The Effect of Exposure on Alpine Treeline Position: a Case Study from the High Sudetes, Czech Republic

Authors: Treml, Václav, and Banaš, Marek

Source: Arctic, Antarctic, and Alpine Research, 40(4) : 751-760

Published By: Institute of Arctic and Alpine Research (INSTAAR), University of Colorado

URL: https://doi.org/10.1657/1523-0430(07-060)[TREML]2.0.CO;2

Arctic, Antarctic, and Alpine Research, Vol. 40, No. 4, 2008, pp. 751–760

The Effect of Exposure on Alpine Treeline Position: a Case Study from the High Sudetes, Czech Republic

Václav Treml and*
Marek Banaš†

*Corresponding author: Department of Physical Geography and Geoecology, Faculty of Science, Charles University in Prague, Albertov 6, CZ-128 43 Prague, Czech Republic
treml@natur.cuni.cz
†Department of Ecology and Environmental Science, Faculty of Science, Palacký University, tř. Svobody 26, CZ-771 46, Olomouc, Czech Republic

Abstract

Using the High Sudetes as an example, we examined whether the position of the alpine treeline is in fact related to the heat load of the site, and whether the temperatures of the air and soil change along slopes with differing exposure to solar radiation. We hypothesized that if there are really strong exposure effects they must be expressed both in significant correlations between treeline elevation and heat load of respective sites and in distinct differences in root zone and tree top temperatures. We found that the highest positions of the alpine treeline were situated in places with the potentially highest heat load. Nevertheless, only weak exposure effects on the soil temperatures during the growing season were detected, both in the closed forest and in the tree groups. Further, air temperatures near the terminal shoots varied significantly less than soil temperatures; however, the margins of the closed forest were especially more favorable at the south-facing slopes. Winter soil temperatures did not seem to be generally more advantageous on sites with high heat load. Direct temperature measurements thus indicated that established positions of the alpine treeline are just slightly influenced by differences in heat load.

DOI: 10.1657/1523-0430(07-060)[TREML]2.0.CO;2

Introduction

The altitudinal position of the alpine treeline (defined according to Körner, 1999) is determined mainly by temperature during the growing season (Tranquillini, 1979; Körner, 1999). In temperate mountains, mean soil temperatures in the alpine treeline vary between 7 and 8°C in the growing season (Körner and Paulsen, 2004). Besides the crucial factor of temperature, other environmental features also affect the alpine treeline position, such as terrain morphology, various types of slope processes, snow accumulation, herbivore browsing, and the occurrence of fires (Holtmeier, 2003). In addition, long-term human impact on the treeline ecotone should be taken into account (Tinner and Theurillat, 2003; Speranza et al., 2000). However, the influence of temperature is more significant than that of other environmental factors, especially with regard to the maximum treeline positions (Plesník, 1971; Malyshev and Nimis, 1997).

The physiological processes which are limited by low temperature and which reduce tree growth intensity at the alpine treeline have not yet been explicitly described. To explain these phenomena, Körner and Hoch (2006) suggested the low soil temperature hypothesis. The question remains, however, to what extent the decrease of tree growth at the forest-tundra ecotone reflects the influence of low air temperatures on meristems in tree tops (Grace, 1989; Paulsen and Körner, 2001; Körner and Hoch, 2006).

In northern temperate mountains with a sufficient amount of precipitation, the dependence of the alpine treeline on temperature implies that the position of the treeline should be different in warmer ("favorable") and colder ("unfavorable") parts of the relief (Aulitzky, 1961; Holtmeier, 2003). Slopes with favorable aspect (south, southwest) are characterized by higher direct radiation (Geiger et al., 2003), and their growing season is longer because of earlier snow melt. However, the assumption that a favorable slope aspect implies a higher treeline position was not confirmed for a large sample of treeline positions in the Swiss Alps (Paulsen and Körner, 2001). These authors suggested that air temperatures in tree tops and shaded soil temperatures at the upper limit of the closed forest do not differ among various slope aspects.

In the present study we focused on the question whether in the High Sudetes (part of the Hercynian Mountains of Central Europe; Grabherr et al., 2003) the highest positions of the alpine treeline occurred in relatively favorable places in terms of potential heat load (*sensu* McCune and Keon, 2002). In addition, we were wondering if there are significant differences in soil and air temperatures along the treeline ecotone on opposite slopes. The initial hypothesis was that in a closed-canopy forest, soil temperatures would not vary substantially among localities with different exposure to solar radiation because of canopy shading (Paulsen and Körner, 2001). If this assumption were correct, the highest positions of the closed-canopy forest should not necessarily occur on slopes with favorable aspect. We further expected that in Norway spruce clonal groups (or solitary trees) above the limit of the closed forest, the warming of the unshaded margins of the spruce groups would be apparent and root zone soil temperatures would thus be higher in favorable aspects.

Methods

STUDY AREA

The highest elevations of the High Sudetes are the only islands of natural alpine forest-free areas between the Scandes in the north and the Alps and West Carpathians in the south (Grabherr et al., 2003; Jeník and Štursa, 2003) (Fig. 1a). The High Sudetes are old Hercynian mountain ranges, the highest of which are the Giant Mountains (the highest peak Sněžka, 1602 m a.s.l.)

