Pollen and plant macrofossil analyses of radiocarbon dated mid-Holocene profiles from two subalpine lakes in the Rila Mountains, Bulgaria

Spassimir Tonkov* and Elena Marinova

(Laboratory of Palynology, Department of Botany, Faculty of Biology, Sofia University St. Kliment Ohridski, 8 Dragan Tsankov bd., Sofia 1164, Bulgaria)

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Abstract: Pollen analysis, plant macrofossil determination and radiocarbon dating were performed on profiles of Holocene age obtained from two subalpine lakes (2320–2340 m a.s.l.) in the Central Rila Mountains, Bulgaria. The palaeovegetational reconstruction dates back to the mid-Atlantic (6500–6700 cal. BP). The plant macrofossil record revealed that groups of *Pinus mugo* and *Juniperus sibirica* were distributed in the subalpine zone. The treeline was shaped by *Pinus sylvestris* and *Pinus peuce* and was higher (up to 2200–2300 m a.s.l.) compared with the present-day. A change to cooler summers and warmer winters after 6700 cal. BP, characterized by a rise in humidity and precipitation, stimulated the formation of a coniferous vegetation belt dominated by *Pinus sylvestris*, *Pinus peuce* and *Abies alba*. The pollen assemblages also indicated a dominance of deciduous trees (*Quercetum mixtum*-*Corylus* phase) at low altitudes until c. 6000 cal. BP. The sub-Boreal was characterized by a wider distribution of *Abies alba* in the lower part of the coniferous belt and a gradual enlargement of the areas occupied by *Fagus sylvatica* and *Picea abies* after 3800–3500 cal. BP. The macrofossil finds of *Picea abies* testify to its expansion after 2800 cal. BP when average temperatures dropped and precipitation increased. Traces of human disturbance in the subalpine area are continuously registered in the pollen and plant macrofossil records since 3770 cal. BP, indicating livestock-grazing, burning of dwarf-pine (*Pinus mugo*) for new pasture land and lowering of the treeline.

Key words: Pollen analysis, plant macrofossils, palaeovegetation, subalpine lakes, Rila Mountains, Bulgaria, mid-Holocene.

Introduction

The development of mountain ecosystems in the temperate regions after the end of the last glaciation is a reflection of dynamic processes related mainly to climate changes, reforestation and human impact. Studies of past environmental change in mountains are extremely important and valuable in this context, owing to the inherent climatic sensitivity of mountain ecosystems (Reasoner *et al.*, 2001). On a continental scale the general picture of this development during the Holocene appears rather diverse for southeastern Europe and the Balkan peninsula in particular, bearing in mind its complex topography, the interaction of several climatic influences, the rich flora and vegetation and, not least, the millennial anthropogenic influence (Lang, 1994; Willis, 1994).

Mountain lakes are amongst the most suitable sites for palaeoecological reconstructions in an attempt to decipher historical records because their sediments often contain a sufficient quantity of well-preserved plant fossils considered as valuable proxies of past environmental changes. For studies tracing the fluctuations in the sensitive ecotone zone between the forest and the subalpine area it seems desirable to combine pollen analysis with plant macrofossil determination in order to obtain more reliable information about the environmental situation at that particular altitude (Lang and Tobolski, 1985).

The key geographical position of Bulgaria in the middle of the Balkan peninsula provides excellent opportunities for understanding the complex mechanisms of vegetation development in postglacial time in this part of southeastern Europe by investigation of high-altitude lakes that are sensitive enough to archive environmental changes. Until recently, the palaeoecological evidence obtained from lake sediments in the Rila Mountains (2925 m), the highest massif on the peninsula, was

*Author for correspondence: (e-mail: tonkov@biofac.uni-sofia.bg)

derived from palynological studies supplemented with radiocarbon dates (Tonkov *et al.*, 1998; Bozilova and Tonkov, 2000). The only exceptions so far, which combine pollen and plant macrofossil analyses, are the investigations of sediments from the peat bog Suho Ezero (1900 m), a former lake in the South Rila Mountains (Bozilova *et al.*, 1990), and from Lake Panichishte (1345 m) in the Northwestern Rila Mountains (Bozilova *et al.*, 2002; Marinova and Tonkov, 2003). The first of these sites spans part of the Lateglacial and the entire Holocene with a detailed radiocarbon chronology for the last 3000 years, while the second site dates back to historical times.

