

# Holocene timberline fluctuations in the mid-mountains of Central Europe

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Central European Hercynian mountain ranges – Krkonoše Mts., Hrubý Jeseník Mts. and Vosges, Schwarzwald, Harz – represent the only islands of alpine forest-free area between the Alps and Western Carpathians in the south and the Scandes in the north. Based on data from previously published pollen profiles and on newly taken cores, comparison of the development of the alpine timberline position is presented. The Labský důl profile in the Krkonoše Mts. spans the whole Holocene, the Keprník profile in the Hrubý Jeseník Mts. brings information from ca 2500 BP to the present. The exceptional position of the Krkonoše Mts. in terms of permanent presence of alpine forest-free area throughout the Holocene was confirmed. In other mountain ranges, the alpine forest-free areas probably vanished or were restricted only to the exposed peaks during the periods of positive temperature anomalies in the Middle Holocene. Later in the period 4000–500 BP, forest free areas reappeared, although the relative contribution of climatic and anthropogenic causes to their formation remains unclear. Taking into account the supposed extent of temperature oscillations in the Middle and Late Holocene and the existing pollen records the authors assume that the alpine timberline in the Hercynian mid-mountains of Central Europe varied only slightly.

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## Introduction

The term alpine timberline refers to the ecotone between forest and alpine belt (Körner 1999) or subalpine shrub formations. The factor determining the absence of forest is the temperature decline related to the increasing altitude (Körner 1999). The alpine timberline ecotone presents a transition zone of varying width and structure (Armand 1992), inferring differences in ecotone response to changing temperature conditions. In general, the response of the alpine timberline to changing temperature conditions is somewhat delayed (Slatyer & Noble 1992; Paulsen et al. 2000). Its position is determined by long-term climatic trends rather than by immediate temperature conditions (Paulsen

et al. 2000). In contrast, local or regional advances of treeline or tree-species line (for more detail, see Körner 1999) as response to the short or mid-term temperature increase can be very rapid (e.g. Bugmann & Pfister 2000; Kullman 2007). Moreover, responses to climatic changes are sometimes opposite, such as advance of timberline due to higher temperature and decline due to higher precipitation or drought (Wilmking et al. 2004).

Certain variations of the alpine timberline position due to climatic oscillations during the Holocene can be detected. In Central Europe, timberline fluctuation is estimated at up to 200 m (Tinner & Theurillat 2003). For the High Sudetes (Krkonoše and Hrubý Jeseník Mts.) and Western Carpathians, oscillations up to 400 m are reported (Firbas 1952;

Ložek 2001) although this phenomenon still remains open.

This study aims at summarising the development of the timberline position in the Hercynian mountains of Central Europe based on detailed interpretation of previously published data and on newly constructed pollen diagrams from Krkonoše and Hrubý Jeseník profiles.

## Methods

### Study area

Hercynian mountain ranges of Central Europe with their primary forest-free areas represent the only alpine islands between the Scandes, the Alps and Western Carpathians (Jeník 1998). They include Vosges, Harz, Krkonoše Mts. (~ Giant mountains/Karkonosze/Riesengebirge) and Hrubý Jeseník Mts. (Fig. 1). Large forest-free area has developed also in the Schwarzwald Mts. but it is probably of secondary origin (Friedmann 2000). The same holds true for the forest-free area on the summit of Šumava (Bayerischer Wald) mountain range. All these mountains are characteristic by relatively high rainfall, from 2200 mm in the highest parts of

the Vosges Mts. to 1500 mm in the Hrubý Jeseník Mts. The average July temperatures range from 8.7 °C in the highest parts of the Krkonoše Mts. (Sněžka 1602 m a.s.l.) to 11.5 °C in the Vosges Mts. (Hohneck, 1363 m a.s.l.). Apart from the Vosges, where European beech (*Fagus sylvatica* L.) is present, the timberline is formed by Norway spruce (*Picea abies* [L.] Karst.). The extent of forest-free area has increased in the past by deforestation in all the mentioned mountain ranges (Jeník & Lokvenc 1962; Jeník & Hampel 1991; Friedmann 2000; Schwartz et al. 2005).

### Pollen analysis and sedimentology

This study presents two new pollen profiles that bring information about history of the alpine belt in the Krkonoše and Hrubý Jeseník Mts. Pollen cores were collected in the Labský důl valley (Krkonoše Mts.) and Keprník Mt. (Hrubý Jeseník Mts.). The locality Labský důl is situated in a lake of glacial origin filled with deposits (Engel et al. 2005). This profile provided the longest pollen record ever analyzed in Krkonoše: from late glacial period to the present. The locality lies close to the timberline which is lowered here by avalanches. The 1283 cm long core (cirque bottom,