1523-0430/08 $7.00

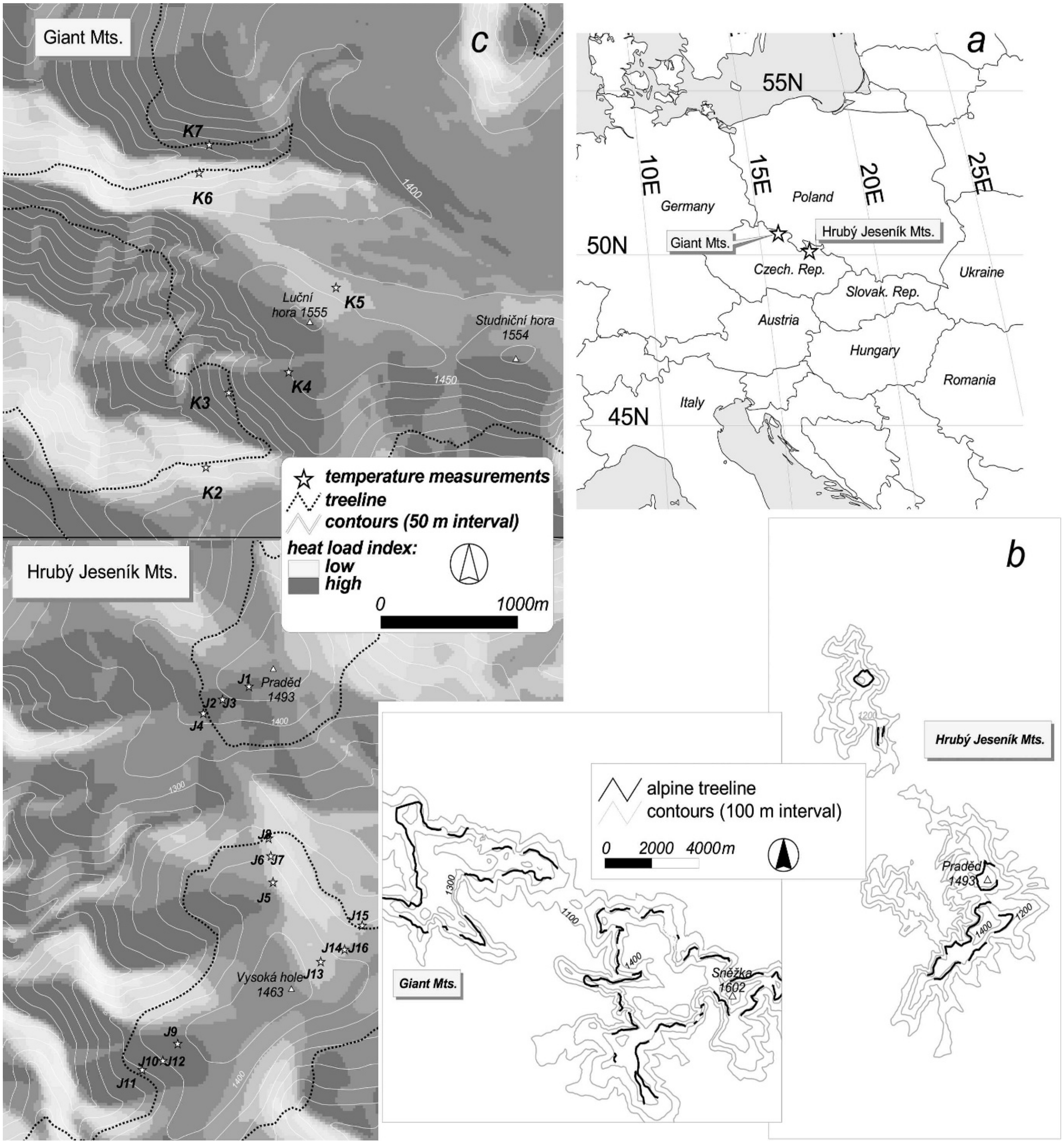

FIGURE 1. Geographical position of the study area (a), the analyzed part of the alpine treeline (b), and the location of individual sites with temperature dataloggers (c).

and the Hrubý Jeseník Mountains (the highest peak Praděd, 1492 m a.s.l.). They consist of high-elevation planated surfaces built by granite, gneiss, and mica schist.

The study area is characterized by relatively high precipitation (around 1300–1500 mm yr^{-1}). Average annual temperatures range from 0.1°C in the highest parts of the Giant Mountains to 1.1°C in the Hrubý Jeseník Mountains. The alpine treeline extends from several tens to several hundreds of meters below the summits, and is thus influenced by the extreme wind conditions associated with locations close to the summits. High winter precipitation (150 to 300 cm deep snow pack) and frequent rime are among further stress factors limiting tree distribution in the High Sudetes (Jeník, 1961; Migala et al., 2002). The alpine treeline is formed by Norway spruce (*Picea abies* [L.] Karst.), and then the ecotone grades either into dwarf pine (*Pinus mugo* Turra) growths in the Giant Mountains or into alpine grasslands (Giant Mountains and Hrubý Jeseník Mountains). The actual treeline position is situated at approximately 1230 m a.s.l. on average in the Giant Mountains and at 1310 m a.s.l. in the Hrubý Jeseník Mountains (Treml and Banaš, 2000).

The extent of the forest-free area has been strongly influenced by humans, who enlarged it in the past through deforestation, pasture, and hay making (Jeník and Lokvenc, 1962; Jeník and Hampel, 1992). After the cessation of direct human influence (60 to 80 years ago), the alpine timberline advanced to its present-day position either by the natural regeneration of Norway spruce or by planting. An extensive part of the alpine treeline ecotone is recently considered not to be anthropogenically disturbed in terms of its current position (Jeník and Hampel, 1992; Treml and Banaš, 2000).

ANALYSIS OF THE RELATIONSHIPS BETWEEN ALPINE TREELINE POSITION AND POTENTIAL HEAT LOAD

To find out whether the highest positions of the alpine treeline (defined *sensu* Körner, 1999) preferably occur in parts of the relief that are favorable in terms of temperature (favorable slope aspect), the calculated heat load of a site was compared with the altitude of the relevant part of the alpine treeline. First, the position of the closed forest was determined by supervised classification of contemporary spectrozonal orthorectified aerial images with 0.3 m resolution (RGB color scheme with a near-infrared channel, Hrubý Jeseník Mountains) or panchromatic orthorectified aerial images of the same resolution (RGB color scheme, Giant Mountains). Classification was then visually inspected on rectified aerial images. To classify an area as "forest," the minimal tree cover had to be ≥50% in a 10 × 10 m square. Then, the alpine treeline was modeled as a continuous line connecting the highest parts of the forest on slopes with different aspect. Aspect was taken as "different" if it changed more than 5 azimuth degrees. In other words, slopes were sectioned according to their aspect every 5° and the highest outposts of forest on adjacent slope sections were consequently connected. The accuracy of the treeline delimitation was verified in the field using a GPS device. Areas where natural factors (avalanches, block fields) or anthropogenic influence (in the surroundings of mountain huts) evidently lowered the treeline were excluded (Fig. 1b). Moreover, to remove those treeline positions affected by wind, we excluded such parts of the treeline which lie less than 50 m of elevation below the summits.

Further, the resulting line connecting the highest outposts of forest was divided into 100-m-long sections, and average altitude and heat load were then determined for each section. The values were set on the basis of the 20-m grid terrain model. The grid of potential heat load was calculated as the heat load index (McCune and Keon, 2002). This index is a more appropriate heat proxy than other indices which usually model direct irradiation (for example Pierce et al., 2005; McCune, 2007). The value of heat load index is relative, depending on the slope orientation, the slope gradient, and the latitude. The aspect was first "folded" about the NE–SW line:

$$\text{Folded aspect} = |180 - |\text{aspect} - 225||. \tag{1}$$

Values of the folded aspect were converted from decimal degrees to radians. Then, the following equation with constants and coefficients applicable for the 30–60° latitudinal range and slopes not steeper than 60° was used according to McCune and Keon (2002):

$$\begin{aligned}\text{Heat load index} = {} & 0.339 + 0.808 * \mathrm{COS}(\text{latitude}) * \mathrm{COS}(\text{slope}) \\ & - 0.196 * \mathrm{SIN}(\text{folded aspect}) * \mathrm{SIN}(\text{slope}) \\ & - 0.482 * \mathrm{COS}(\text{folded aspect}) * \mathrm{SIN}(\text{slope}).\end{aligned} \tag{2}$$

Computations were performed using AVENUE script (ESRI, 2002) compiled by Parks (2003).

