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CONTROLLING FACTORS LIMITING TIMBERLINE POSITION AND SHIFTS IN THE SUDETES: A REVIEW

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Abstract

Three isolated massifs in the Sudetes, Central Europe, are elevated sufficiently high to allow for the development of the treeline ecotone. These are the Karkonosze/Krkonoše in the West Sudetes and Hruby Jeseník and Masyw Śnieżnika/Králický Sněžnik in the East Sudetes. The upper limit of closed tree stands (i.e. timberline) is located at c. 1250 m a.s.l. on average in the Krkonoše, but with significant variability spanning more than 500 m. In the East Sudetes the respective elevation is higher, above 1300 m a.s.l., and the variability is smaller. While temperature is the primary factor governing the uppermost tree stands, second-order climatic factors play an important role in shaping treeline ecotone position, particularly wind and snow accumulation patterns. Active surface processes such as debris flows and snow avalanches force the timberline to descend and account for its locally very irregular course. There is a history of long-term human impact on the position of the timberline, with its peak in the 17-19th centuries when high-mountain meadows were extensively used for grazing and haymaking. In the last century the overall trend of timberline ascent associated with abandonment of agricultural land and temperature rise has been interrupted by the episode of catastrophic forest decline due to air pollution.

Key words

treeline ecotone • Karkonosze • Hrubý Jeseník • Masyw Śnieżnika • mountain ecology

Introduction

The Sudetes, shared by the Czech Republic and Poland, constitute the highest area within the Central European mountain and upland belt that extends broadly parallel to the Alps and the Western Carpathians, from the Vosges in France in the west to the South Polish Uplands in the east. Three individual massifs within the Sudetes rise above

1200 m a.s.l. (Fig. 1) into a climate belt sufficiently cool to hamper the growth of trees. As a consequence, treeline ecotone is present on these massifs and plays the role of an important ecological and geomorphic boundary, separating forested slopes below and treeless ridges and summit plateaus above. The alpine treeline ecotone is a transitional zone between the upper limit of closed forest (i.e. alpine timberline) and the upper limit of occurrence of tree species (Körner 2012). Whereas the position of the alpine timberline results from the interaction of several factors including climatic variables and disturbances, the location of the altitudinal tree species limit is governed by temperature (Holtmeier 2009; Körner 2012). An intermediate position within the treeline ecotone is represented by the alpine treeline, which is conventionally delineated as a line connecting all the uppermost locations of tree stands (Körner 2007). The exact definitions differ slightly among the studies referred to in our review (Treml & Banaš 2003; Treml 2007b; Treml & Chuman 2015) and in this review the definition of the alpine timberline is based on minimum canopy cover.

The characteristics of treeline ecotone in the Sudetes and the variety of factors controlling its position have long been of interest to various scientific disciplines and therefore considerable knowledge has accumulated. While most of the older work was largely qualitative, significant advances in understanding the treeline ecotone have been made in recent years through the use of various quantitative indices. The aim of this paper is to provide an overview of these recent achievements with the focus on three interrelated aspects:

1) the location of the timberline and its key characteristics;
2) controlling factors limiting its current position and shifts;
3) assessment of anthropogenic influences on the course of the timberline and treeline.

All three massifs which rise above the timberline – Karkonosze/Krkonoše (Polish/Czech names, respectively), Hrubý Jeseník and Masyw Śnieżnika/Králický Sněžník – are considered (Fig. 1).

Study areas

The Sudetes as a whole are elongated NW – SE and are divided into a large number of minor geographical units, distinguished on the

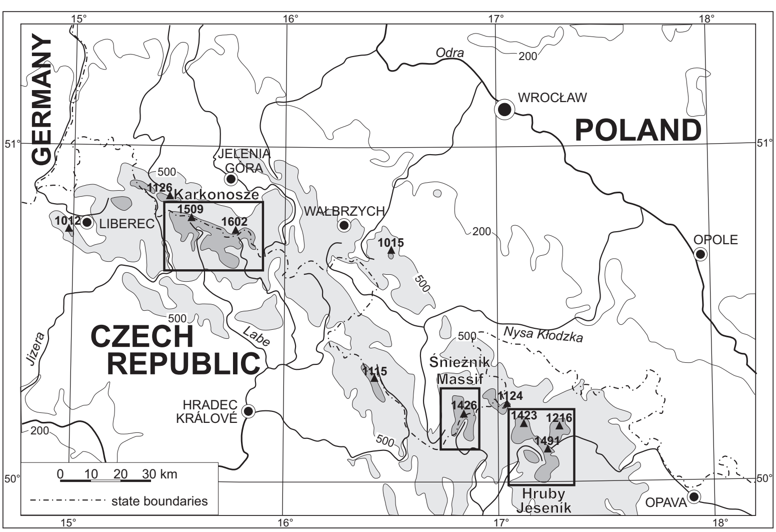

Figure 1. General topography of the Sudetes and location of the three massifs which rise above the timberline in their most elevated parts. Light grey areas indicate the extent of terrain above 1000 m a.s.l.

basis of their distinctive geomorphology and clear morphological boundaries, usually related to main fault lines or important lithological contacts. The contemporary elevation differences between these units are primarily attributed to complicated patterns of Neogene to Quaternary uplift and subsidence, with the highest massifs interpreted as uplifted most (Demek 1975; Demek et al. 2007; Zuchiewicz et al. 2007; Migoń 2008, 2011). Thus, all three massifs hosting the timberline are regarded as major horsts.

