequent vegetation history of the eastern bogs has been changed in contrast with the western mires, being marked by Alnus-Betula carrs since the Atlantic, 6000 years ago. Summit plains exposed to high precipitation and strong wind differed in the formation of plant cover, which in the Rybárenská Mire began as late as in the beginning of the Holocene, 10,000 years ago. In the Šumava Mts., continuous vegetation development since the Late Glacial is essential for reconstruction of the unique forest history that varied remarkably according to the local effects of vertical zonation, microclimate, and water regime.*

KEY WORDS: mountain mires, present-day biodiversity, pollen analyses, vegetation development, Late Glacial, Holocene, Šumava Mts., Czech Republic.

Introduction

Mires arise as semiterrestrial ecosystems where accumulation of organic matter prevails above its decomposition. Ecological balance of these contradictory processes is rather complicated being controlled by several factors, such as amount and seasonal course of precipitation, mean, annual and diurnal temperature, occurrence of dominant plants, geological bedrock and/or hydrological design. Disintegration of the accumulated material, enriched by trapped pollen grains (Svobodová, 1998), is negligible and its redeposition is rare. As a result, mire ecosystems store information on past ecological conditions that might be dated and the evolution of the mire itself and of its surroundings might be potrayed (Frenzel, 1983).

In Central Europe, the history of mires started in the Late Glacial. In the last 15,000 years, a variety of mires developed from the forested bogs and saline or calcareous fens to open patterned mires with blanket and palsa-like structures and mixed kettle-hole bogs in glacial cirques. At present, the majority of growing mires is confined to mountain areas of the Hercynian middle-mountains with mainly ombrotrophic mires (bogs), namely to Bohemian Forest, Ore Mountains, Black Forest, the Vogesen, Jeseníky, Iser Mts., Giant Mts., Czech-Moravian Highlands, Harz and Ardennes. Their remarkable biodiversity includes occurrence of endemic species and communities (Hadač and Váňa, 1967; Dierssen and Dierssen, 1984; Hölzer, 1977).

Among them, Bohemian Forest (Šumava in Czech, Böhmerwald in German), middle-mountain range astride the boundaries of Czech Republic, Germany and Austria reaching up to 1456 m, represents one of the most important peatland regions where mires cover more than 15% of the area (Schreiber, 1924). Orography and geomorphology hand in hand with climate transitional between oceanic and subcontinental (Nekovář, 1969), temperature gradient, distribution of precipitation and wind speed, predisposed differentiated altitudinal development of its numerous mires (Rudolph, 1929; Soukupová, 1996), where relic boreal populations co-exist together with the immigrant species from the Alps in the endemic communities (Sofron, 1980; Šula and Spitzer, 2000). Though first paleoecological research of mires in Bohemian Forest has been carried out already in the 1930s (Klečka, 1928; Ruoff, 1932), only few modern paleoecological data have been gained from so many well-preserved mire ecosystems during the last thirty years, except for the southern Bavarian side (Stalling, 1987). In this study, comparison of basic mire types of Bohemian Forest and their environments in the Late Glacial and Holocene is given for different altitudinal, geomorphologic and mesoclimatic situations.

Environmental predisposition

Mires in the Šumava are spread within a wide altitudinal range of 700 m, with mean annual precipitation reaching from 729 to 1552 mm. In lower altitudes where material from retrograde erosion was deposited (Šebesta, 1996), terrestrialization was active in the development of valley-raised bogs behind natural levees, e.g. Mrtvý Luh Bog, Malá Niva Bog, Chalupská Bog, Hůrecká Bog. As it is documented by pollen analyses, formation of these bogs might start already in the Late Glacial (Svobodová, 1995). Peat depth attains up to 7.5 m. At present, most of valley-raised bogs are partly or completely forested by the *Pino rotundatae-Sphagnetum*. Open central parts are usually lacking bog-lakes. This type is marked by prominent laggs with communities of the alliance *Sphagno recurvi-Caricion canescentis, Betulion pubescentis* and *Calthion*.

Paludification was decisive for the establishment of patterned mires on suitable gentle slopes of extensive plain paleorelief in the central Šumava (between 1000 and 1200 m). High precipitation (annual mean between 1000 to 1500 mm), and relatively low temperature with annual mean between 3 and 4 °C (Nekovář, 1969) predisposed the process (e.g. Rokytecká Mire, Blatenská Mire, Rybárenská Mire, Luzenská Mire). The mires

mostly include several smaller bog centers with bog-lakes; peat depth reaches up to 5.5–6.5 m (Pohořal, 1964). They are marked by occurrence of *Pinus x pseudopumilio* (*P.mugo x P.rotundata*) krummholz, belonging usually to the association *Sphagno magellanici-Pinetum mughi.* Open central parts are mostly covered by the alliance *Oxycocco-Empetrion hermaphroditi* (namely by the *Sphagno magellanici-Trichophoretum caespitosi*). Several communities of the *Leuko-Scheuchzerion* occupy numerous depressions (see below) (Sofron and Šandová, 1972; Sofron, 1980; Soukupová, pers.observ.).