Subsequently, the Pearson correlation coefficient between heat load index and treeline elevation was calculated. In addition, differences in heat load values within the elevation quartiles were checked using ANOVA.

DIRECT TEMPERATURE MEASUREMENTS

Two vertical transects across a natural alpine treeline ecotone were chosen in the area of Praděd–Vysoká Hole (Hrubý Jeseník Mountains), and the soil temperature and air temperature at tree tops of selected Norway spruce individuals were measured on slopes with favorable (S–SW) and unfavorable (N–NW) orientations (Fig. 1c). Measurements were carried out in three locations with regard to the alpine treeline ecotone: (1) at the upper limit of the occurrence of solitary trees/clonal groups with a minimum height of 2 m (e.g. "outpost tree groups"), (2) in clonal spruce groups at the upper limit of trees higher than 5 m (i.e. tree limit defined by Jeník and Lokvenc, 1962), and (3) at the limit of the closed forest (Table 1). While the outpost spruce groups were usually formed by 3 to 6 upright woody stems, the number of trees in tree groups in the middle part of a transect was markedly higher (6 to 11). The clonal groups in corresponding positions of the transects had similar altitude as well as physiognomy (height of trees, number of upright stems, diameter).

To compare temperatures of soil not shaded by trees, stands dominated by *Calamagrostis villosa* were chosen which were situated in open spaces of the alpine forest-free area close to groups of 5-m-high spruce (Table 1). Measurements were also carried out in six localities in the eastern part of the Giant Mountains. In the Hrubý Jeseník Mountains the treeline was situated 70–110 m below summit plateaus at slopes with analyzed transects. In the Giant Mountains the elevation distance between summits and treeline position was slightly higher (110–220 m). Except for the highest measurement points (upper limit of 2-m-high trees), tree groups or solitary trees were not significantly deformed by wind action (presence of prominent flag trees, etc.).

Measurement points have been located in parts of the alpine treeline with either stable (transect "B," sites K6 and K7) or ascending tendency (transect "A," sites K3 and K4; Table 1) for the last 60 to 70 years (Treml, 2007). The elevation of the treeline at these sites is 40 to 100 m higher than the average treeline position. With respect to the significantly higher positions of the treeline at most measured localities, we suppose that these studied sections of the alpine treeline ecotone are probably temperature limited. However, sites K7 and K6 were exceptional, because the treeline at these slopes is depressed by deep snow accumulations, sliding snow, and small-scale avalanches. Until the end of the 19th century, the sites were under direct human influence, either by grazing (Hrubý Jeseník Mountains) or by hay production (both mountain ranges; Jeník and Hampel, 1992).

Temperature sensors with an accuracy of ±0.2°C connected to dataloggers EMS MINIKIN (produced by Environmental Measurement Systems, Inc.) were used. Soil temperatures were measured 10 cm under the surface, i.e. approximately at the root growth zone (Holtmeier, 2003; Körner and Paulsen, 2004;

TABLE 1

Characteristics of the measurement points in the alpine treeline ecotones in the High Sudetes (see also Fig. 1).

Transect	Site code (Fig. 3)	Site characteristics	Elevation (m a.s.l.)	Slope aspect	Slope inclination (degrees)	The beginning of the growing season 2006/2007
A	J1	highest positioned spruce groups > 2 m	1468	SW	10	16.5./20.5.
	J2	tree groups with trees > 5 m	1443	SW	11	9.5./20.5.
	J3	treeless area within the zone of tree groups > 5 m	1443	SW	11	
	J4	trees below the closed-forest limit	1411	SW	12	19.5./14.5.
	J5	highest positioned spruce groups > 2 m	1429	NE	13	13.5./20.5.
	J6	tree groups with trees > 5 m	1390	NE	14	16.5./20.5.
	J7	treeless area within the zone of tree groups > 5 m	1390	NE	14	
	J8	trees below the closed-forest limit	1361	NE	17	17.5./19.5.
B	J9	highest positioned spruce groups > 2 m	1436	SW	10	20.5.
	J10	tree groups with trees > 5 m	1400	SW	15	11.5.
	J11	trees below the closed-forest limit	1348	SW	19	6.5.
	J12	treeless area within the zone of tree groups > 5 m	1399	SW	15	
	J13	highest positioned spruce groups > 2 m	1424	NE	12	18.5.
	J14	tree groups with trees > 5 m	1391	NE	12	20.5.
	J15	trees below the closed-forest limit	1355	NE	14	19.5.
	J16	treeless area within the zone of tree groups > 5 m	1391	NE	12	
KA 1	K2	trees below the closed-forest limit	1300	N	31	
	K3	trees below the closed-forest limit	1304	S	28	
KA 2	K4	highest positioned spruce groups > 2 m	1491	S	11	
	K5	highest positioned spruce groups > 2 m	1477	N	16	
KA 3	K6	trees below the closed-forest limit	1218	N	32	
	K7	trees below the closed-forest limit	1229	S	32	

Maděra, 2004). Sensors were calibrated by measuring the temperature of water chilled with ice (0°C) to determine their accuracy, which varied from 0 to 0.1°C. All sensors were placed under an equally thick layer of plant litter and in the same soil horizon (Ah) of fine-grained soil with 10 to 20% volume of debris. Localities showed similar moisture conditions. They were situated in sloping, but not concave or convex parts of the surface. This soil temperature measurement design enabled us to assume the same depth-temperature gradient in all monitored areas. Sensors were installed at places where the soil surface was shaded by branches all day. In two locations (sites J5 and J9; Table 1), soil temperatures were alternatively measured at two neighboring spruce groups. Difference in average temperature was 0.1°C, which may have been caused by poorly located sensors, or different soil characteristics.

To measure air temperature, hanging EMS MINIKIN sensors with a radiation shield were used. The sensors were always placed on the northern side of the trunk, close to the tree top. Only trees with tops not damaged by mechanical breakage were chosen.