Karkonosze/Krkonoše. They are located in the West Sudetes and reach the highest elevation within the entire range, at Mt. Śnieżka/Sněžka whose summit is 1602 m a.s.l. (Fig. 1). The highest part is an extensive, gently rolling plateau at 1300-1500 m a.s.l., whose continuity is however broken by the existence of mountain passes and residual hills. In a few localities the edges of the plateau are undercut by glacial cirques, which are the morphological testimony to Pleistocene glaciation. To the south the plateau gives way to broad convex ridges sloping gently southward, separated by deeply incised valleys. In terms of the present-day geomorphic environment, various morphogenetic domains are distinguished. On the plateau cryogenic processes of frost heaving and sorting play a significant role, whereas steep slopes below the plateau edges are modelled by soil creep, occasional snow avalanches and debris flows, as well as rock fall in glacial cirques. For a more thorough presentation of the environment of the area the reader is referred to recent syntheses edited by Flousek et al. (2007) and Knapik and Raj (2013).

Hrubý Jeseník. This is the second highest mountain massif in the Sudetes, located in its eastern part, where the most elevated spot – Mt. Praděd – attains 1491 m a.s.l. In contrast to the Krkonoše, no comparable extensive summit plateaus occur in the Hrubý Jeseník. Instead, long and sinuous ridges run from south to north, with several shorter branches running east and west (Fig. 1). Mountain top surfaces are broad convexities, nearly planar along the axis, and for long distances they retain an elevation above 1300 m a.s.l. Nevertheless, they are rather narrow (< 500m) on a regional scale. Convex slope breaks connect gentle ridge tops with long and steep slopes below, whose height may reach 600-700 m. Because of the limited snow accumulation area on the summit parts the Pleistocene glaciation was relatively underdeveloped and only one distinct glacial cirque exists (Velká kotlina). Otherwise the ridges are undercut by deeply incised valley heads, not uncommonly as steep as 30-40°, moulded by occasional debris slides, flows, and snow avalanches. On the ridges themselves inherited periglacial landforms are abundant and some contemporary cryogenic activity is recorded. A more thorough presentation of the geology and geomorphology of the area can be found in Czudek (1997) and Roštínský (2010).

Masyw Śnieżnika/Králický Sněžník. The third highest massif in the Sudetes straddles the Czech/Polish boundary in the western part of the East Sudetes. Its homonymous most elevated spot reaches 1426 m a.s.l. (Fig. 1). As in the Hrubý Jeseník, a widespread mountain-top plateau is absent and the general morphology is one of a series of broadly convex, largely forested ridges radiating from the central elevation. Those extending to the south are longer and higher, retaining an altitude of 1200-1300 m a.s.l. for 4-6 km. Slopes below are steep (25-35°) and connect with valley floors located as much as 500-600 m below. In comparison with the other two massifs, the Králický Sněžnik experiences much less contemporary geomorphic activity, despite slope steepness. Only a few historical debris slides occurred, all within the forest belt.

Methods of mapping treeline ecotone

Since treeline ecotone is a transition zone, the definition of any line such as the timberline or treeline depends on conventional criteria (Körner 2007). In our review, we refer to a number of studies with varying methodologies applied to define the position of treeline ecotone (Tab. 1). Treelines and timberlines were mostly mapped based on minimum tree

Table 1. Methods and parameters applied in treeline ecotone mapping in the Sudetes

Source	Minimum tree height [m]	Minimum forest canopy cover (canopy percentage on a given area size)	Source for determination of forest canopy cover	Classification method	Region
Jeník and Lokvenc (1962)	5	50 % on 100 m^2	Field survey	Not applied	Karkonosze
Alblová (1970)	5	50 % on 100 m^2	Field survey	Not applied	Hrubý Jeseník
Zientarski (1993)	8	40 % on 1000 m^2	Field survey	Not applied	Karkonosze
Treml and Banaš (2003)	5	50 % on 100 m^2	Grey-scale orthogonal aerial images, field survey	Image thresholding	Sudetes
Treml (2007b)	5 m - alpine timberline 2 m - upper limit of tree occurrence	50 % on 100m^2	True-color and grey-scale orthogonal aerial images, field survey	Supervised classification	Sudetes
Král (2009)	Not applied	51-75 % on 1000 m^2	Color-infrared orthogonal aerial images	Supervised classification	Hrubý Jeseník
Treml and Chuman (2015)	Not applied	50 % on 100m^2	True-color and grey-scale orthogonal aerial images	Image segmentation and classification	Karkonosze, Hrubý Jeseník

height and minimum forest canopy covering an area of a certain size. In the pioneer studies, the above mentioned parameters were determined directly in the field (Jeník & Lokvenc 1962; Alblová 1970; Zientarski 1993). Later on, aerial images were interpreted together with field surveys (Treml & Banaš 2003). Recent approaches are based on the classification of orthogonal aerial imagery with variable spectral resolutions (Král 2009; Treml & Chuman 2015). Exact comparisons of treeline ecotone positions between different studies usually fail because of differences in criteria used in the delineation of treeline ecotone. Temporal and spatial comparison of treeline ecotone positions is possible only using input data of identical resolution and classified according to the same method (e.g. Treml & Chuman 2015).