This paper presents the results from the palaeoecological study of the sediments of two subalpine lakes, undertaken as a part of the Mountain Research Initiative (MRI) in collaboration with Past Global Changes (PAGES), aiming to obtain through a multidisciplinary approach new information on the Holocene vegetation dynamics and climate change at high altitudes in the Central Rila Mountains, an area that has not been sufficiently investigated. Moreover, this palaeovegetational reconstruction throws additional light on the dynamic Holocene forest development in the high mountains on the peninsula in evaluating more precisely the role of ecological, climatological and anthropogenic factors.

Study area

Geography, geology, climate and modern vegetation

The Rila Mountains range is situated in Southwestern Bulgaria (lat. $41^{\circ}52'30''$ – $42^{\circ}21'40''$ N, long. $23^{\circ}01'22''$ – $24^{\circ}01'E$), surrounded by the basins of three main rivers that divide it into four parts (Figure 1). The mountain is geologically complex, being composed of Palaeozoic metamorphic rocks (crystalline schist and marble) and intrusive rocks (granite). Plentiful geomorphological evidence is available for the last two glaciations, when the activity of the mountain glaciers led to the formation of typical glacial relief forms with cirques, numerous lakes (approximately 140), moraines and trough river beds. It was suggested that the valley glaciers stretched down to approximately 1300 m (Glovnja, 1968; Velchev, 1995). The exact timing of the start of deglaciation is still unknown but the most recent palynological evidence suggests that the accumulation of sediments in the glacial lakes began earlier than 13 000 yr BP (Bozilova and Tonkov, 2000).

The climate below 1000 m is transitional between continental and submediterranean. Above 1000 m the microclimate becomes montane and the mean temperature drops by 0.5°C with each 100-m increase in altitude. The mean annual precipitation is 800–1000 mm, much of it snow at higher altitudes (Tishkov, 1976).

The present vegetation of the Rila Mountains has six vegetation altitudinal belts (Velchev and Tonkov, 1986; Bondev, 1991). A comprehensive description of the structure and composition of these vegetation belts in the Central Rila Mountains has been presented in earlier publications (Tonkov *et al.*, 1998, 2000).

It is worth noting that above the xerothermic and xeromesophilous oak and hornbeam belts (up to 1000 m) dominated by *Quercus cerris*, *Q. pubescens*, *Q. frainetto*, *Q. dalechampii*, *Carpinus orientalis*, *Carpinus betulus* with an admixture of *Ulmus glabra*, *Acer platanoides* and *Acer pseudoplatanus*, fragments of beech forests (*Fagus sylvatica*) are found. Beech also forms mixed woodstands with *Abies alba* and *Picea abies* at altitudes of 1400–1600 m. The coniferous belt (1600–2000 (2200 m)) is the most compact and well-developed vegetation belt, and is composed mainly of forests of *Pinus sylvestris* and

Figure 1 A. Location of Rila Mountains (solid triangle) on the Balkan peninsula. Scale bar, 100 km. B. Morphographic map of Rila Mountains and the location of sites (solid circles) mentioned in text: 1, peat bog Suho Ezero (Bozilova and Smit, 1979; Bozilova *et al.*, 1990; Bozilova, 1995); 2, Lake Suho Ezero (Tonkov *et al.*, 1998); 3, Lake Sedmo Rilsko (Bozilova and Tonkov, 2000); 4, Lake Panichishte (Bozilova *et al.*, 2002; Marinova and Tonkov, 2003); solid triangle, the study area of Lakes Ostrezki. Scale bar, 10 km. C. Central Rila Mountains showing the group of Lakes Ostrezki (open rectangle). Scale bar, 200 m

Picea abies. The Balkan endemic *Pinus peuce* forms a sub-belt and shapes the treeline in the western and southern parts of the mountain. Within this zone communities of *Abies alba*, *Betula pendula*, *Populus tremula* and *Juniperus sibirica* also occur.

The subalpine belt (2200–2500 m) on northern slopes, particularly in the central and eastern parts, is dominated by thick impenetrable formations of *Pinus mugo* (dwarf-pine) with *J. sibirica*, *Vaccinium myrtillus* and herbaceous communities on

open areas. *Alnus viridis* is mainly restricted to mountain brooks along the steep, rocky slopes. The alpine belt (2500–2925 m) is dominated by the herbaceous communities of *Carex curvula*, *Festuca airoides*, *F. riloensis*, *Dryas octopetala*, *Salix herbaceae*, etc.

Today the vegetation in almost all belts is influenced by anthropogenic activity and, in many places, the treeline has been artificially lowered.