Temperatures were recorded at 1-hour intervals. Average temperatures from the monitored period and average daily temperatures ($\Sigma T_{0-23}/24$) were used as basic temperature characteristics. The length of measured temperature series was different for technical reasons, and therefore only periods measured simultaneously were compared. Temperature measurements were carried out from June 2006 to October 2007 at most locations. Records were taken during two growing seasons. Data from winter season were also included in the case of the Hrubý Jeseník Mountains (winter seasons 2005/2006 and 2006/2007, transect A; winter season 2006/2007, transect B).

To determine the winter temperature characteristics of the alpine treeline ecotone the following indices were evaluated: average temperature of the period with daily means of soil temperature lower than 3.2°C (e.g. dormancy period), and number of days with average temperature lower than 0°C. The beginning of growing season was defined as the beginning of a continuous period with mean daily soil temperature higher than 3.2°C (Körner and Paulsen, 2004).

RELATION BETWEEN HEAT LOAD AND MEASURED TEMPERATURES

For each measurement point, potential heat load was analyzed (see above) for the surrounding area with a 10-m radius. Subsequently, relationships between measured air and soil temperatures and the potential heat load of the site were assessed. Evaluation was carried out using the Pearson correlation coefficient either for all sites together or for individual types of sites. To account for the influence of different elevations, all temperature values were normalized to an altitude of 1000 m a.s.l. with the use of a vertical temperature lapse of 0.73°C/100 m for average air temperatures in the growing season. The lapse value was calculated from the data measured in Velká Kotlina (1175 m a.s.l.) and in Praděd (1493 m a.s.l.) (Lednický et al., 1973), which are very close to the studied transects in the Hrubý Jeseník Mountains. A lower temperature lapse of 0.4°C/100 m was applied to soil temperatures, according to data from Germany, where altitudinal gradients of summer soil temperature are 0.2–0.4°C lower than gradients of air temperatures (Green and Harding, 1980). Unfortunately, local soil temperature lapse values are not known.

Results

ALPINE TREELINE POSITION AND HEAT LOAD

In the monitored alpine treeline sections, only a slight linear relationship was found between the elevation of the treeline and the potential heat load of the site (the Giant Mountains: $r = 0.29$, $p < 0.05$; Hrubý Jeseník Mountains, $r = 0.24$, $p < 0.05$). However, if we consider the distribution of potential heat load values in four

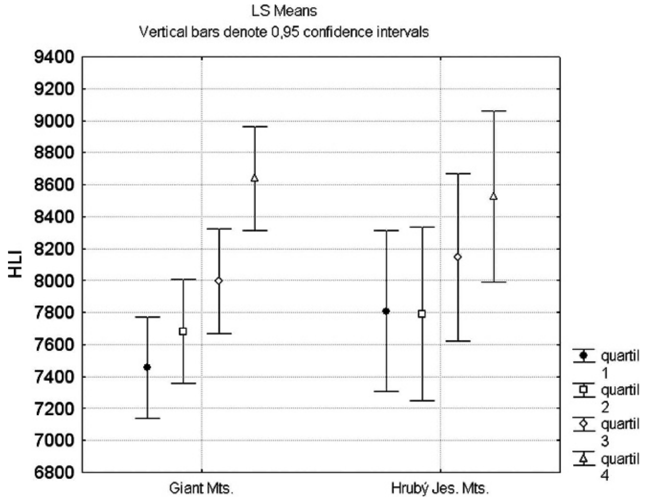

FIGURE 2. Least squared means with confidence intervals for potential heat load values (HLI) in altitudinal quartiles of sections of the alpine treeline (1—lowest sections … 4—highest sections).

statistical quartiles of the treeline altitudes, some regular patterns can be found in both mountain ranges (Fig. 2).

The highest sections of the alpine treeline are more likely situated in favorable parts of slopes in terms of temperature. The differences in potential heat load of treeline sections in individual quartiles are significant only in the case of the Giant Mountains (ANOVA, $F = 15.8$, $p < 0.05$) and not for the Hrubý Jeseník Mountains ($F = 2.3$, $p = 0.07$).

MEASURED TEMPERATURES, HEAT LOAD, AND SITE POSITION IN THE ECOTONE

Very similar temperatures were found at both the favorable and unfavorable slope aspects. This was true not only for the sites situated at the upper limit of the closed forest but even for the tree groups above the treeline. Nevertheless, sites on south-facing slopes seem to be slightly warmer than those on north-facing slopes (Fig. 3). More pronounced differences regarding both air and soil temperatures were found in the "B" transect, with steeper slopes and thus more differing heat load. Root zone soil temperatures of south-facing slopes usually increased more (0.23°C on average if outliers are removed) due to exposure effect than air temperatures are (0.13°C on average). In the highest outposts of tree groups, the differences of soil temperatures between both slope orientations are ambiguous. Higher temperature values in a given measure point are seen in both the favorable and unfavorable slope orientations, which could be caused by local microclimatic conditions. The almost 0.5°C warmer southern slope at sites K6 and K7 is somewhat outstanding due to fragmentation of the forest by avalanches and block fields.

As expected, soil temperatures are more favorable in free, unshaded areas (Fig. 3) and these places also show significantly higher exposure effects on temperatures.

Air temperatures at the tree tops are practically identical for all positions. A slight difference in the "B" transect (at the upper margin of the closed forest and in the tree groups above the treeline) as well as in the closed forest stands K2 and K3 (Giant Mountains) is caused by markedly steeper slopes in comparison with the "A" transect. Thus, the radiation heating of the surface may be more intense and the heated atmospheric layer above the surface may be thicker. At the highest point of the transect ("outpost tree groups"), where stronger air flow may be expected, this difference was not seen.

A comparison of the distribution of soil and air temperatures (after eliminating the elevation bias) with relevant values of potential heat load shows that the variation in air temperature is markedly lower compared to soil temperatures (Fig. 4), with the exception of the uppermost tree groups at the K4 and K5 measurement points. Those sites are probably strongly affected by their position close to the exposed summit. Nevertheless, it seems that under similar conditions of potential surface heating, temperatures of soil shaded by spruce branches differ more than the air temperatures at the tree tops. No relation between heat load and soil temperatures could be observed even if outliers are removed. Regarding air temperatures, there is a moderate correlation with the potential heat load of the site ($r = 0.64$, $p < 0.05$) if outlaying data of the K4 and K5 measurement points are eliminated. This relation is more significant within treeline sites themselves ($r = 0.73$, $p < 0.1$) and probably also at tree groups above the treeline ($r = 0.84$; only four sites were analyzed). No correlation between air temperatures and heat load was found in outpost tree groups ($r = 0.17$).