Characteristics of the treeline ecotone

Krkonoše

Tree stands in the treeline ecotone are dominated by Norway spruce *Picea abies* [L.] Karst. Rowan (*Sorbus aucuparia*) and sycamore maple (*Acer pseudoplatanus*) occur occasionally, particularly on sites characterized by high snow loads and within snow avalanche paths. Scattered stands of European beech (*Fagus sylvatica*) were planted in the treeline ecotone on the south-facing slope of Mt. Zlaté Návrší (western part of Krkonoše, Vacek & Hejcman 2012). At several locations, the last remnants of planted stone pine (*Pinus cembra*) remain. Extensive stands of prostrate dwarf pine (*Pinus mugo*) are widespread across the alpine treeline ecotone (Fig. 2A). Scattered polycormons

Figure 2. Typical treeline ecotones in the Krkonoše Mts. (A); in Masyw Śnieżnika (B); and in the Hrubý Jeseník Mts. (C)

of low-stature dwarf pine can be found even at the highest locations of the Krkonoše Mts. The herbal layer in the treeline ecotone is mainly formed of *Calamagrostis villosa* mats, and on the north-facing slopes *Athyrium alpestris* is also frequent. With increasing altitude these plant communities are replaced by communities typical for the cryo-vegetation zone of arctic-alpine tundra (Soukupová et al. 1995). Uppermost specimens of spruce can even be found in the cryo-aeolian zone of arctic-alpine tundra.

Concerning treeline physiognomy, the treeline in the Krkonoše is formed either by 'diffuse' or 'islands' treeline ecotones (according to terminology of Harsch & Bader 2011). However, at many locations the form of the treeline is probably strongly affected by past human activity. Clonal groups of spruce together with extensive, often closed stands of dwarf pine typically occur in the treeline ecotone. At the timberline, 9 to 7 m high spruce trees with upright stems prevail. With increasing altitude across the treeline ecotone, spruce trees tend to show numerous symptoms of biomass loss due to wind browsing, such as flag-crowns or table-like crown forms. At extremely wind-affected locations prostrate forms of spruce can even be found. Candelabra-like forms of stems and multi-stemmed spruce trees are also common within the treeline ecotone.

Treeline ecotones delimit two large and five small forest-free enclaves (Fig. 3). The average altitude of the timberline in the Krkonoše is about 1240 m (Zientarski 1993; Treml & Banaš 2003; Treml 2007b; Migoń & Parzóch, 2008), whereas the average altitude of the treeline (defined as a line connecting the uppermost alpine timberline positions on adjacent slope sections differing in aspect) is 1278 m (Treml 2007b), based on an analysis of aerial images from 2003. Computed elevations refer to the entire course of treeline ecotone including sections lowered by past human interventions and by snow avalanche activity. Based on aerial images from 2005, the maximum timberline elevation was 1462 m on the south-west facing slope of Mt. Sněžka. Trees higher than 5 m have recently been found at elevations of about 1500 m. The least elevated sections of the timberline are situated in the valley bottoms (Labský důl, Obří důl), where its elevation may be as low as 900 m (Treml & Banaš 2003). The variability of timberline position on the northern slopes is smaller and the minimum and maximum values are 1036 m and 1340 m, respectively (Zientarski 1993).

The current treeline ecotone position and physiognomy are, however, related to the past dynamics of tree stands. The position of the alpine timberline was reconstructed from several pollen profiles that contain the record of the entire Holocene period (e.g. Engel et al. 2010). Based on pollen and sedimentary records, the timberline is inferred to have been situated at 1000 m a.s.l. during the period 9200-8800 BP (Treml et al. 2008). After 7400 BP the timberline advanced to at least 1320 m a.s.l., which is the altitude of the Pančava peat bog