Sites of investigation

The group of Ostrezki Lakes (42°08'N, 23°28'E) on the Central Rila Mountains comprises several lakes with a permanent water surface and half a dozen smaller ones that dry up during summer. The group is located in the subalpine belt above the present treeline on the western slope of a large cirque (Figure 1C). Lake Ostrezko-2 (2320 m) has an elliptic shape with peaty shores and an area of about 1.5 dka (Figure 2). The water depth is 1.5 m. Lake Ostrezko-3 (2340 m) has a circular shape with an area of about 1.0 dka and water depth of 1.7 m. The distance between the lakes is 150 m. Today the lakes are surrounded by groups of *Pinus mugo*, *J. sibirica* and herb vegetation composed of *Nardus stricta*, *Poa alpina*, *Deschampsia caespitosa*, *Carex nigra*, *Carex echinata*, *Campanula alpina*, *Geum coccineum*, *Geum montanum*, *Ranunculus montanus*, *Potentilla ternata*, *Dianthus microlepis*, *Plantago gentianoides*, *Primula deorum*, *Gentiana pyrenaica*, etc.

Materials and methods

Coring and lithology

The material for analyses from Lake Ostrezko-2 was obtained from the northern peaty shore. The core length was 200 cm. The material consists of lake mud overlain in the uppermost 25 cm by undecomposed *Sphagnum* peat. The second coring was done in the southern periphery of Lake Ostrezko-3 at water depth of 70 cm. The core retrieved was 180 cm long. The sediment consists of lake mud. The equipment used was a Dachnowski hand-operated corer.

Pollen analysis

Both cores were sampled at 5–10 cm intervals, and a volume of 2 cm³ for each sample was treated with HF acid with subsequent acetolysis (Faegri and Iversen, 1989). The pollen

sum (PS) used for percentage calculations is based on total terrestrial pollen (AP+NAP). In most instances a PS of 500–600 was achieved. Spores of mosses and pteridophytes, and pollen of aquatics and Cyperaceae were excluded from the PS. Their representation is expressed as percentages of the PS as defined above. Taxa with low frequencies or of less importance are not shown in the pollen diagrams (Figures 3 and 4). The identification of spores and pollen was made using the reference collection of the Laboratory of Palynology and the keys in Beug (1961), Faegri and Iversen (1989) and Moore *et al.* (1991). For calculation and drawing of the pollen diagrams the programs TILIA and TILIA*GRAPH were used (Grimm, 1991). The subdivision of the pollen diagrams into Local Pollen Assemblage Zones (LPAZ) and their subsequent correlation was performed by the application of CONISS (Grimm, 1987). The zones are numbered from the base upward and prefixed by the site designation OSTR.

Plant macrofossil analysis

The samples for plant macrofossil analysis were taken every 10 or 20 cm. After soaking in KOH the material was sieved in two fractions through meshes of 0.4 and 0.16 mm. The plant remains were studied at magnification 10–40×. Sections from wood fragments larger than 0.5 cm, were analysed under light microscope. The identification was performed using the reference collection kept in the Herbarium of Sofia University (SO) and several literature sources (Beijerinck, 1947; Katz *et al.*, 1977; Schoch *et al.*, 1988; Schweingruber, 1990; Tobolski, 2000). Cuticular analysis was also applied in an attempt to distinguish between the needles originating from *Pinus mugo* and *Pinus sylvestris* (Struzkova, 2002). The results are graphically plotted as two diagrams (Figures 5 and 6) using TILIA and TILIA*GRAPH programs (Grimm, 1991). Macrofossils such as fruits and seeds are presented in absolute numbers per 20 ml (Lake Ostrezko-2) and per 40 ml (Lake Ostrezko-3). The abundance of wood fragments and remains of vegetative parts (stems, leaves, etc.) is shown on a relative scale by black dots.

Radiocarbon dating

Five ¹⁴C dates were determined on bulk peat and lake mud samples in the Radiocarbon Laboratory at the University of Bern, Switzerland (Lake Ostrezko-2) and in the Radiocarbon AMS Laboratory at Max-Planck Institute for Biogeochemistry,

Figure 2 A view of Lake Ostrezko-2

Figure 3 Percentage pollen diagram from the core Lake Ostrezko-2

Jena, Germany (Lake Ostrezko-3). The dates have been calibrated to calendar years with the computer program OxCal v3.5 (Bronk Ramsey, 2000). The results are shown in Table 1. The dates in the discussion are given as calibrated radiocarbon years BP (cal. BP) unless otherwise stated.