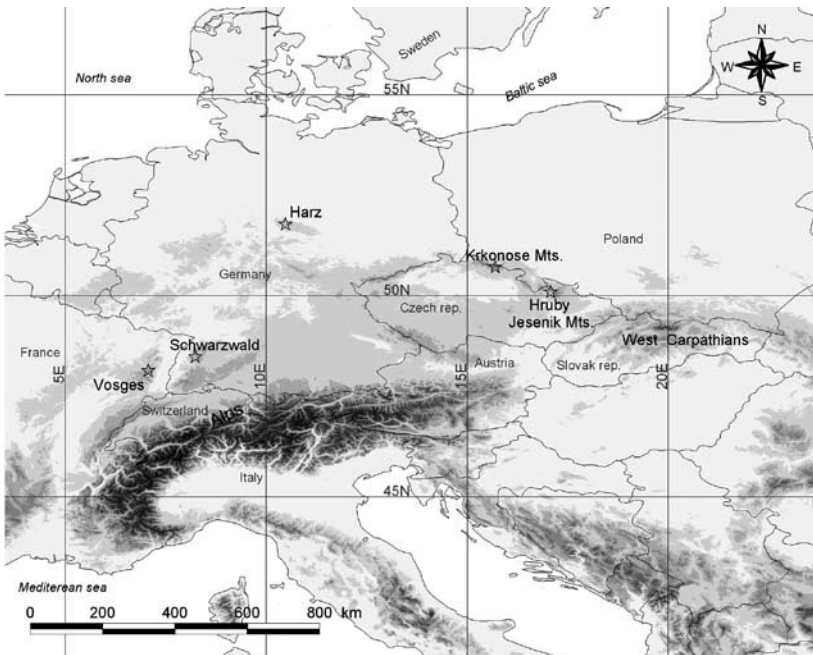


Fig. 1. Locations of the investigated Central European Hercynian mid-mountains.

50°45'N, 15°33'E, 990 m a.s.l.) was collected with Russian peat sampler. Except for the peat layer up in the profile, the core contained mainly of inorganic matter. The section between 810 and 830 cm contaminated during sampling and was discarded from analyses.

The profile from Mount Keprník (50°10'N, 17°07'E, 1429 m a.s.l.) was taken from a pit dug in an earth hummock. The organic sediment had a peaty character with sedge remains. The locality is situated on a plateau in the northern part of the mountain range at a distance of 200 m (60 m of altitude) above the timberline.

The samples for pollen analysis were processed with standard acetolysis method (Moore et al. 1991), and pollen grains were identified according to the handbook by Beug (2004). Pollen diagrams including stratigraphic zones were created using TILIA (Grimm 1992) software. The sediment from Labský důl was analysed for organic matter content (determined by loss-on-ignition, LOI) and particle size distribution (determined by wet sieving). Based on these two indicators, the lithostratigraphic units (segments with similar characteristics e.g., particle size distribution, organic matter proportion, colour) of the profile were determined. Radiocarbon dating ( $^{14}\text{C}$ ) was carried out by laboratories in Erlangen, Poznan (for accelerator mass spectrometry, AMS) and at the Faculty of Science of the Charles University in Prague (for conventional  $^{14}\text{C}$ ) (Table 1). Absolute data are expressed, if not indicated otherwise, as uncalibrated radiocarbon years BP. Linear age-depth model ( $R^2 = 0.98$ ) from uncalibrated radiocarbon data was, in the case of Labský důl, created for the depth ranging from 205

to 963 cm. Chronostratigraphic zones are used according to Lang (1994).

### Interpretation of the alpine timberline altitudinal shifts

When interpreting the pollen diagrams in relation to the timberline position, main emphasis was put on the proportion between woody species and herbs (AP/NAP). This proportion allows approximate determination between the dominance of forests and forest-free areas in the vicinity of the profile. Macroscopic remains of plant species (macrosubfossils), however, would provide better information about the timberline position (Tinner & Theurillat 2003). Unfortunately, macroremains of plant species were not mentioned in the majority of previously published studies, so we had to concentrate on the AP/NAP percentage when interpreting the timberline fluctuation.

Concerning the AP/NAP rate, critical arboreal proportion was considered to be 70–80%, representing the approximate value of woody species proportion in the central European profiles situated at or just below timberline (e.g., Gouillé Rion, Gouillé Loéré, Grande Tsa [Tinner et al. 1996; Tinner & Theurillat 2003; Wright et al. 2003], and the northern side of Vysoké Tatry Mts. [Obidowicz 1993]). For variations of AP/NAP, it was always taken into account whether the change of the value was due not only to the change of dominant species with different (higher or lower) pollen production. In a case where timberline was constituted by spruce at the time, a propor-

Table 1. Radiocarbon data from Labský důl and Keprník sites.

Site	Depth (cm)	Lab. No.	Dated material	$^{14}\text{C}$ Age (uncal. BP)	Laboratory
Labský důl	205	ERL 6295	peat	4080 ± 49	Phys. Inst. der Uni. Erlangen
Labský důl	230–250	CU 1916	peat	4380 ± 148	Radiocarbon Laboratory KHIG PříUK
Labský důl	354	ERL 6318	peat	5024 ± 53	Phys. Inst. der Uni. Erlangen
Labský důl	438	ERL 6319	wood fragment	5272 ± 57	Phys. Inst. der Uni. Erlangen
Labský důl	547	Poz-13708	wood fragment	5780 ± 60	Poznań Radiocarbon Laboratory
Labský důl	797	ERL 7380	plant macroremnant	8216 ± 94	Phys. Inst. der Uni. Erlangen
Labský důl	963	ERL 6184	plant macroremnant	9572 ± 54	Phys. Inst. der Uni. Erlangen
Keprník	50–51	Poz-13744	peat	2090 ± 35	Poznań Radiocarbon Laboratory

tion of  $\geq 50\%$  spruce pollen was also considered indicative of closed stands at the locality (Obidowicz 1993).

