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Thermal characteristics of alpine treelines in Central Europe north of the Alps

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ABSTRACT: Alpine treeline ecotones north of the Alps in Central Europe occur in 11 mountain ranges, including the Harz Mountains (Germany), mountain chains of the High Sudetes (Czech Republic and Poland) and the Western Carpathians (Czech Republic, Poland and Slovakia). These mountains are characterized by pronounced maritime–continental gradients, large differences in the mass elevation effect, and varying distance between the treeline and summits. We evaluated how these factors influence treeline temperatures and thus treeline elevation. We compared various treeline temperature metrics for all mountain ranges in the study region both among the mountain ranges and with treeline temperatures in the Alps. Our results show that treelines along the 50th parallel increase their elevation by approximately 94 m per 100 km towards the east, a reflection of a rise in elevation of isotherms of growing season temperatures along the maritime–continental gradient and with increasing mass elevation effect. Among the majority of evaluated mountain ranges, growing season treeline temperatures did not differ significantly, suggesting identical thermal limitation of tree growth in these ranges. However, we identified 4 regions (the Harz, Králický Sněžník, Hrubý Jeseník and Velká Fatra Mountains) where the uppermost tree stands are situated below the common treeline isotherm, an indication that trees are limited by other factors (e.g. biomass loss). Based on a comparison of various treeline temperature metrics, we suggest that to reliably describe treeline climates in regions with pronounced maritime–continental gradients, it is necessary to use metrics capturing the entire growing season. Such metrics show that treeline temperatures in the study region are similar to those in the Alps.

KEY WORDS: Treeline · Sudetes · Carpathians · Harz · Alpine areas · Temperature metrics

1. INTRODUCTION

The treeline ecotone is a prominent vegetation transition zone where tree size and density progressively decrease from the upper margin of closed forest towards the treeless alpine zone (Körner 2012). On the global scale, alpine treelines (i.e. idealized lines situated approximately in the middle of the alpine treeline ecotone) are characterized by growing season air temperatures of approximately 6.7 ± 0.8°C (Körner & Paulsen 2004). However, on a regional scale, the highest tree stands are often situated at elevations lower than that of the isotherm that still allows tree growth (Macias-Fauria & Johnson 2013, Case & Duncan 2014). Increased dieback and constraints on seedling establishment and survival might prevent trees from reaching their uppermost potential elevations (Harsch & Bader 2011). Factors locally or regionally hampering the advance of trees to thermal growth-restricted positions (i.e. so-called second-order factors of treeline position; Harsch & Bader 2011) include wind action, winter desiccation, irregular distribution of snow and the effect of drought or various disturbances (Holtmeier & Broll 2007). However, differentiation between purely temperature-limited treelines and uppermost tree stands limited by climatic factors other than temperatures alone is crucial for predicting how treelines will react to increasing temperatures.

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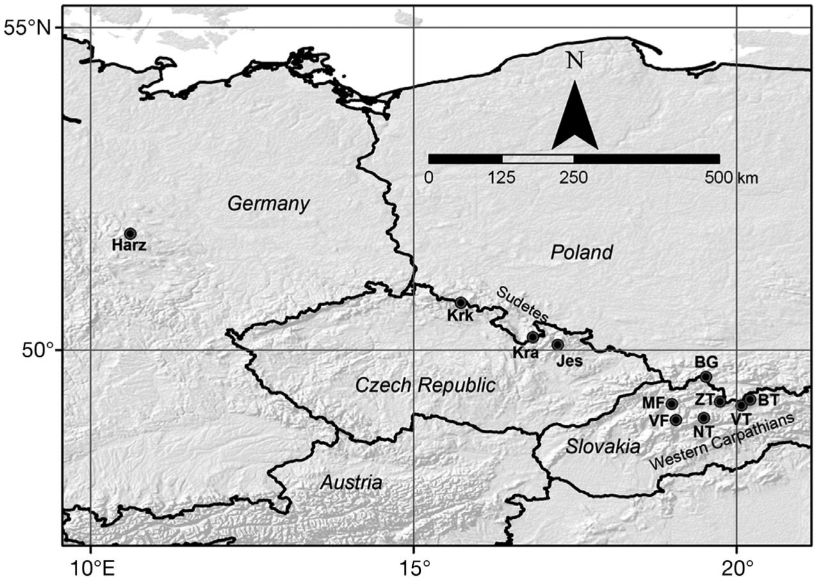