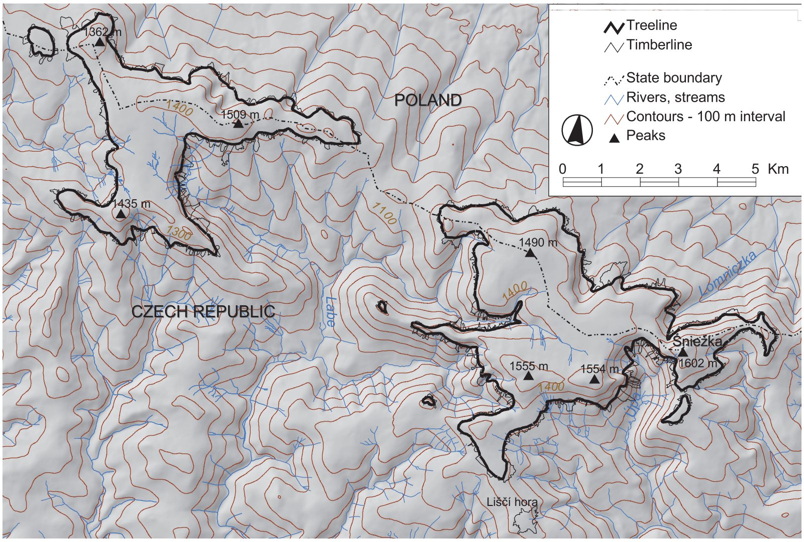

Figure 3. Timberline and treeline positions in the Krkonoše Mts. Lines were derived from aerial images dated to 2005 based on the minimum canopy criterion. For details see Treml and Chuman (2015) and Table 1. Note that in the south-eastern tip of the summit area, only timberline was delineated at the isolated enclave of Mt. Liščí hora, because the uppermost closed stands of spruce reach the summit plateau on the west-facing slope. Therefore, the treeline (i.e. the line connecting the uppermost parts of the timberline), could not have been defined

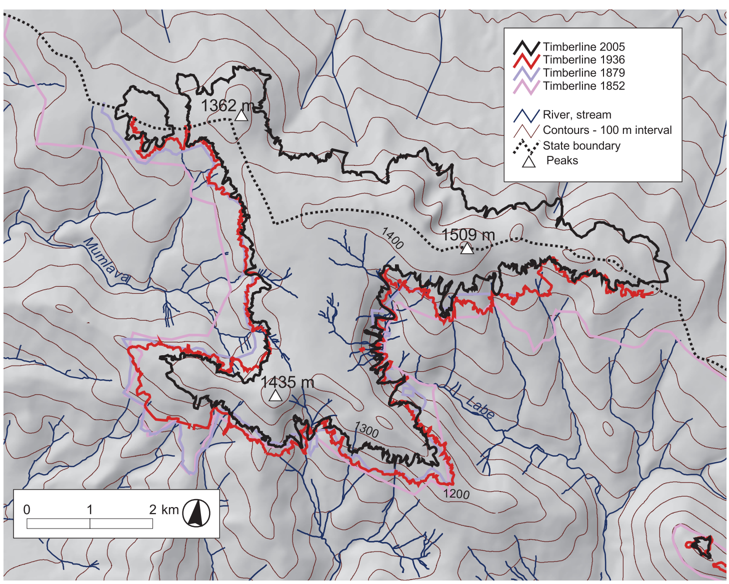

Figure 4. Successive timberline positions in the western part of the Krkonoše Mts. since the 19th century (dating from 1852, 1879, 1936 and 2005). The1852 timberline is derived from maps of the so called *Stable cadastre* and the *Second military mapping* (Vágner 2013). Data for both sources were compiled between the 1820s and 1840s. The 1879 timberline is based on the Forest map of the *Jilemnice large farm* (Vágner, 2013). Timberline positions in 1936 and 2005 were derived from aerial images (Treml & Chuman 2015), see Table 1

(Huettemann & Bortenschlager 1987; Treml et al. 2006). According to Treml et al. (2006, 2008), the maximum timberline position in the Krkonoše was never higher than 1450 m a.s.l. (the lower limit of well developed sorted patterned ground formed in the Late Glacial). The same authors suggested that in the time interval 4000-800 BP the alpine timberline had probably been continuously situated below the Úpa peat bog (1420 m).

Since at least the Late Middle Ages the treeline ecotone has been under human pressure, generally leading to the lowering of its position (Speranza et al. 2000; Treml et al. 2008). It was probably at its lowest during the 18th century as a consequence of strong anthropogenic pressure and in response to cold oscillations within the Little Ice Age (Lokvenc 1995; Treml et al. 2014). Based on old maps, Vágner (2013) reported the mean altitude of the timberline position as 1106 m in the 1750s and 1145 m in the 1850s in the western part of Krkonoše, as well as 1167 m in the entire Czech part of Krkonoše (Fig. 4).

Since the 1930s the alpine timberline in the Krkonoše has showed an average annual upward advance of 0.43 m assuming linear shift (Treml & Chuman 2015). The dominant process associated with the upward advance of the alpine timberline was the densification of the lower part of the treeline ecotone. However, this timberline advance was relatively small if compared with other European mountains. Treml and Chuman (2015) argue that the high cover of prostrate dwarf pine shrubs and the presence of convex parts of slopes with extreme microclimatic conditions are important constraints on forest advance.

Králický Sněžník and Hrubý Jeseník

Similarly to the Krkonoše Mts., the treeline ecotone in the Králický Sněžník and Hrubý Jeseník Mts. is dominated by Norway spruce, whilst rowan (*Sorbus aucuparia*) and sycamore maple (*Acer pseudoplatanus*) are occasionally present as well (Fig. 2B,C). Within snow avalanche paths in the Hrubý Jeseník, extensive stands dominated by Carpathian birch (*Betula carpatica*) can be found. In the Malá kotlina valley (SE part of the main ridge), the snow avalanche path is bordered by natural stands of European beech. Both in the Králický Sněžník and the Hrubý Jeseník, the last remnants of planted, non-indigenous stone pine (*Pinus cembra*) have persisted. In contrast to the Krkonoše, dwarf pine stands in the treeline ecotone result exclusively from planting in the 19th and 20th century (Hošek 1973). Before planting, this species had not been present here at least during the late Holocene (Rybníček & Rybníčková 2004; Novák et al. 2010). Besides dwarf pine, other shrub communities dominated by *Empetrum hermaphroditum* and *E. nigrum* are relatively frequent. Isolated individuals of juniper *Juniperus communis* ssp. *alpina* can be found in the treeline ecotone as well (Zeidler et al. 2009). The most common dwarf shrub in the treeline ecotone is however the European blueberry *Vaccinium myrtillus*, which forms the most abundant species in understory. Together with *Calamagrostis villosa*, these species dominate the herb layer (Zeidler et al. 2012).