Mountain mesoclimate, apart of the altitudinal effect, differs between the wind-exposed Northwest and leeward valleys of the Southeast (Ložek, 1998). For comparison of vegetation development during the last 15,000 years and of the present-day biodiversity three representative mires were selected on the bedrock of gneiss. They are situated in the windward northwestern upslope (Hůrecká Bog: 870 m), central summit plain (Rybárenská Mire: 1060 m), and from the southeastern valleys (Velká Niva and Malá Niva Bogs: 760 m). Assessment of plant communities was performed by means of phytosociological description (Moravec et al., 1994).

Hůrecká Bog represents a forested domed raised-bog in the western Bohemian Forest, located in the leeward position behind the topmost crests of Grosser Arber (1456 m) and Královský hvozd Ridge (1343 m). Elevation of the bog is rather high, between 861 and 882 m. Mean annual temperature attains 5.1 °C. Mean annual precipitation in the region reaches 807 mm with July maximum of 107 mm. Permanent snowpack persists for 60 days. The mire is located in the transition zone between gneiss and granites where both upwelling and alluvial surface waters are active. Peat deposits deeper than 0.5 m cover the area of 62.2 ha, their volume reaches $1.1x10^6$ m³ (Havelka and Březina, 1996). Bottom sediment of limnic gyttja relies on sand and clay, most of the profile is formed by sedge and sedge-cotton grass peat (Svobodová, 1995).

The entire complex of Rybárenská Mire is situated on the eastern outcrop of the topmost summit plains of Modrava on gneiss above the confluence of Roklanský and Javoří brook. It covers about 134 ha in the zone of transition between the montane mixed beech forests and coniferous taiga where mean annual precipitation reaches to 1100 mm and mean annual temperature to 3.7 °C, and continuous snow pack lasts for 6.5 months. Peat deposit reaches to 6.5 m, peat volume $2.8x10^6$ m³ (Havelka and Březina, 1996). From the base of gray clay the profile is formed by gyttje, overlying by sedge peat with *Sphagnum* remains and brown mosses (*Hypnaceae).* The majority of the upper part of the profile is built up of sedge-cotton grass peat.

Malá and Velká Niva Bogs, the two raised-bogs are placed to the East of central Šumava plains in the deep valley between the Radvanický Ridge and Boubín Massif in the floodplain of Teplá Vltava River that separates them. Each of them covers about 140 ha, and peat deposit reaches up to 6.4 m and to 3.4, respectively. Peat volume in Malá Niva reaches to $2.5x10^6$ m³, and to $1.6x10^6$ m³ in Velká Niva. Mean annual temperature attains 5.2 °C, annual precipitation total is 757 mm with July maximum of 102 mm. Permanent snowpack lasts for 50 days. Bottom sediment of limnic gyttja relies on gray sandy clay, one third of profile is formed by mixed peat, in the upper part sedge-cotton grass and sedge peat prevails.

At present, the Šumava have altogether 17 new pollen profiles analyzed palynologically by Svobodová et al. (in press). The peat profiles were sampled for the purpose of pollen analyses by the Russian Intorf sampler or extracted from the open profile to the metal boxes (500x100x100 mm). The peat samples are stored in the small plastic bags or directly in the metal boxes. Samples of 1 cm³ volume were treated by classic methods of Erdtman and Overbeck (Berglund and Ralska-Jasiewiczowa, 1986). In each pollen sample the minimum number of 500 pollen grains of arboreal pollen were counted. The absolute pollen counts are stored in the European Pollen Database.

Results

Mires of the northwest

Among the forested mires of the Northwest, Hůrecká Mire represents a well-developed and best-preserved raised-bog complex. According to the detailed vegetation analysis, most of the mires is covered by bog-pine forest with trees of the age 180 years. The association *Pino rotundatae-Sphagnetum* is marked by establishment of *Molinia caerulea*. The mire lacks open central expanse, *Sphagnum fuscum* and *S.rubellum* are scarce as well as *Calluna vulgaris*. In few rill fen species occur, such as *Eriophorum angustifolium, Carex canescens, C. echinata,* or *Phragmites australis*. Its well-developed lagg is relatively species-rich and is occupied by a mosaic of tall-sedge communities, namely by *Eriophoro vaginati-Sphagnetum recurvi, Carici rostratae-Sphagnetum apiculati, Caricetum goodenowii,* and *Agrostio caninae-Caricetum diandrae.* On several drier lagg sites, birch woods of the alliance *Betulion pubescentis* have established. Brooks are accompanied by stands of *Alnus incana*, and whole mire is surrounded by extensive waterlogged spruce stands belonging to *Mastigobryo-Piceetum* (Sofron 1980; Neuhäuslová 1998) and *Calamagrostio villosae-Piceetum*.