TEMPERATURE DURING THE COLDEST PART OF THE YEAR, BEGINNING OF THE GROWING SEASON

Measurements of soil winter temperatures indicated their high inter-annual variability which is probably related to variations in snow pack amount. While temperatures and frozen

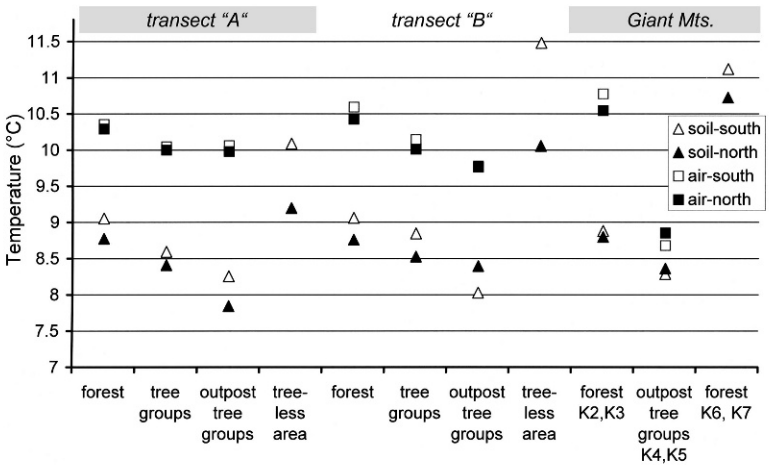

FIGURE 3. Average soil and air temperatures in the period 8 June to 10 October 2006 and 16 June to 12 October 2007. Temperatures of transect "A" sites are modified to the same altitude of the respective measurement points using temperature lapse 0.73°C/100 m (air temperatures) and 0.4°C/100 m (soil temperatures).

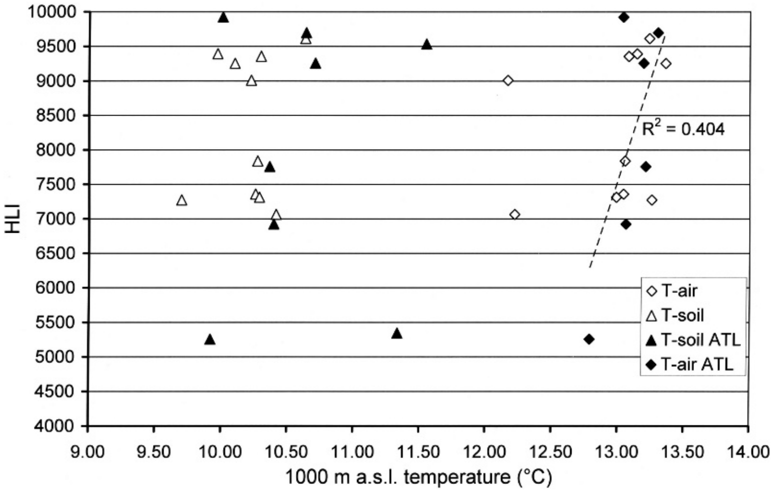

FIGURE 4. Mean soil and air temperature modified by altitudinal lapse to 1000 m a.s.l. in relationship to the potential heat load (HLI); values marked ATL refer to the upper limit of the closed forest.

soil period of related sites were similar during the snow-rich winter of 2005/2006, soils of south-facing slopes were frozen longer as well as temperatures were generally lower there than those on north-facing slopes in the snow-poor winter of 2006/2007 (Fig. 5). On south- and southwest-facing slopes the snow was periodically melting and thus the unprotected soil was more exposed to freezing. This is reflected by the numbers of days with temperatures below 0°C.

The pattern of the beginning of the growing season also was affected by snow amount. In winter 2005/2006 the growing season started later in the closed forest than in the tree groups (Table 1), and this delay was more pronounced on southwestern slopes. While snow melt was faster on treeless sites on south-facing slopes, no differences were observed in the closed forest where snow cover was shaded. On the contrary, in 2007 the growing season started first at the lower elevation parts of southwest-facing slopes (upper limit of the closed forest, tree groups; Table 1). We suppose that this distinct pattern of the growing season beginning was due to the overall low amount of snow in 2007. It probably also melted quickly in the forest, where the amount of snow had been even lower than in forest-free areas.

Discussion

HIGHEST POSITIONS OF THE ALPINE TREELINE

Only a slight dependence on the potential heat load was identified for the alpine treeline in the High Sudetes. In other words, a higher alpine treeline does not necessarily have to be situated in sites that are potentially more heat favorable. This corresponds to findings from the Central Alps (Paulsen and Körner, 2001). The very highest positions of the treeline, however, were generally located on southwest-facing slopes in both ranges studied in the High Sudetes. This finding shows that favorable slope aspect may shift the limit of the forest up in altitude.

Maximum elevated treeline outposts situated on south- to southwest-facing slopes originated probably in consequence of higher direct radiation. The radiation heating of the surface has a positive impact, especially on low-stature vegetation (Körner, 1999), including conifer seedlings, unless it is accompanied by extreme surface desiccation or radiation cooling at night (Germino et al., 2002). Because surfaces oriented towards the south quadrant are heated more, an easier survival of seedlings in those areas (with enough precipitation to prevent soil drying) can be assumed. This also implies a faster upward shift of the forest on favorable slope aspects as a consequence of the general temperature increase (Holtmeier and Broll, 2005). On the other hand, it is not clear to what extent long-term human influence (present at least since the 15th–16th centuries; Lokvenc, 1995; Jeník and Hampel, 1992) has resulted in this distribution of the alpine treeline sections within the elevation intervals. However, during the past 60 years human intervention in the alpine treeline has not been substantial.

In the High Sudetes, the fact that the uppermost positions of the alpine treeline are found on southwestern slopes of the highest peaks (Sněžka, Praděd; see Treml and Banaš, 2000) may also be important. On the sides of these highest summits, the treeline runs rather in the middle parts of the slopes, which are more favorable in terms of temperature than the upper margins (Aulitzky, 1967; Obrebska-Starkel, 1984). In the case of the maximum treeline position in the Giant Mountains, situated on the leeward side of the anemo-orographic system, the mesoclimatic specificity of the locality may also play a part (Jeník and Lokvenc, 1962). Those spatial characteristics are disregarded by the heat load index. Nevertheless, we believe that they play a role only at some specific locations, and use of the heat load index is thus generally appropriate. Regarding the above-mentioned suggestions, the maximum treeline positions in the High Sudetes result probably from favorable slope exposure to solar radiation and advantageous position in the middle parts of slopes.