According to the terminology of Harsch and Bader (2011), *diffuse* and *islands* treeline ecotones occur in the Hrubý Jeseník and the Králický Sněžník. Sharply delineated ecotones can be found at some locations as a consequence of past human interventions. Small clonal groups of spruce trees are widespread in the intermediate and upper parts of the treeline ecotone (Šenfeldr & Maděra 2011; Šenfeldr et al. 2014) and often display flag-crown morphology as a result of wind-browsing. Candelabra-like stems of spruce are also common. Their presence results from frequent apical breaks caused by high snow loads, rime and/or wind action.

In comparison with the Krkonoše, the treeline ecotones in the Hrubý Jeseník and the Králický Sněžník are narrower and the variability in timberline altitudes is smaller (Treml & Banaš 2003). Further, in the Hrubý Jeseník Mts. the forest-free areas are very fragmented, constituting one large (the southern part of the main ridge) and four relatively small enclaves with alpine treeline ecotones

(Fig. 5). The average timberline altitude is 1320 m in the Králický Sněžník and 1302 m in the Hrubý Jeseník, based on aerial images from 2005 (Treml 2007c). The treeline in the Hrubý Jeseník defined by the same approach as in the Krkonoše is situated at an altitude of about 1320 m (Treml 2007c). The maximum timberline position is attained on the west-facing slope of Mt. Praděd (1420 m). Even in the vicinity of the highest peaks, trees higher than 3 m can be found. The lowest sections of alpine timberline are situated within runout parts of snow avalanche paths in the Malá Kotlina valley (Hrubý Jeseník, 1070 m) and in the Morava valley (Králický Sněžník, 1220 m).

Available records providing data on treeline dynamics span approximately the last 4000 years (Rybníček and Rybníčková, 2004; Dudová et al., 2013). The only sedimentary profile covering the Late Glacial period is situated at 850 m a.s.l., at the southern tip of the main ridge, and this pollen record documents

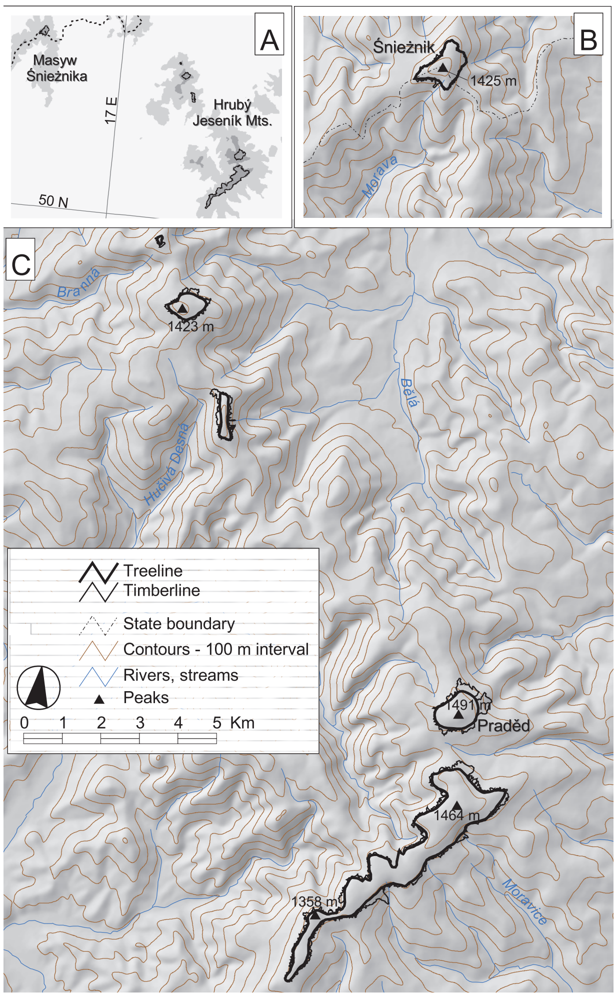

Figure 5. (A) Location of treeline ecotone areas in the eastern part of the Sudetes. Timberline and treeline positions in the Hrubý Jeseník Mts. (B) and in Masyw Śnieżnika (C). Lines were derived from aerial images dated 2005 based on the minimum canopy criterion. For details see Treml and Chuman (2015) and Table 1