The mire originated in the depression from the initial small lakes (*Algae, Myriophyllum alterniflorum, M. spicatum, M.verticillatum).* In the Late Glacial cold oscillation of the Younger Dryas, brought the tundra- steppe vegetation. With the decline of pollen curves of *Juniperus*, *Betula nana*, *Chenopodiaceae*, *Artemisia*, *Thalictrum* and *Helianthemum,* the Holocene begins with the Preboreal and the development of *Pinus-Betula* light forest. The Boreal period is characterized by the spread of *Corylus*, and *Corylus-Picea* forests. In the climatic optimum of the Atlantic pollen curve of *Picea* and later *Fagus* suggest the development of *Picea-Fagus* forests. The climatic indicators of *Hedera helix* and *Viscum album* complete the Atlantic pollen spectrum. The *Picea, Fagus,* and *Abies* form the spruce-beech woodland of the Subboreal and of the Older Subatlantic. The *Abies* made only a mixture in these forests. In the Younger Subatlantic the settlement and agricultural activities are reflected by pollen of cultural plants *Secale cereale* and *Triticum.* That corresponds to German colonization of the 13th century. In the Late Subatlantic the *Fagus-Picea-Abies* forests were replaced with expanding *Pinus* or plantations of *Picea*.

Local development began with the small oligotrophic lakes in the depressions, characterized by gyttja of the Late Glacial and of the Boreal. At the second half of the Boreal the change to the raised bog was marked by *Carex* peat, which demonstrates small sedges The layer of charcoals of the Boreal period characterized the some fire events and subsequently the appearance of *Vacciniaceae* and *Calluna vugaris*. During the whole period of the Atlantic and part of the Subboreal *Pinus* trunks

were deposited in the mire. That demonstrates the change of the water regime and the development of the *Pinus* forest, with a lot of decaying woods. Vegetation of open sites was formed by the species of *Carex, Eriophorum, Vaccinium* and *Calluna vulgaris*. In the middle of the Subboreal the next change to the *Sphagnum* layer - *Cyperaceae* dry peat is marked, which means change to the submontane raised bog again. The next moist layer is formed by *Eriophorum* peat and the development of the submontane raised bog continued in the Subboreal and Older Subatlantic periods. The last layer is the similar *Eriophorum* peat, but again with the *Pinus* trunks and, and with the great development of *Pinus* loose and forest on the mire of the Young Subatlantic. The layer of charcoals shows the human activities around the mire and from this time the period of the Late Subatlantic begins, which is not younger than 300 years. The shrubs of *Vacciniaceae* and *Calluna vugaris* demonstrate the type of the vegetation on the mire.

Summit plains of central Šumava Mts.

Among vast complexes of patterned mires that developed in the elevated summit area of the Šumava range, Rybárenská Mire represents the easternmost archipelago in the Modrava Plains. The complex includes five separate bog centres, covered by krummholz of *Pinus x pseudopumilio* accompanied by *Vaccinium uliginosum, V. myrtillus* and *V.vitis-idaea* and on dry margins with *Betula nana*. Mire expanse of the best-developed centres is open, marked by stripped pattern of elevated hummocks (with the *Empetro hermaphroditi-Sphagnetum fusci*), ridges (with the *Eriophoro vaginati-Sphagnetum medii, Andromedo polifoliae-Sphagnetum magellanici*), flat lawns (with the *Eriophoro vaginati-Trichophoretum caespitosi*), shallow hollows, intermittently or permanently inundated pools (with the associations of the alliance *Leuko-Scheuchzerion*) and bog-lakes (where 82 species of algae were observed).

The vegetation development of the complex of montane raised bogs of the summit plains (e.g. Rybárenska slat' Mire) started later, at the beginning of the Holocene, in the Preboreal. In the Preboreal vegetation of *Betula-Pinus mugo* communities covered the central plains. The Boreal is characterized by the local expansion of *Corylus* and *Pinus*. The Atlantic is presented by appearance of *Picea*, and later of *Fagus*. The development of climax spruce-beech and spruce forests is evidenced. In the immense *Picea-Fagus-Abies* forests, where mainly *Abies* formed the mixed forests, marked the period of the Subboreal and the Older Subatlantic. The density of Abies here is much higher in comparison with the western part of the Šumava Mountains. The Younger Subatlantic is characteristic with the decline of *Abies* and *Fagus* and increase of *Picea* and *Pinus*.