Results

Radiocarbon chronology

The radiocarbon measurements indicated that the bottom part of the sequence from Lake Ostrezko-3 was older than 5700 BP (6500 cal. BP). A depth–age model constructed by linear interpolation for the sequence from Lake Ostrezko-2 shows an age of *c.* 6000 cal. BP (Figure 7). This model also implies somewhat faster rates of sedimentation for the time intervals 3770–2800 cal. BP and from 1240 cal. BP to the present. Important changes in the pollen stratigraphy of both cores are clearly identified and tied to the corresponding radiocarbon age.

Pollen stratigraphy

The palynostratigraphical correlation of the sequences analysed is feasible because of the presence of reliable markers, i.e., similarities in the behaviour of the main pollen curves, the delimitation of LPAZ by CONISS and the application of the depth–age model constructed by linear interpolation. As a result five LPAZ (OSTR-1 ... OSTR-5) are recognized and their description is summarized in Table 2. The oldest LAPZ OSTR-1 (180–115 cm) is present only in the pollen diagram from Lake Ostrezko-3 (Figure 4).

Plant macrofossils

The analysis was focused on the core from Lake Ostrezko-2 (Figure 5) which is bound to a radiocarbon chronology. Regarding the core from Lake Ostrezko-3 (Figure 6), the main interest was concentrated on the lowermost part (180–115 cm) that corresponds to the oldest LPAZ OSTR-1. The results from the macrofossil determination allow three Local Macrofossil Assemblage Zones (LMAS) to be distinguished and their description is summarized in Table 3.

Discussion

The palaeoecological record derived from pollen and plant macrofossil analyses of the sediments studied extends back to *c.* 6500–6700 cal. BP, i.e., the mid-Atlantic. This is a characteristic benchmark of the Holocene vegetation dynamics in the high central area of the Balkan peninsula (Rila, Pirin and Rhodopes Mountains), when important changes in forest composition and altitudinal vegetation zonation began to take place (Bozilova, 1996). At that time mesophilous deciduous forests, dominated by *Quercus* with abundant *Tilia*, *Ulmus* and *Corylus*, were distributed in the Central Rila Mountains at low altitudes (LPAZ OSTR-1, *Quercetum mixtum-Corylus* phase). The absence of a dense forest canopy above this vegetation belt, where pioneer forests of *Betula* with stands of *Pinus* were spread, has facilitated the air transport of deciduous tree pollen upslope to the subalpine zone. The end of this deciduous forest phase is determined at *c.* 6000 cal. BP (zone boundary OSTR-1/2), this age is in good conformity with previous investigations in the Rila Mountains (Bozilova *et al.*, 1990; Bozilova and Tonkov, 2000). The decline in the percentage of *Betula* pollen marks the end of the vast spread of birch at mid and higher altitudes for nearly 4000 years after the onset of the Holocene (Bozilova, 1996).

Figure 5 Plant macrofossil diagram from the core Lake Ostrezko-2

The reasons for this late establishment and subsequent expansion of *Picea* in the central parts of the Balkans are complicated and still debatable. The palynological investigations cited above suggest that the closest refugial areas for *Picea* were located in the northernmost parts of the Balkan

peninsula – Slovenian Alps, Dinaric Mountains and Carpathian Mountains (Lang, 1994; Farcas *et al.*, 1999; Björkman *et al.*, 2003) from where it slowly migrated to the south and southeast. On the other hand, the hypothesis that local residual populations of spruce could also have existed during the

Figure 6 Plant macrofossil diagram from the core Lake Ostrezko-3

Table 1 Results of radiocarbon measurements

Lab. no.	Depth (cm)	Age (BP)	Calendar age (cal. BP)	Material dated
<i>Lake Ostrezko-2</i>				
B-6101	53–67	1290 ± 40	1270–1175 (1238)	peat
B-6617	95–105	2720 ± 40	2853–2776 (2831)	lake mud
B-6099	146–154	3510 ± 40	3833–3702 (3776)	lake mud
B-6098	175–185	4830 ± 40	5599–5490 (5590)	lake mud
<i>Lake Ostrezko-3</i>				
P-174	150–156	5700 ± 35	6620–6406 (6455)	lake mud

Lateglacial in isolated interior montane areas on the Balkan peninsula where moisture was sufficient, also deserves attention (Ravazzi, 2002; Tonkov, 2003).