TEMPERATURES IN THE SITES WITH DIFFERENT HEAT LOAD

Our observation that there is no clear relation between treeline elevation and modeled heat load may be explained by the similar temperatures found in the closed forest, so that insolation-induced favorability becomes unimportant. This has been suggested by Paulsen and Körner (2001). Under the closed-canopy forests, only minor soil temperature differences were found for opposite slope aspects; nevertheless, south-oriented slopes were usually moderately warmer. Similarly, in the tree groups above the treeline, soil temperatures between the opposite slopes differ only slightly (not more than 0.3°C). South-oriented slopes are found to be warmer in this case as well. Weak temperature differences in tree groups situated on opposite slopes are fairly surprising, as it has been assumed that a closed canopy forest would have greater influence on soil cooling than more isolated tree groups (Körner, 1999), which are heated by the surrounding surface (Holtmeier and Broll, 1992). When comparing non-shaded treeless sites, the soil is much warmer on slopes of the south-facing quadrant.

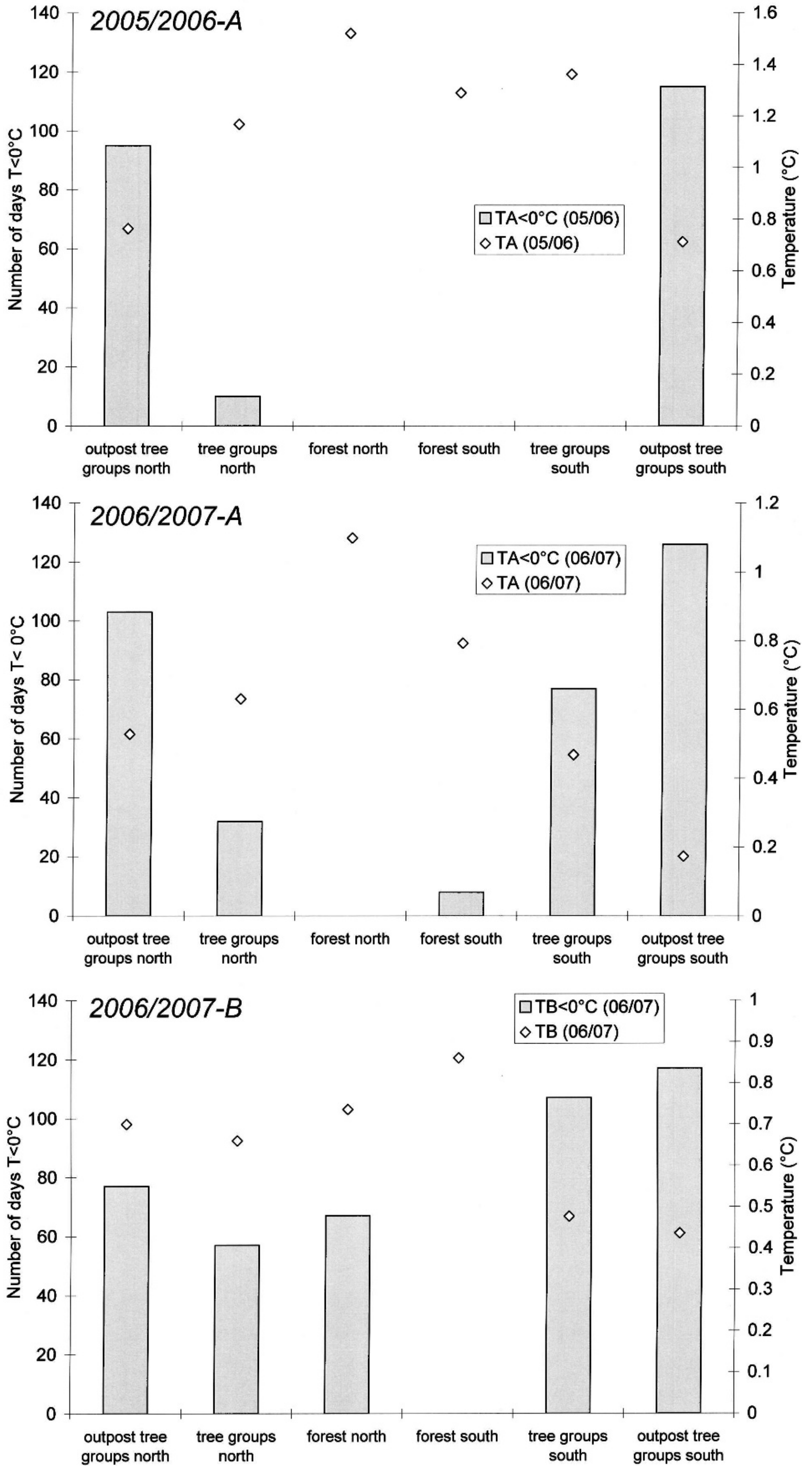

FIGURE 5. Number of days with an average soil temperature lower than 0°C (TA, TB < 0°C), and average temperature in the dormancy period (TA, TB). Data from winter seasons 2005/2006 and 2006/2007. Hrubý Jeseník Mountains, transects A and B.

The above-mentioned results indicate that forest splitting into tree groups thus may not be explained simply by an "effort" to improve temperature conditions, even if part of the root system extends over the margins of the groups (Holtmeier, 2003; Maděra, 2004). Another possible explanation of this phenomenon may be the hypothesis that tree groups above the closed-forest limit are remnants of the former closed forest, or they may be consequences of favorable climatic oscillations, which enable trees to establish themselves above the treeline (Slatyer and Noble, 1992). In any case, this suggestion needs to be supported by more extensive data sets.

Air temperatures varied among studied sites less than soil temperatures. This confirms the suggestion that air temperatures at tree tops are coupled rather to free atmosphere temperature (Paulsen and Körner, 2001) and are less influenced by local topographic or vegetation irregularities. On favorably exposed, especially steeper, slopes, there was a greater heating of the active surface (in a meteorological sense; Geiger et al., 2003), which also influenced temperature at the spruce tree tops. More pronounced are the differences in air temperatures near tree tops at sites situated in closed forest, which simultaneously display great differences in heat load. This suggests that at the closed-forest margins, heating of the active surface apparently occurred—the air in favorable slope aspects could have been heated from the tree tops of the closed-forest areas (external active surface layer according to Geiger et al., 2003).

It could be concluded that measured temperatures generally show only weak exposure effects not comparable with a treeless area. A similar pattern was recently found for canopy temperatures also by Rossi et al. (2007).

MODIFICATIONS OF DOMINANT TEMPERATURE PATTERNS

There were some exceptions from the above-mentioned temperature patterns regarding both soil and air temperatures. They generally result from site specific conditions. Great differences in soil temperatures at sites K6 and K7 (Důl Bílého Labe valley in the Giant Mountains) could be attributed to the character of the treeline there, which consists of narrow protruding belts of trees among avalanche tracks, debris flows, and block fields. Trees often do not branch in the lower part of their trunks, so direct solar radiation can penetrate into the stands (though the measurement sensors were shaded by branches). This can contribute to a generally warmer microclimate in the inner space of the forest on the southern slope.