The local conditions seem to be easier with comparison of the western mires and the eastern bogs. From the beginning the complex of the central mires of the Šumava region developed as the ombro-oligotrophic bog and remained like this throughout the whole Holocene. In the Boreal the charcoal layer was marked, the timing of which corresponds to that one of the Hůrecka Mire. The fire events are suggested in that time over the Šumava region. In the consequence of the fire the shrubs of *Vacciniaceae, Ericaceae* and *Calluna vulgaris* covered the central parts of the mire together with *Cyperaceae* and *Filipendula*. The local development continues to the moss layer of the Atlantic period. The moss layer with *Eriophorum* was developed in the Subboreal and persisted to the Subatlantic period.

Mire complexes of the southeast

Malá and Velká Niva bogs belong to characteristic treed raised-bogs of the eastern Šumava. The shape of both mires is elongated with asymmetric laggs. In the former bog that is well preserved, the lagg adjacent to river is cut off due to river erosion. Similarly for the latter mire, the lagg on side to river was developed obviously only poorly; at present it is partly disturbed by the road. The opposite laggs, sitting at the foot of neighbouring hills, are fully developed, being formed mostly by communities of the alliance *Betulion pubescentis*. Inner bog is mostly covered by the stands of *Pino rotundatae-Sphagnetum* with bog pine trees up to the age of 309 years. Central mire expanse is loose in trees with the rare association *Empetro hermaphroditi-Sphagnetum fusci*.

The system of bogs in the Southeast of the Šumava Mts., situated along the upper Vltava River (Svobodová et al., in prep)., includes the oldest mires of the range. The Late Glacial is dated to 13,000 years BP, covering the period of the Older Dryas, the Alleröd and the Younger Dryas. The Holocene differs from the regions described above with the local development of *Alnus-Betula* carrs from the Atlantic and with remarkable dense *Abies* forestation from the Subboreal, forming the beech-fir forests.

Local development of the bogs started with sandy-clay sediments in the Late Glacial. The bottom of the bog is composed of very decayed peat of *Sphagnum* and *Eriophorum*. In the Atlantic the *Carex* communities covered central parts of the peat bog. Very significant feature of the development of eastern bogs is the development of *Alnus* and *Betula* carrs from beginning of the Atlantic. The change towards the communities with *Eriophorum* characterized the Younger Atlantic. The Subboreal is marked by *Carex* communities and by the change to eutrophic and mesotrophic conditions. In the Subatlantic the layers with *Eriophorum* appeared again and then than the layer with *Sphagnum*, which formed the final phase of the forested or open raised bogs.

Discussion and conclusions

Formation and plant cover of mires in the Šumava Mts. differs both in relation to the altitude and with regard to their location in the range. The mires of the topmost Šumava Mts. differ strikingly. Presence and composition of plant communities in them shows high biodiversity of the open central parts with occurrence of relic species on bogs where pine krummholz does not cover the entire bog. The mires of lower elevations belong to domed raised bogs and are marked by occurrence of bog forests formed by the central European endemic *Pinus rotundata*. It is recognized that growth of trees depends on the sufficient length of season, and season of the summit areas is too short to enable the growth of trees. The raised bogs in the windward northwestern upslope part of the mountains are noted by open lagg and closed-canopy expanses. In the leeward valleys of the Southeast the lagg of raised bogs is composed of *Betula pubescens* woods, central mire expanse remains open being exposed to large fluctuations of surface temperatures (Soukupová pers. observ.). This pattern of the mire corresponds to the more continental mesoclimate in this part of the mountains.

The development of the mires in the last 13,000 years in the Šumava Mts. was complicated. The mires began to develop in the eastern part where the oldest ones are situated, dated back to the Older Dryas, 13,000 years ago. Then the mires of the

western part began to appear at the end of the Late Glacial, in the period of the Younger Dryas, 11,000 years ago. Finally, the great complex of the mires in the central part of the Šumava Mountains began its development at the beginning of the Holocene, in the Preboreal, 10,000 years ago. The change from the oligotrophic to the eutrophic conditions has been done several times during the Late Glacial and the Holocene on the mires and bogs of the eastern and western part. The central part remained oligotrophic from the beginning of the development to the end. The eastern and western bogs were changed to the waterlogged woods of decaying *Pinus* trees or *Alnus-Betula* carrs. The mires in the central part have never been forested and stayed open during the Holocene. The spruce forests of the Atlantic, and later, from the Subboreal and the Older Subatlantic the immense forests of *Abies* and *Fagus* are remarkable in this part of Europe.

Despite the overwhelming course of climate in Central Europe in the last 15,000 years (Firbas, 1949, 1952; Berglund, 1986), in mountains the development of mires and surrounding landscape differs notably according to diversification of the mesoclimate. According to the composition of vegetation, the mires in the windward upslope suggest to be exposed to higher wetness than the leeward valleys; the formation mires of summits has been influenced a very short growing season and high precipitation. In extrapolations of palaeoecological data in mountains the diversification of biotic development has to be in account.

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