In the southernmost mountains of Europe, the expansion of the *Abies–Picea* forest was limited to the mid–late Holocene, owing to increased climatic humidity. However, in forest environments, competition with other trees, notably *Abies*, was the main factor accounting for reduced migration rates of *Picea* (de Beaulieu *et al.*, 1994). In the diagrams from Ostrezki Lakes a stepwise decline of *Abies* pollen begins at c. 3500 cal. BP accompanied by a rise of *Picea* pollen and the appearance of the first macrofossils (needles) of spruce. The main reason for the expansion of *Picea* at the sub-Boreal/sub-Atlantic transition in the northern temperate regions is considered a climate change to lower temperatures and higher precipitation, synchronous with an abrupt increase in radiocarbon in the atmosphere c. 850 cal. BC as a result of increased solar activity (van Geel *et al.*, 1998). This climate change facilitated the enlargement of the coniferous forests in the high Bulgarian mountains and the formation of numerous peat bogs.

The last spread of *Picea* forest in the late Holocene is recorded after 1250 cal. BP when it started to descend, replacing *Abies* at many places in the Rila Mountains in the altitudinal zone 1400–1600 m (Bozilova *et al.*, 2002).

The Holocene distribution pattern of *Fagus* in the Rila Mountains appears similar to that of *Picea*. It is worth noting that the climate change in the mid-Holocene has also had a positive effect on the final establishment of *Fagus* in the Central Rila Mountains c. 5700 ± 35 BP (6450 cal. BP) (Figure 4). The enlargement of areas occupied by *Fagus* at mid altitudes (1000–1400 m) began at c. 3800 cal. BP. Beech has formed pure stands, or mixed stands with either *Abies alba* or *Carpinus betulus*, predominantly on north-facing slopes in the transitional zone between the coniferous and deciduous vegetation belts. When discussing the distribution of *Fagus* it is important to pay attention to the high capabilities of efficient air-transport of its pollen grains upslope, as has been shown by

4.5–8.4% abundance in surface moss samples collected at the modern treeline and in the subalpine belt between 2000 and 2200 m (Tonkov *et al.*, 2000). The present wider distribution of beech forests in the study area at lower altitudes has taken place rather late, around 500–400 cal. BP, coincident with the climate cooling during the ‘Little Ice Age’ (Bradley and Jones, 1992) (LPAZ OSTR–5, Figure 4).

Evidence for human presence in the subalpine zone at this altitude is observed in both pollen and macrofossil diagrams. The continuous pollen curves of taxa such as *Plantago lanceolata*, *Rumex*, *Scleranthus*, *Urtica*, considered as indicators of human disturbance in mountainous areas, alongside cereals (Bozilova and Tonkov, 1990), appear at the beginning of LPAZ OSTR–3 at 3770 cal. BP (Figure 3). This complex of pollen types may also include part of the Poaceae, *Artemisia* and Chenopodiaceae pollen. Numerous wood charcoal fragments are counted just before 3770 cal. BP and c. 2800 cal BP. It is logical to presume that some of the forest fires, especially those after 2800 cal. BP, were initiated by the local population in order to increase the area of high mountain-pasture land by burning dwarf-pine (*Pinus mugo*), a management widely practised until c. 50 years ago (Bozilova and Tonkov, 2000). The various macrofossil finds of heliophilous herbs such as *Potentilla* sp., *Thymus* sp., *Dianthus* sp., *Silene* sp., *Doronicum austriacum*, etc. (zone MacroOstr–2), accompanied by a decrease of the macrofossil records from conifers (*Pinus sylvestris*, *Pinus peuce*), indicate openings in the vegetation and lowering of the treeline.

The poor macrofossil record, comprising only needles of *Pinus mugo*, *Juniperus sibirica* and other occasional finds, in the uppermost sections of both cores for the period after 1240 cal. BP (zone MacroOstr–5) reflects the characteristics of the present-day vegetation that dominates around the lakes in the subalpine belt.

Conclusions

In the context of the intensive ongoing research during the last decade on postglacial sequences in the montane areas of the Balkan peninsula, the following main conclusions could be drawn concerning the palaeovegetation reconstruction in the Central Rila Mountains for the last 6700–6500 years as a result of the multidisciplinary approach combining pollen analysis, plant macrofossil determination and radiocarbon dating.

- (1) The formation of a coniferous vegetation belt dominated by *Pinus sylvestris*, *Pinus peuce* and *Abies alba* began after 6700 cal. BP. The treeline shaped by *Pinus sylvestris* and *Pinus peuce* was higher, up to 2200–2300 m, compared with the present-day. Groups of *Pinus mugo* and *Juniperus sibirica* among patches of herb vegetation were distributed in the subalpine zone.