the occurrence of open forests with *Pinus cembra*, birch and *Larix decidua* at the end of the Late Glacial (Dudová et al. 2014). In contrast to the Krkonoše, larch had been present in timberline stands of the Hrubý Jeseník at least until 580 BC (Dudová et al. 2013). As regards the long-term treeline ecotone dynamics, Rybníček and Rybníčková (2004), Treml et al. (2008), and Novák et al. (2010) showed that the uppermost parts of the Hrubý Jeseník were likely forest-free during the period between ca 2200 BP and 900 AD. Between 530 and 900 AD there is evidence for depressed timberline in Mezikotlí valley (1250 m), likely resulting from snow avalanche activity. The first indications of human intervention affecting the treeline ecotone come from 900 AD and during the subsequent early High Middle Age period the timberline was locally depressed to about 1250–1350 m (Novák et al., 2010). Extensive human intervention affecting the treeline ecotone and resulting in timberline descent are dated to the Late Middle Ages (ca 1300-1500 AD; Rybníček & Rybníčková 2004; Novák et al. 2010; Dudová et al. 2013).

In the Králický Sněžník, before the first human-induced interventions affecting the treeline ecotone (around 900 to 1000 AD), the extent of forest-free ecosystems had been very limited. They were probably restricted to the uppermost summit part of Mt. Králický Sněžník, as testified by relict patterned ground (sorted nets type, Křížek 2007), which is a landform easily destroyed by root action and uprooting – both phenomena associated with forest stands.

In the 18th and at the beginning of the 19th century the timberline was depressed to its lowest position, with individual forest-free areas in the southern and northern part of the Hrubý Jeseník ridge connected and constituting two large forest-free zones (Jeník & Hampel, 1991). The same situation was found on the ridges of the Králický Sněžník where the majority of areas above ca 1250 m were forest-free (Treml 2007c). Later on, forest stands advanced upwards, both due to plantations and due to spontaneous succession. Since the 1940s, the alpine timberline in the Hrubý Jeseník has advanced upwards at an overall rate 0.30 m yr^{-1} assuming a linear shift; the treeline position, however, has remained stable (Treml & Chuman, 2015).

Natural controlling factors limiting timberline position

Climatic controlling factors

In general, heat deficiency determines the formation of treeline ecotone (Körner 2012). On a regional scale, however, there can be other climatic stressors (i.e. second-order factors of treeline formation) preventing the advance of trees to their maximum temperature-limited positions (Holtmeier 2009). In the global perspective, the growing season ground temperatures at the treeline are in most cases around 6.7±0.8°C (Körner & Paulsen 2004). In the cold temperate regions of Europe, particularly in the Alps, these temperatures are ca 1°C higher (Körner & Paulsen 2004). The comparison of both ground temperatures (Treml et al. 2015) and air temperatures (Treml 2007c) between the Sudetes and the Alps reveals that treeline temperatures are ca 0.5°C higher in the Sudetes than at the highest treeline positions in the Alps. Therefore, the second-order factors influencing treeline position should also be considered. Air temperatures in the alpine treeline ecotone are listed in Table 2.

Since the current position of the treeline ecotone is related to climatic conditions over the past tens to hundreds of years rather than solely to the current climate (Holtmeier 2009), past temperature fluctuations should also be taken into consideration. Over the last century, there has been a significant rising trend of summer temperatures in the Sudetes, estimated at 0.07°C/10 years (Głowicki 1997, based on data from Mt. Śnieżka station, Fig. 6). Prior to the 20th century, tree-ring-based temperature reconstruction showed that decadal means of June-July temperatures in the Sudetes were likely to have been 4°C lower at the beginning of the 18th century and around 1820, compared to the most recent period

Table 2. Air temperature variables characterising the highest positions of the alpine timberline in the Krkonoše Mts. and the Hrubý Jeseník Mts. Temperatures (1961-1990) from meteorological stations Śnieżka (1602 m a.s.l., Głowicki, 1997) and Praděd (1491 m a.s.l.) were scaled to the timberline position using appropriate monthly lapse rates derived by Květoň (2001)

Mountain range	Maximum timberline elevation [m a s.l.]	Growing season temperature (May-Sep) [°C]	Warmest month temperature [°C]
Krkonoše Mts.	1462	7.2	9.1
Hrubý Jeseník Mts.	1420	8.0	9.9

2000-2009 (Treml et al. 2014). Such strong negative temperature anomalies associated with the Little Ice Age probably hampered tree growth and succession in the summit parts of the Sudetes.

In addition to cold climate, there is abundant evidence that second order factors of treeline formation play an important role in the Sudetes (Jeník 1961; Jeník & Lokvenc 1962; Treml et al. 2012; Treml & Chuman 2015). This idea is also supported by relatively weaker temperature-growth responses of treeline trees in comparison to timberline trees (Treml et al. 2012). Treml et al. (2012, 2015) have argued for a strong effect of wind action on tree growth at the treelines. Nevertheless, additional climatic stress agents should also be taken into account, e.g. frequent rime and fog (Błaś & Sobik 2000; Błaś et al. 2002; Migała et al. 2002). Treml and Chuman (2015) suggest that wind action induced a relatively small rate of timberline advance in the Sudetes over recent decades – less than what could have been expected according to the trend of rising temperature. Besides temperatures and wind action, tree