## Results

### Krkonoše Mts.

The profile from Labský důl allows reconstruction of the early Holocene timberline. The simplified pollen diagram (Fig. 2) shows data from Late Glacial period to ca 8000 BP corresponding to the profile depth from 1283 cm to 790 cm. According to the pollen analyses from lower parts of the profile, the markedly different pollen composition between 810 and 830 cm (Jankovská 2004) is due to contamination from the upper parts of the core (ca. 500–650 cm). Pollen curves of *Salix*, *Juniperus*, *Betula nana* type, *Ephedra distachya* and *E. fragilis* type and also the presence of *Pinus haploxylon* type (i.e. *Pinus cembra*) clearly delimit the forest-free stage in the profile. Higher pollen curve of *Pinus sylvestris* type is produced by pollen from local *Pinus mugo* stands or by influx of *P. sylvestris* from lower altitudes, or by combination of both factors. In this period (i.e. before ca 9500 BP), alpine timberline was probably situated clearly below the investigated site. The first significant oscillation of AP/NAP curve is recorded at around 1200 cm (LD1). Before this period (early stage after deglaciation), closed pine forests have probably not occurred in the vicinity of the lake and thus, regional (climatic) rather than local driving factors are suggested.

At around 9600 BP (LD2), a markedly lower proportion of arboreal pollen was recorded. It is not clear whether the decrease of AP curve was caused by local disturbance or by climatic influence.

During the following period, the AP curve approaches 80% and passes it constantly at 8200 BP. At the same time, the proportion of organic matter in the lake sediment rises from 7–9% to 20–25%. Apparently, the timberline composing of pioneer woody species *Pinus* and *Betula* passed the level of Labský důl profile as late as around 9200–8800 BP.

Another decrease of AP pollen takes place at 8200 BP (LD3), set off by resedimentation below this part of the profile. Other parameters also, such as increase of *Betula nana* type and *Juniperus*, and lower organic content in the sediment, probably

indicate the increase of forest-free area either due to local disturbance or climate.

The AP/NAP oscillation mentioned above represents only minor wiggles in AP/NAP curve in the range from 85 to 95% arboreal pollen. These slight shifts in the AP/NAP curve probably reflect local vegetation changes and/or avalanche events. Hence, more elevated localities can give more evidence about the alpine timberline position during the most part of Middle and Late Holocene.

Norway spruce has been sporadically present at the Labský důl site (based on stomata) since 7500 BP, more abundantly from 6800 BP, and as a major timberline forming species since the Atlantic period (Jankovská 2004).

### Hrubý Jeseník Mts.

The investigated pollen profile taken from an earth hummock at the summit of the Keprník Mt. covers a time span since ca 2500 BP and hence, it records a period similar to other pollen profiles analysed in the Hrubý Jeseník Mts. (Rybniček & Rybničková 2004).

At the summit of Mount Keprník, the AP proportion in the mentioned time period was between 70 and 80% (zone K1, K2, Fig. 3). At the same time, no woody species stomata were found in the investigated profile. The profile shows a regression of woody species typical for mixed oak forests and progression of beech and fir in the K2 zone. Direct indicators of human activities are present in the uppermost layers (K3). In the whole profile, there are only minor shifts in AP/NAP curve. With respect to the absence of spruce stomata remnants and AP < 80% (in exposed windy position with potentially high pollen influx from lower areas), it can be concluded that closed forest has not been present in the summit area of the Keprník Mt. during the last 2500 years. Other evidence includes occurrence of earth hummocks since at least 2090 BP. These landforms are usually quickly destroyed after colonisation by trees (Treml & Křížek 2006).

## Discussion

### Evolution of the alpine timberline in the Krkonoše Mts. and the Hrubý Jeseník Mts.

In the Krkonoše Mts., the alpine timberline position during the Younger Dryas can be estimated at 500–600 m according to the equilibrium line alti-

Labský důl, Krkonoše Mts., Czech republic  
 50°46' N, 15°33' E, 990 m asl.  
 Simplified pollen diagram