On the other hand, ambiguous variations in temperatures on sites with opposite exposure to solar radiation were found in the highest outposts of tree groups. Local microclimatic differences exerted a more significant influence on soil temperatures. Therefore, there was a greater variation in temperatures among sites with both favorable and unfavorable slope aspects, in both directions (both higher and lower temperatures in S–SW–facing slopes compared to N–NE–facing slopes). Further, more intense air flow completely leveled air temperatures near tree tops. Prevailing strong winds (Jeník, 1961) and frequent fogs (Blas and Sobik, 2000) in the summit areas generally influence the uppermost outposts of the alpine treeline ecotone in the High Sudetes, limiting atmospheric heating near the surface layer. This is because the alpine treeline runs relatively close below the exposed summit plateaus.

When interpreting temperature measurements, it must be noted that the growing season in 2006 was considerably warmer than the long-term average in the Hrubý Jeseník Mountains and Krkonoše Mountains (about 1.9°C higher temperature between May and October 2006 than the mean from 1961–1990; Czech Hydrometeorological Institute, 2007). In the monitored period, however, there was both radiative-type weather (most of July and September) and cloudy weather with high precipitation (August). Therefore, we suppose that the differences recorded among individual sites do not differ from periods with normal meteorological characteristics. The growing season in 2007 was normal regarding temperatures (Czech Hydrometeorological Institute, 2007).

TEMPERATURES IN THE COLDEST PART OF THE YEAR

Not only growing season temperatures but also winter conditions may considerably influence the position and dynamics of the alpine treeline ecotone (Meshinev et al., 2000; Kullman, 2007). We recorded a distinct pattern of soil temperatures during both measured winter seasons, which could be ascribed to differences in quantity of snow. Season 2005/2006 was characterized by moderately cold temperatures and an extremely high snow pack, whereas winter season 2006/2007 was mild with a low snow pack.

The growing season of 2006 began notably later at the closed-forest limit than in higher-positioned tree groups. Nevertheless, the highest positions of the tree groups displayed a much more extreme development of winter soil temperatures and longer period with frozen soil. This is mainly due to snow distribution, since snow accumulates at the border of the closed forest (Štursa et al., 1973; Körner, 1999; Holtmeier, 2003). On the contrary, the margins of summit plateaus, where the outpost tree groups are located, are wind swept, and thus deeper freezing of soil is facilitated (Harčarik, 2002). Earlier snow melting was rather prominent in tree groups above the closed forest limit on south-facing slopes, which was also reflected in higher soil temperatures in this part of the ecotone.

A delayed beginning of the growing season in closed forest was not recorded during the winter of 2006/2007. Snow melted earlier there due to the low depth of the snow pack. The low snow pack also repeatedly melted during the winter, especially on south-facing slopes. Thus, the bare ground was not protected against freezing, and consequently lower soil temperatures as well as a higher number of days with frozen soil were recorded on south-facing slopes compared to north-facing slopes.

It seems that the generally earlier beginning of the growing season on slopes with favorable exposure to solar radiation (Holtmeier, 2003) may not be significant in closed forest sites. Further, the potential advantageousness of slopes with high heat load is weakened during snow-poor winters because of the exposure of snow-free patches to deep freezing.

Conclusions

In the High Sudetes, the highest positions of the alpine treeline are situated on slopes with favorable exposure to solar radiation; however, in general the position of the treeline correlates only slightly with the potential heat load of the site. This implies that there really could be some exposure effects on maximum treeline positions. Nevertheless, as soon as forest or even tree groups are established, differences in growing season soil temperatures in the root zone between favorable and unfavorable slope aspects are reduced. Tree crowns shading the underlying surface impede exposure effects on soil temperatures which are pronounced on treeless sites. Similarly, air temperatures near the tree tops are not significantly affected by slope aspect due to their distance from the heated ground. Besides growing season temperatures, soil temperature measured in the winter period do not seem to be generally more favorable at south-facing slopes, either. Ascertained growing season temperature patterns indicate that only low stature trees or seedlings could profit from strong exposure effects. In this context, the maximum treeline positions situated on southwest-facing slopes could be explained.

We are aware that these findings result from relatively short-term measurements and the specific conditions found in mountains where the alpine treeline runs close to planated summit surfaces on relatively gentle slopes. Nevertheless, we believe that the temperature patterns recorded at lower parts of the alpine treeline ecotone could be generally valid also for other temperate mountains.

Acknowledgments

This research would not have been possible without the support of grant projects VaV MZP SM/6/70/05 and MSM 0021620831. The authors wish to thank Prof. Jan Jeník for helpful comments on earlier versions of the manuscript and to David Hardekopf for his help with the translation. Two anonymous reviewers and the associate editor are acknowledged for their detailed suggestions and comments. Agencies of the Krkonoše National Park and Jeseníky Landscape Protected Area are appreciated for their technical support and for permission to conduct research in strictly protected areas.

References Cited

Aulitzky, H., 1961: Lufttemperatur und Luftfeuchtigkeit. *Mitteilung der Forstlichen Bundesversuchsanstalt Mariabrunn*, 59: 105–125.

Aulitzky, H., 1967: Lage und Ausmass der ''warmen Hangzone'' in einen Quertal der Innenalpen. *Annales Meteorologicae*, 3: 159–165.

Blas, M., and Sobik, M., 2000: Fog in the Giant Mountains and selected European massifs. *Opera Corcontica*, 37: 35–46 (in Polish).

Czech Hydrometeorological Institute, 2007: *Meteorological Data for the Czech Republic between 1961 and 2007*. (http://www.chmi.cz/meteo/ok/infklim.html) (in Czech).

ESRI, 2002: *Using Avenue*. Redlands: Environmental Research Institute, 239 pp.

Geiger, R., Aron, R. H., and Todhunter, P., 2003: *The climate near the ground*. Langham: Rowman & Littlefield Publishers, 584 pp.

Germino, M. J., Smith, W. K., and Resor, C., 2002: Conifer seedling distribution and survival in an alpine-treeline ecotone. *Plant Ecology*, 162: 157–168.

Grabherr, G., Nagy, L., and Thompson, D. B. A., 2003: An outline of Europe's alpine areas. *In* Nagy, L., Grabherr, G., Körner, Ch., and Thompson, D. B. A. (eds.), *Alpine biodiversity in Europe.* Ecological Studies. Berlin Heidelberg New York: Springer-Verlag, 3–12.

Grace, J., 1989: Tree lines. *Philosophical Transactions of the Royal Society, London Ser. B*, 324: 233–245.