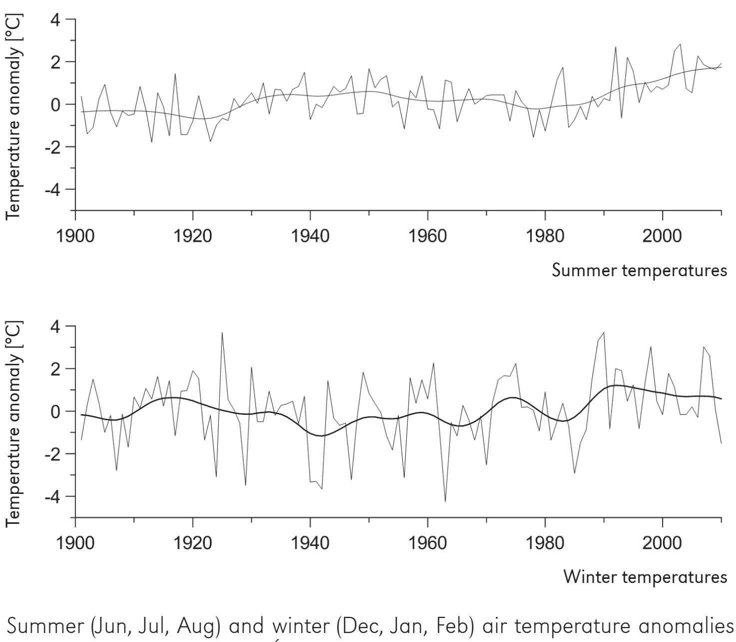

Figure 6. Summer (Jun, Jul, Aug) and winter (Dec, Jan, Feb) air temperature anomalies relative to the normal period 1961-1990 from the Mt. Śnieżka meteorological station (1602 m a.s.l.). Homogenized data published by Głowicki (1997) were used. Bold lines denote 20-yr Gaussian low-pass filters

growth and seedling survival in the Sudetic treeline ecotones is limited by irregular distribution of snow on windward and leeward sites (Jeník 1961), which determines the basic pattern of timberline configuration, particularly in the Krkonoše. There, in the leeward parts of relief, the timberline usually attains its minimum altitude as a consequence of snow avalanche activity (Jeník 1961; Kociánová & Spusta 2000).

Biotic controlling factors

In the Sudetes, biotic controlling factors of treeline ecotone dynamics include in particular competition and facilitation between trees and shrubs (Callaway et al. 2002), the impact of snow fungi on seedling survival (Holtmeier 2009), and grazing pressure from large herbivores (Cairns & Moen 2004). Extensive stands of prostrate *Pinus mugo* slow the upward expansion of spruce as they physically hamper both vegetative and generative reproduction of spruce (Treml & Chuman 2015). However, in the upper part of the treeline ecotone, dwarf pine stands promote height growth of spruce due to their protective role (Šenfeldr et al. 2014). The newly established spruce ramets and seedlings suffer from fungal infections, especially on snow-rich and waterlogged sites (Vacek et al. 2012; Šenfeldr et al. 2014). Recruitment of spruce in the treeline ecotone is further reduced by the intense grazing pressure of red deer (Vacek 1990).

Geomorphic controlling factors

Geomorphic factors are most evident in influencing the position of the timberline (i.e. the upper limit of a closed forest) in the High Sudetes and may be divided in two categories. The first one comprises passive factors such as slope shape and steepness, the occurrence of sheltered locations within otherwise exposed slopes, and inherited characteristics of soil and regolith cover which do not change on medium (centennials) to short (decadal) time scales. They define the local environment, which may or may not be suitable for tree stands to establish themselves and thrive. The second includes active surface processes, which exert an impact on tree stands and species, usually leading to tree/forest damage or destruction. Among the processes acting across the timberline in the Sudetes are debris flows, debris slides, snow avalanches, and rather infrequent rock slides and rock falls. Whilst they are typically initiated above the timberline, relief energy allows them to reach lower elevations located within the forest belt. Local topographic conditions dictate that they preferentially occur within slope hollows of various origin (glacial, nival, preferential weathering) and along erosional ravines, hence in terrain concavities.

Several relationships between the position of treeline ecotone and local relief have been quantitatively evaluated by Treml (2007a). It was demonstrated that, among other conclusions, the elevation of the both timberline and treeline is lower within concave landforms (valley heads, slope hollows) than it is on convex hillslopes. However, extreme convexity of hillslope surfaces (hence, exposure) results in local descent of the treeline too. Furthermore, the treeline takes a lower altitudinal position within valley floors than on the adjacent open slopes, although the variability was not found to be statistically significant. The effect of slope steepness is not very pronounced, although it had been found that the treeline on steeper slopes tends to show more evident oscillations at the decadal timescale. On the Polish side of the Krkonoše, Migoń and Parzóch (2008) observed that forest stands rarely occur on slopes steeper than 30° and suggested that the likely explanation lies in the efficacy of throughflow in coarse regolith covers. More generally, the presence of coarse slope deposits (blocky moraines, rock glaciers, block fields and block streams) causes a significant lowering of the timberline, locally by as much as 110 m in respect to the reference datum of 1250 m a.s.l., as well as contributing to its local shifts up- and downslope.