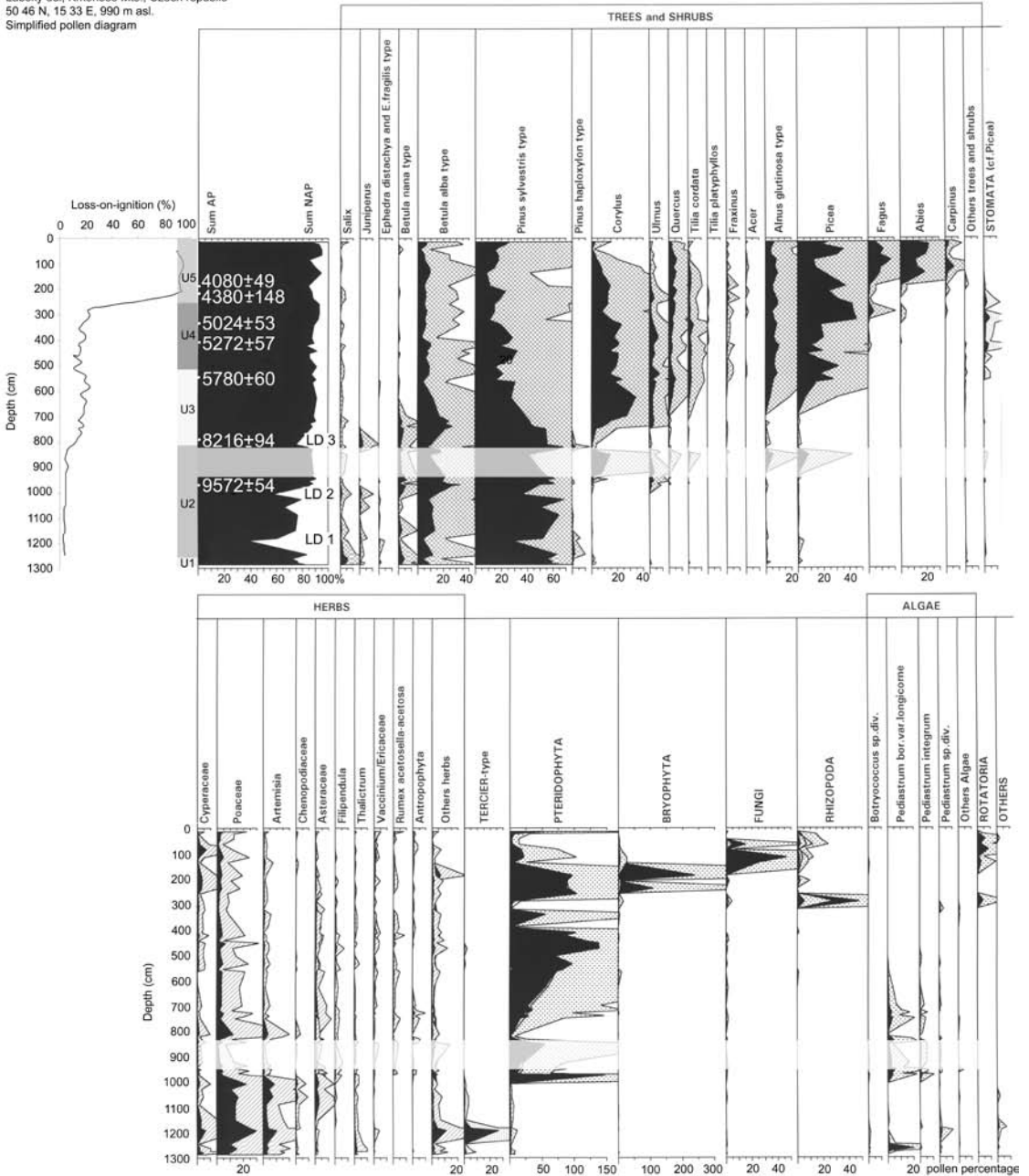


Fig. 2. Simplified pollen diagram, radiocarbon data, loss-on-ignition and litostratigraphic units (U1–U5) in the “Labský důl” core. Light rectangle across pollen diagram indices contaminated part of the profile (810–830 cm depth).

tude at approximately 1200 m a.s.l. It follows that the timberline reached the upper locations with a time lag which corresponds to the relatively late deglaciation (Bourlés et al. 2004). Three distinct

oscillations of AP/NAP curve were detected before the timberline finally passed the Labský důl cirque bottom. It is suggested that the first one (LD1) represents a climatically driven timberline descent

Keprník (Hrubý Jeseník Mts.)  
50°10'N, 17°07'E, 1429 m asl  
Czech Republic  
Simplified pollen diagram

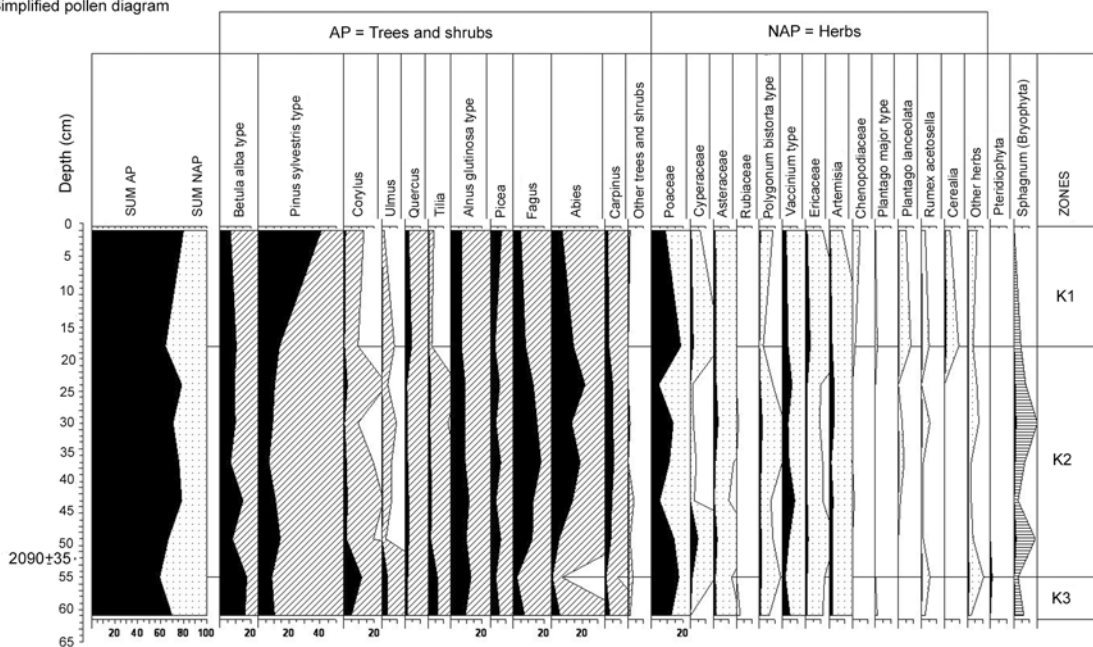


Fig. 3. Simplified pollen diagram, summit of Mt. Keprník (1429 m a.s.l.).