Green, F. H. W., and Harding, R. J., 1980: Altitudinal gradients of soil temperatures in Europe. *Transactions of Institute of British Geographers*, 5: 243–254.

Harčarik, J., 2002: Microclimatic relationships of the arctic-alpine tundra. *Opera Corcontica*, 39: 45–68.

Holtmeier, F. K., 2003: *Mountain timberlines. Ecology, patchiness and dynamics*. Dordrecht: Kluwer, 370 pp.

Holtmeier, F. K., and Broll, G., 1992: The influence of tree islands on microtopography and pedoecological conditions in the forest-alpine tundra ecotone on Niwot Ridge, Colorado Front Range, U.S.A. *Arctic and Alpine Research*, 24: 216–228.

Holtmeier, F. K., and Broll, G., 2005: Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. *Global Ecology and Biogeography*, 14: 395–410.

Jeník, J., 1961: *Alpine vegetation of the High Sudetes: theory of Anemo-Orographic systems*. Prague: Nakl. NČSAV, 409 (in Czech).

Jeník, J., and Hampel, R., 1992: *Die waldfreien Kammlagen des Altvatergebirges (Geschichte und Ökologie)*. Stuttgart: MSSGV, 104 pp.

Jeník, J., and Lokvenc, T., 1962: Die alpine Waldgrenze im Krkonoše Gebirge. *Rozpravy Československé Akademie věd, Praha, ser. Math.–natur.*, 72(1): 1–65.

Jeník, J., and Štursa, J., 2003: Vegetation of the Giant Mountains, Central Europe. *In* Nagy, L., Grabherr, G., Körner, Ch., and Thompson, D. B. A. (eds.), *Alpine biodiversity in Europe.* Ecological Studies, 167. Berlin Heidelberg New York: Springer-Verlag, 47–51.

Körner, Ch., 1999: *Alpine plant life: functional plant ecology of high mountain ecosystems*. New York: Springer, 290 pp.

Körner, Ch., and Hoch, G., 2006: A test of treeline theory on a montane permafrost island. *Arctic, Antarctic, and Alpine Research*, 38: 113–119.

Körner, Ch., and Paulsen, J., 2004: A world wide study of high altitude treeline temperatures. *Journal of Biogeography*, 31: 713–732.

Kullman, L., 2007: Tree line population monitoring of *Pinus sylvestris* in the Swedish Scandes, 1973–2005: implications for tree line theory and climate change ecology. *Journal of Ecology*, 95: 41–52.

Lednický, V., Pivoňová, R., and Ujházy, F., 1973: Temperature of the air on Praděd. *Campanula*, 4: 175–202 (in Czech).

Lokvenc, T., 1995: Analysis of anthropogenic changes of woody plant stands above the alpine timber line in the Krkonoše Mts. *Opera Corcontica*, 32: 99–114 (in Czech).

Maděra, P., 2004: Growth and population strategy of Norway spruce (Picea abies (L.) Karsten) at alpine timberline in the Praděd nature reserve, Větrná louka site. *Geobiocenologické spisy*, 10: 51–70 (in Czech).

Malyshev, L., and Nimis, P. L., 1997: Climatic dependence of the ecotone between alpine and forest orobiomes in southern Siberia. *Flora*, 192: 109–120.

McCune, B., and Keon, D., 2002: Equations for potential annual direct incident radiation and heat load. *Journal of Vegetation Science*, 13: 603–606.

McCune, B., 2007: Improved estimates of incident radiation and heat load using non-parametric regression against topographic variables. *Journal of Vegetation Science*, 18: 751–754.

Meshinev, T., Apostolova, I., and Koleva, E., 2000: Influence of warming on timberline rising. A case study in *Pinus peuce* Griseb. in Bulgaria. *Phytocenologia*, 30: 431–438.

Migala, K., Liebersbach, J., and Sobik, M., 2002: Rime in the Giant Mts. (The Sudetes, Poland). *Atmospheric Research*, 64: 63–73.

Obrebska-Starkel, B., 1984: Reflection of the orographic patterns in the micro-and mesoclimatic conditions. *GeoJournal*, 8: 259–263.

Parks, S., 2003. Heat Load Index script (http://arcscripts.esri.com/).

Paulsen, J., and Körner, Ch., 2001: GIS-analysis of tree-line elevation in the Swiss Alps suggests no exposure effect. *Journal of Vegetation Science*, 12: 817–824.

Pierce, K. B., Lookingbill, T., and Urban, D., 2005: A simple method for estimating potential relative radiation (PRR) for landscape-scale vegetation analysis. *Landscape Ecology*, 20: 137–147.

Plesník, P., 1971: *Upper timberline in the High and Belanské Tatry Mts*. Bratislava: Nakl. SAV, 475 pp. (in Slovak).

Rossi, S., Deslauriers, A., Anfodillo, T., and Carraro, V., 2007: Evidence of threshold temperatures for xylogenesis in conifers at high altitudes. *Oecologia*, 152: 1–12.

Slatyer, R. O., and Noble, I. R., 1992: Dynamics of montane treelines. *In* Hansen, A. J., and Di Castri, F. (eds.), Landscape boundaries, consequences for biotic diversity and ecological flows. *Ecological Studies*, 92: 327–345.

Speranza, A., Hanke, J., van Geel, B., and Fanta, J., 2000: Late-Holocene human impact and peat development in the Černá Hora bog, Krkonoše Mountains, Czech Republic. *The Holocene*, 10: 575–585.

Štursa, J., Jeník, J., Kubíková, J., Rejmánek, M., and Sýkora, T., 1973: Snow cover in the west Krkonoše Mts, during the exceptional winter season 1960/1970 and its ecological significance. *Opera Corcontica*, 10: 111–146 (in Czech).

Tinner, W., and Theurillat, J.-P., 2003: Uppermost limit, extent, and fluctuations of the timberline and treeline ecocline in the Swiss Central Alps during the past 11,500 years. *Arctic, Antarctic, and Alpine Research*, 35: 158–169.

Tranquillini, W., 1979: Physiological ecology of the alpine timberline. Tree existence at high altitudes with special reference to the European Alps. *Ecological Studies*, 31: 131.

Treml, V., 2007: The effect of terrain morphology and geomorphic processes on the position and dynamics of the alpine timberline. A case study from the High Sudetes, Czech Republic. *In* Kalvoda, J., and Goudie, A. D. (eds.), *Geomorphologic variations*. Prague: P3K, 339–360.

Treml, V., and Banaš, M., 2000: Alpine timberline in the High Sudetes. *Acta Universitatis Carolinae Geographica*, 15(2): 83–99.

MS accepted May 2008