The lower position of the treeline/timberline in terrain concavities, although partly explained by topoclimatic factors, is certainly influenced by geomorphic processes too. Both snow avalanches and debris flows damage the trees, forcing the timberline to descend down the respective avalanche/debris flow track. The Łomniczka Cirque in the Krkonoše, with the lower elevation of the timberline on its western shoulder affected by frequent mass movements, provides a good example. In fact, in both the Krkonoše and Hrubý Jeseník different gravity-driven mass transport processes tend to use the same concave topographic features exerting a synergic effect on timberline elevation. However, except for specific locations, the frequency of mass movements is not high enough to cause the permanent lowering of the timberline position, as known from alpine terrains. Rather, debris flow/avalanche tracks are slope sections where the oscillations of the treeline position are most evident and both the furrows and lateral ramparts are landforms preferentially colonised by new trees after an event. In consequence, lobate or linear upslope projections of the timberline can be identified, especially in the Krkonoše (Treml 2007a).

Anthropogenic influences

The long history of human occupation and land use in the Krkonoše has also had its effect on the timberline. The earliest human activity in montane forests is documented from 1100 AD (Speranza et al. 2000). However, significant human-induced alterations of the treeline ecotone are of a later age and dated to the Late Middle Age period (Speranza et al. 2000; Treml et al. 2008). Gentle slopes at high elevations (>1000 m a.s.l.) were found attractive for grazing and animal husbandry as early as in the 17th century, a trend that intensified in subsequent centuries. In consequence, tree stands near the natural timberline were cut down and replaced by open meadows (Fabiszewski 1985). In some locations the resultant lowering of the timberline was by as much as 150-200 m, e.g. at Hala Szrenicka or Hala Pod Łabskim Szczytem. Data provided by Vágner (2013) indicate comparable downslope shifts in the 18th century (Fig. 4). In more recent times, in the 1970s and 1980s, considerable lowering of the timberline in several parts of the Krkonoše occurred due to anthropogenic forest dieback caused by atmospheric pollution (Zientarski 1993). The pollution-induced lowering of timberline was, however, significantly smaller in the Czech part of the Krkonoše (Treml 2007b). Both in the Krkonoše and Hrubý Jeseník the timberline descent in the period of the 1970s and 1980s was particularly characteristic for climatically stressed stands, i.e. at the most elevated timberline positions, on north-facing slopes and on the most convex parts of the slopes (Treml & Chuman 2015).

In contrast to the Krkonoše, reliable evidence of the first human activity affecting treeline ecotone is dated to the early medieval period in the Hrubý Jeseník and the Králický Sněžník (ca 700-900 AD; Novák et al. 2010). Based on charcoal and pollen indicators both Novák et al. (2010) and Dudová et al. (2013) speculated about possible human-induced alterations of the treeline ecotone even earlier, in the Late Iron Age. The most pronounced depression of timberline due to burning and subsequent pasture was dated to the Late Middle Ages. The permanent use of pasture grounds prevented the succession of trees (Hošek 1973). Similarly to the Krkonoše, in the eastern part of the Sudetes, human impact was also strongest on the summit on gently rolling surfaces. The general advance of the alpine timberline in the Sudetes during the last 70 years is associated particularly with the termination of pasture and hay making (Treml & Chuman 2015).

Conclusions

The presence of various upper limits of tree growth in the Sudetes makes this mountain range distinctive among other mountain terrains of the Hercynian belt of Central Europe. Differential uplift and subsidence in the late Cenozoic has brought three isolated massifs within the Sudetes to such altitudes that a clear pattern of geoecological belts could have developed during the Holocene. Inherited relief dictates that treeless terrains occupy an extensive mountain-top plateau (Krkonoše), a long watershed ridge (Hrubý Jeseník), or the most elevated part of a central dome (Králický Sněžník). Consequently, the treeline and the timberline are mostly located on steeper slopes at lower elevations, characterised by a significant geomorphic and topoclimatic variability which influence the position of the upper limits of tree stands. Temperature, patterns of snow accumulation, the exposure factor, competition of spruce and prostrate dwarf pine, and surface processes such as debris flows and snow avalanches are the dominant controlling factors limiting the position of the treeline/timberline, accounting for its wide range of elevation, from as low as ca 900 m a.s.l. to as high as 1462 m a.s.l.

Prehistoric and historic fluctuations of the timberline have been caused both by natural factors and human interference, with the latter more clearly identified in various types of records. There is no evidence that the summit plateau of the Krkonoše has ever been under forest in the Holocene, even during the climatic optimum. Humans have been affecting the position of the timberline since early medieval times, with the impact intensified from the 17th century onwards when grazing and hay making on the high-elevation surfaces were at their peak. Temporary descent of the timberline, especially in the Krkonoše, occurred in the late 20th century, being the consequence of forest dieback due to air pollution. Nevertheless, in the last century the timberline has been advancing upwards at a rate of 0.3-0.4 m yr^{-1}, apparently in response to agricultural land abandonment and overall temperature rise.

Editors' note:
Unless otherwise stated, the sources of tables and figures are the authors' on the basis of their own research.

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