rather than a result of local disturbances. The second significant oscillation of AP/NAP curve (LD2) also reflects regional rather than local cause. Before this period, timberline had still remained below the Labský důl site and therefore, local disturbance in closed pine-birch forest would not be significantly manifested in the AP/NAP curve. The third oscillation (LD3) could be correlated with the central European oscillation CE 2 (Haas et al. 1998), which was recorded also in the High Tatra Mts. (Kotarba & Baumgart-Kotarba 1999).

The Labský důl profile gives insight to timberline position from deglaciation until ca 8000 BP, whereas other pollen profiles from the summit areas of the Krkonoše Mts. (Fig. 4) cover a time period since  $7600 \pm 130$  BP, which is the time span of the Pančava peat bog profile (Huettemann & Bortenschlager 1987). This peat bog is located on an exposed highly elevated planated surface and thus, it is supposed a prominent part of its pollen is brought by wind from windward valleys (Jeník 1998). High proportion of herb and dwarf shrub pollen was detected (25–30% Gramineae, 10% *Calluna*) at the bottom of this profile (Huettemann

& Bortenschlager 1987). This suggests that at the given time (~ 7600 BP), either the timberline had not yet reached the Pančava peat bog (1300 m a.s.l.) or that it had already been lowered below this level. In the following period (after 7400 BP according to Huettemann & Bortenschlager 1987), the alpine timberline reached at least the level of the Pančava peat bog and since varied apparently only a little. Nevertheless, according to Speranza et al. (2000) there was a colder period between  $2640 \pm 60$  and  $2480 \pm 35$  BP, but there is no evidence of a timberline shift due to this temperature oscillation.

In the following period, no marked trend in forestation or deforestation was detected in the highest parts of the Krkonoše Mts. At less elevated Pančava peat bog, AP reaches 90% of the pollen spectrum (Jankovská 2001), and at Úpa peat bog (1430 m a.s.l.) it reaches approximately 80% (Svobodová 2004). Considerable proportion (20–30%) of the pollen spectrum belongs to pine, mainly from local *Pinus mugo* stands.

At the Pančava peat bog, *Picea* pollen represents about 10–20% during 4000–800 BP (Jankovská

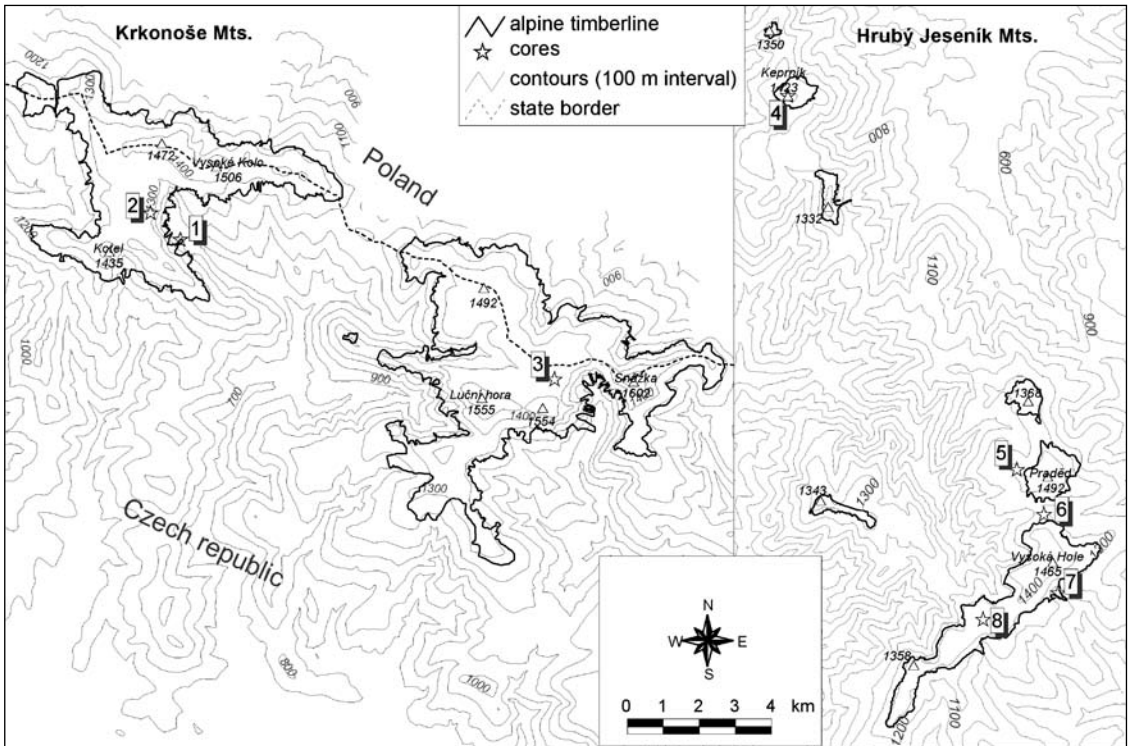


Fig. 4. Positions of described pollen profiles within the Krkonoše and Hrubý Jeseník Mts. (1) Labský důl; (2) Pančava peat bog (Huetteman & Bortenschlager 1987; Speranza et al. 2000; Jankovská 2001); (3) Úpa peat bog (Svobodová 2004); (4) Keprník; (5) Velký Děd; (6) Barborka; (7) Velká kotlina; (8) Velký Máj (5–8; Rybniček & Rybničková 2004).