Figure 7 Age as a function of depth for core Lake Ostrezko-2

Table 2 Description of the LPAZ

LPAZ Ostrezko 2/3 Depth (cm)	Age range (cal. yr BP)	Main features of the LPAZ
OSTR-1 180–115	~ 6500–6000	Dominance of <i>Pinus diploxylon</i> 40–45%, presence of <i>Abies</i> 10%, <i>Pinus peuce</i> 4% and deciduous tree pollen (<i>Corylus</i> 10–25%, <i>Tilia</i> , <i>Ulmus</i> , <i>Carpinus</i>); appearance of the <i>Fagus</i> curve; NAP represented by Poaceae 5–10%, <i>Artemisia</i> , <i>Centaurea</i> , <i>Dianthus</i> , etc.
OSTR-2 200–145/115–75	6000–3770	Increase in <i>Abies</i> up to 30% and <i>Pinus diploxylon</i> 40–60%; decline in deciduous tree pollen (particularly <i>Corylus</i>); appearance of the <i>Picea</i> curve
OSTR-3 145–105/75–55	3770–2800	Short maximum for <i>Pinus peuce</i> (6–10%); decline in <i>Abies</i> , synchronous increase in <i>Picea</i> ; great variety of NAP and appearance of anthropogenic indicators (<i>Rumex</i> , <i>Plantago lanceolata</i> , <i>Urtica</i>)
OSTR-4 105–53/55–25	2800–1240	Maximum for <i>Picea</i> (6–10%), high values for <i>Pinus diploxylon</i> 50–60%, strong decline in <i>Abies</i> (5–8%); great variety of NAP including taxa of local origin (<i>Sphagnum</i> , <i>Selaginella</i> , Cyperaceae)
OSTR-5 53–0/25–0	1240–0	Rise in <i>Fagus</i> (10%) and partly for <i>Picea</i> ; appearance of <i>Castanea</i> , <i>Juglans</i> ; increase in the anthropogenic indicators (<i>Artemisia</i> , Cichoriaceae, <i>Plantago lanceolata</i> , <i>Rumex</i> , <i>Secale</i> , <i>Hordeum</i>)

Table 3 Description of the LMAZ

LMAZ Ostrezko 2/3 Depth (cm)	Main features of the LMAZ
OstrMacro-1 200–145/180–115	Needles, seeds and female cones of <i>Pinus mugo</i> , <i>Pinus peuce</i> ; needles of <i>Pinus sylvestris</i> ; wood of <i>Pinus</i> sp.; fruits of <i>Alnus viridis</i> ; seeds, fruits of herbs (<i>Dianthus</i> , <i>Silene</i> , <i>Thymus</i> , etc.); charcoal particles
OstrMacro-2 145–60/115–25	Abundance of needles of <i>Pinus mugo</i> , <i>Pinus sylvestris</i> , <i>Juniperus sibirica</i> ; first records of <i>Picea abies</i> and <i>Abies alba</i> (needles); seeds of herbs (<i>Cardamine</i> , <i>Cirsium</i> , <i>Doronicum</i> , etc.); moss remains
OstrMacro-3 60–0/25–0	Poor macrofossil content: sporadic finds of needles of <i>Pinus mugo</i> , <i>Pinus sylvestris</i> , <i>Juniperus sibirica</i> ; vegetative parts of mosses (<i>Sphagnum</i> , <i>Drepanocladus</i>)

- (2) The mid-Holocene pollen assemblages at low altitudes were dominated by deciduous trees (*Quercetum mixtum-Corylus* phase) that lasted until c. 6000 cal. BP.
- (3) The wide distribution of *Abies alba* in the lower part of the coniferous belt was confined to the time window 6000–2800 cal. BP, i.e., during the sub-Boreal, with a maximum at c. 3800 cal. BP.
- (4) The establishment of *Fagus sylvatica* and *Picea abies* took place at c. 6500 and 4500 cal. BP, respectively. Both tree species began gradually to enlarge their areas after 3800–3500 cal. BP. The final expansion of the beech forests at low altitudes took place c. 500–400 cal. BP, coincident with the climate cooling during the ‘Little Ice Age’.
- (5) Traces of human impact are continuously registered in the pollen and plant macrofossil records since 3770 cal. BP. In historical times the changes in the vegetation cover at higher altitudes, and the lowering of the treeline, were primarily caused by increasing anthropogenic activities, indicating livestock-grazing and burning of dwarf-pine (*Pinus mugo*).

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