2001, 2004), while at Úpa peat bog it reaches only 5–15% (Svobodová 2004). This is probably a consequence of longer distance between the Úpa peat bog and the timberline during this period. Moreover, both Pančava and Úpa pollen profiles show significantly smaller number of *Picea* pollen, as compared with sites recently surrounded by spruce forest (Labský Důl, Barborka). This indicates that at least Úpa peat bog was situated above the alpine timberline during 4000–800 BP. Human-induced changes in vegetation are present in the above mentioned pollen profiles since the Medieval Period (Jankovská 2004).

Based on existing data, it is not possible to determine the exact level that the closed forest reached during the climatic optimum of the Holocene (i.e. Atlantic chronozone, Lang 1994). Most likely, a closed tall-trunk stand cannot be expected at locations where well developed sorted patterned ground is present (above ca. 1430–1450 m a.s.l.). Should these landforms become overgrown by trees, they usually lose their raised cen-

tre morphology, which is not the case of the above mentioned patterned ground (Sekyra et al. 2002). The maximum elevation of closed forest could, therefore, have been only about 100 m higher than today.

Profiles from the Hrubý Jeseník Mts. (Fig. 4) contain pollen record from 4620 BP onwards. High proportion of hazel pollen indicates hazel stands at the summit locations (about 1300 m a.s.l.) during the period 4620–3500 BP (Rybniček & Rybničková 2004), although direct evidence in the form of macroscopic remains is missing.

Some presently forest-free localities show relatively low proportions of arboreal pollen also during the period 1945–800 BP: approximately 60% at Velká Máj (peat bog on the summit plateau) and at Velká kotlina (peat bog on the cirque bottom), where the oscillations of AP/NAP curve were more pronounced (Rybniček & Rybničková 2004). This indicates permanently forest-free areas during this period, although significant local changes in timberline position probably took place in the area of

the Velká kotlina cirque. Compared to both the above mentioned sites, the proportion of arboreal pollen was higher at Mt. Keprník (70–80%). However, the presence of earth hummocks at the summit of Keprník since at least ca. 2100 BP is considered a proof of absence of forest, as such landforms could not persist the physical action by tree roots in a closed forest (Treml & Křížek 2006). Similar earth hummocks of the same age occur also on the summit of Praděd Mt. at 1492 m a.s.l. (Treml et al. 2006).

At presently forested localities such as Barborka and Velký Děd (Rybníček & Rybníčková 2004), the AP proportion between 3700 and 800 BP fluctuates at around 85%. The noticeable decrease of woody species pollen, namely beech and fir, observed in most profiles at around 500 BP (zone K3 in the case of Keprník), can be ascribed to human influence. However, a synergic action of the last Little Ice Age could be involved aside human influence in the uppermost locations of the Hrubý Jeseník Mts. during the last 800–500 years (Hošek 1972).

Based on the evidence from all mentioned pollen profiles, it can be concluded that in the Hrubý Jeseník Mts. the alpine timberline did not advance to the most exposed summits (e.g. Keprník Mt., Velký Máj Mt.) during the period ca 2000–800 (500) BP and that forest free areas also persisted on steep slopes of the Velká kotlina cirque. The rest of the presently forest-free areas, however, were forested and remained so until as late as 800–500 BP.

### **Alpine timberlines in the neighbouring mid-mountains: Vosges, Schwarzwald and Harz**

The extent of alpine forest-free area in the neighbouring Hercynian mid-mountains is quite limited (Tables 2 and 3). In the Vosges Mts., forest-free areas of natural origin are found only in the highest exposed parts of the summit plateaus (Carbiener 1963). Large part of the area previously called “chaumes primaries” originates from deforestation during the Iron Age (Schwartz et al. 2005). During Younger Dryas, timberline altitude is estimated at 500 m (Schloss 1979), ascending rapidly to at least 1100 m in the early Holocene with the advance of pine and birch (Schloss 1979; Edelman 1985). At the beginning of the Boreal period (ca. 9000 BP), timberline reached an altitude of ca. 1200 m a.s.l. (Lemée 1963). In the Vosges Mts., the early Holocene timberline development may have been af-

ected by mesoclimatic phenomena of some valleys with glaciation relicts (Mercier et al. 1999). According to Schwartz et al. (2005), *Tilia* occurred at an altitude of 1060 m at around 8000 cal. BP (ca 7200 BP), whereas at present its occurrence does not exceed 900 m. This fact suggests warmer climate than at present. During the climatic optimum (8000–4500 BP), even the highest parts were forested. After ca. 4500 BP, beech stands in the highest parts thinned down and the timberline reappeared (De Valk 1981). At the most exposed locations, it existed until the beginning of summer farming activities (grazing, hay making, forest clearance), which resulted in timberline lowering and formation of the majority of the present-day forest-free areas at around 1400–1200 BP (Schwartz et al. 2005).

In Schwarzwald, the altitude of the timberline in the Younger Dryas is estimated at 750 m (Lang 2006). During the early Holocene it advanced rapidly to the level of the highest peaks where closed stands of pine and birch were formed. Present forest-free area is probably secondary and originates from the period of expansion of the summer farming to the highest parts at around 1000 AD (Bogenrieder 1982; Friedmann 2000).

In the Harz Mts., the summit of Brocken Mt. (1141 m a.s.l.) was forested during the climatic optimum of the Holocene (Firbas 1952; Beug et al. 1999). Altogether four treeless periods are documented in the Brocken summit area (Beug et al. 1999): 1) from Younger Dryas to 9700 BP, 2) from ca 5700 to 5300 BP, 3) from 2900 to 2800 BP and 4) after 500 BP. The latest forest-free period is documented from the 16th century, i.e. before the intensified human influence (Tackenberg et al. 1997). However, the evidence for a natural origin of the forest-free area at the Brocken summit is mainly floristic (Haeupler 1970) and historical (Tackenberg et al. 1997). Although direct evidence (archaeological findings, soil charcoal, etc.) of early anthropogenic impact is missing, human contribution to the formation of the forest-free area at Brocken summit can not be excluded (Beug et al. 1999).

### **Extent of the alpine belt during the Holocene**

Based on the present vertical extent of the alpine belt in various Hercynian mountains of Central Europe (Table 3) it can be assumed that the most “endangered” alpine forest-free areas during the Holocene were situated in the Harz and Vosges



Table 2. List of sources and sites which were used for reconstruction of alpine timberline position.

Mountain range	Site/Source	Age start of record	Proxy used for treeline reconstruction	Author of study
Vosges	Gazon de Faing, 1230, 1290 m	only relative biostratigraphic dating – since Boreal	pollen	Lemée 1963
Vosges	Altenweiher 926 a.s.l., Moselotte 1290	ca 8000 BP resp. 2500 BP	pollen	De Valk 1981
Vosges	Sewensee 500 m	late glacial	pollen	Schloss 1979
Vosges	Rosberg 1190 m	7600 BP – the oldest charcoal	charcoals – soil profiles	Schwartz et al. 2005
Vosges	Goutte Loiselot 850 m	late glacial	pollen	Edelman 1985
Vosges	several sites on Hautes Chaumes (above 1200 m)		soil profiles	Carbiener 1963
Schwarzwald	9 sites (654–1280 m)	late glacial	pollen	Lang 2006
Harz	Brocken summit area		historic data	Tackenberg et al. 1997
Harz	Brocken summit area		floristic data	Haeupler 1970
Harz	several sites in Brocken area (highest 1100 m)	late glacial	pollen	Beug et al. 1999
Krkonoše	Labský důl 990 m	late glacial, first <sup>14</sup> C date 9200 BP	pollen, stomata	this study
Krkonoše	Pančavské rašeliniště 1325 m	7600 BP	pollen	Huettemann & Bortenschlager 1987
Krkonoše	Pančavské rašeliniště 1320 m	3100 BP	pollen, pollen concentration	Speranza et al. 2000
Krkonoše	Pančavské rašeliniště 1325 m	3995 BP	pollen	Jankovská 2001
Krkonoše	Úpské rašeliniště 1420 m	3440 BP	pollen	Svobodová 2004
Krkonoše	summit plateaus (above 1430–50 m)	persisted from late glacial	soils	this study
Hrubý Jeseník	Velký Máj 1350 m	1945 BP	pollen	Rybníček & Rybníčková 2004
Hrubý Jeseník	Velká Kotlina 1400 m	ca 1700 BP	pollen	Rybníček & Rybníčková 2004
Hrubý Jeseník	Barborka 1315 m	ca 3700 BP	pollen	Rybníček & Rybníčková 2004
Hrubý Jeseník	Velký Děd 1395 m	4600 BP	pollen	Rybníček & Rybníčková 2004
Hrubý Jeseník	Keprník 1423 m	2090 BP	pollen	this study
Hrubý Jeseník	Keprník 1415–1423 m, Praděd 1450–1490 m	2100 BP	earth hummocks – soils	this study, Treml et al. (2006)

Table 3. Recent vertical extent of the alpine belt in Hercynian mid-mountains of Central Europe – difference between elevation of the highest peak and the uppermost outposts of the timberline. Values in brackets correspond to the average height of natural nondepressed alpine timberline (Treml &amp; Banaš 2000).

	Maximal elevation of the alpine timberline (m a.s.l.)	T** (°C)	Vertical extent of the alpine belt (m)	Corresponding gradient of summer temperature (°C)
Vosges	1360	8.0	60	0.3–0.4
Harz	1125*	7.8	20	0.1–0.2
Krkonoše	1370	7.1	210 (300)	1.2–1.3 (1.8)
Hrubý Jeseník	1430	7.2	60 (140)	0.3–0.4 (0.8)

\* ... sensu Tackenberg et al. (1997)

\*\* ... average temperature April–September (growing season, 1981–1990) at the maximal elevation of the alpine timberline, calculated from data published by Migala (2005), with temperature lapse 0.6°C/100 m.

Mts. During the latter half of the Holocene, when the woody species constituting the timberline today were already present in the Harz and Vosges Mts., there were probably no naturally treeless areas during periods 0.5–1°C warmer than today. The existence of such positive temperature anomalies is likely, considering the recent Holocene temperature estimates from Central Europe (Haas et al. 1998; Hierl et al. 2003).

This hypothesis is supported also by the pollen analyses. They show that during the Holocene, the alpine timberlines in Hercynian mountain ranges of the Central Europe developed in different ways. In the Krkonoše Mts. large forest-free areas were present throughout the Holocene, whereas in the Harz and Vosges Mts., even the uppermost locations (except for steep slopes, rocks, block fields or exposed peaks) were forested during the climatic optimum (De Valk 1981; Beug et al. 1999). The alpine forest-free areas in the Vosges reappeared after 5000 BP (De Valk 1981). In the Hrubý Jeseník Mts., according to recent temperatures and Holocene temperature estimates (e.g., Hierl et al. 2003), the alpine forest-free area probably had a very limited extent during the warmer periods of the Holocene. It expanded most likely before 2000–2500 BP, which is the age of the part of the pollen profile documenting forest-free areas at summit localities (Velký Máj, Velká Kotlina – Rybníček & Rybníčková 2004, Kepník). Presence of treeless areas at the summits of the Hrubý Jeseník is also proved by an earth hummock rise around 2100 BP. In the Schwarzwald Mts. the actual relatively large forest-free area is of anthropogenic origin (Friedmann 2000).

The history of alpine areas can be related to present-day biodiversity. For example, the butterfly communities of the Krkonoše Mts. differ greatly from those present in the Harz, Hrubý Jeseník and Králický Sněžník Mts. They are more similar to those of the West Carpathian mountain ranges (Mařák & Kuras 2006). This fact could confirm the notable distinctions of the forest-free area development in the Krkonoše Mts. as compared to other mentioned Hercynian mountain ranges. The presence of many plant species and diversified communities dependent strictly on forest-free areas in all those mountain ranges (Jeník 1998) indicates that long lasting forest-free enclaves have been in existence. Nevertheless, the presence of these forest-free patches depend on soil conditions, water regime or slope inclination rather than on temperature.

## Rate of timberline fluctuation

The maximum amplitude of timberline oscillations in Central European mid-mountains is governed by their low altitude and a very limited space between their summits and the timberline. In the Krkonoše Mts., the presence of a closed forest cannot be expected at sites with well developed sorted forms of patterned ground at altitudes above 1450 m a.s.l. Sorted forms of patterned ground formed here at the end of the last glacial stage (Traczyk & Migoň 2003). The maximum difference in the timberline position compared to the present is, therefore, less than 100 m. In other Central European Hercynian mountain ranges, the timberline ascended to its highest locations. Minimum difference in the timberline position ranged therefore from 25 m (Harz Mts.) to 40–150 m (Hrubý Jeseník Mts.). However, it is possible that during some of the cold oscillations recorded in the Central Europe (for example CE 8, Haas et al. 1998) the timberline was situated lower than today and the total fluctuation would therefore be several tens of meters. As for the Vysoké Tatry Mts., Obidowicz (1993) argues that during the climatic optimum, the alpine timberline was only 50 to 100 m higher than today. The above mentioned smaller timberline oscillations correspond to temperature reconstructions (Haas et al. 1998; Hierl et al. 2003) that estimate the extent of summer temperature fluctuations in mid and late Holocene to 1 °C. Nevertheless, the changes in timberline position in this period may not have been as vigorous as earlier in the Holocene (Tinner & Kaltenrieder 2005) due the well established stable communities strongly influenced by competition. This is true for the Krkonoše Mts. even today: as temperature increases, the timberline ascends first at disturbed localities with low herb cover (such as old debris flow tracks) and higher rates of seedling establishment (Treml 2004).

## Conclusions

During the Holocene, Harz, Vosges, Schwarzwald and Hrubý Jeseník Mts. were prone to disappearance of alpine forest-free areas in the periods of favourable climatic conditions. Most likely, a temperature dependent alpine belt was absent from these areas during the climatic optimum. In contrast, a large alpine area was maintained throughout the Holocene in the Krkonoše Mts. In the Hrubý

Jeseník Mts., a temperature dependent forest-free area existed at least since 2000 BP to the present.

In the Krkonoše Mts., alpine timberline gradually advanced from 500–600 m in the Younger Dryas to 1000 m (9200–8800 BP). After 7400 BP timberline ascended at least to 1320 m, which is the altitude of the Pančava peat bog. Maximum timberline position in the Krkonoše Mts. has not exceeded 1450 m a.s.l., as this is the lower limit of well developed sorted patterned ground formed in the late glacial. Therefore, it has passed the present maximum by 60 m only, and the average positions of the natural timberline by 150 m. During 4000–800 BP, the alpine timberline was situated probably below the Úpa peat bog (1420 m a.s.l.). In the Labský důl profile, three distinct oscillations of AP/NAP curve were recorded during the early Holocene. Of these, at least two (LD1 and LD2 – 9600 BP) oscillations are believed to be timberline descends due to climatic shifts rather than local disturbances.

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