Fig. 1. Location of the mountain ranges studied in Central Europe. BG: Babia góra and Pilsko; BT: Belianské Tatry; Jes: Hrubý Jeseník; Kra: Králický Sněžník; Krk: Krkonoše; MF: Malá Fatra; NT: Nízké Tatry; VF: Velká Fatra; VT: Vysoké Tatry; ZT: Západné Tatry

Treelines are characterized by very similar thermal growing season conditions (Körner & Paulsen 2004), which are determined by multitude of geographical factors. For example, the position of isotherm that limits tree stature varies along a latitudinal gradient and also in the longitudinal direction in response to changing continentality (Paulsen & Körner 2014, Zhao et al. 2014). Further variation is attributed to the mass elevation effect, which suggests treelines are found at lower elevations in small isolated massifs compared with extensive mountain ranges (Holtmeier 1973). Tree limits near mountain summits may exist at relatively high growing season temperatures compared with true temperature-limited treelines (summit syndrome, sensu Körner 2012), because intense wind action and/or unfavourable soil conditions near summits preclude tree growth irrespective of thermal conditions (Holtmeier 2009, Takahashi 2014).

In the Central-European mountain ranges north of the Alps (hereafter CENA), the Western Carpathians, the Sudetes and the Harz Mountains have well-developed treeline ecotones (Fig. 1) (Ellenberg 1988, Grabherr et al. 2003). These mountain ranges differ by factors that affect the positions of the growing season isotherms. For example, they are situated along a west–east maritime–continental gradient (Mikolášková 2009), with some small, isolated massifs (e.g. the Harz Mountains) but also relatively extensive mountains (the Vysoké Tatry Mountains) with substantial climatic contrasts between outer and inner, windward and leeward parts of the mountain range (Konček 1974, Büntgen et al. 2007). And last but not least, the vertical distance between the uppermost tree stands and summits varies greatly, simply because summits differ in elevation.

In this study, we evaluate the thermal characteristics of treelines in CENA and compare them with published or computed temperature data for treelines in the Alps. The main objectives of this study are to: (1) find the uppermost positions of tree groups and define their climate characteristics; (2) compare temperature characteristics of CENA treelines and treelines of the Alps; and (3) determine the influence of summit syndrome and maritime-continental gradients on treeline temperatures. We hypothesize that if the treelines under study are particularly influenced by a heat deficiency, thermal metrics characterizing treeline position should have approximately the same values irrespective of the mountain range. Treeline elevation was derived from the position of the uppermost tree groups in each mountain range as the best approximation of what might be a natural (climatic) upper tree limit (rather than the result of anthropogenic disturbance).

2. METHODS

2.1. Study area

This study focuses on treeline ecotones in CENA, approximately 48–51° N and 10–20° E (Fig. 1, Table 1). Only areas with palaeoecological evidence for climate-driven forest-free zones have been included (Beug et al. 1999, Treml et al. 2006, Novák et al. 2010). The mountain ranges under study comprise Hercynian mountains with elevations ranging from 1100 to 1600 m and the Western Carpathians, which exceed 2000 m. Hercynian mountain ranges (the Harz, Krkonoše, Králický Sněžník and Hrubý Jeseník Mountains) are composed of acidic crystalline rocks, and their topography is characterized by flat summit surfaces and adjacent moderately steep slopes. The Western Carpathians include limestone lithologies (Velká, Malá Fatra, Nízké and Belianské

Table 1. Basic characteristics of each mountain range studied. Timberline elevations were derived using different methodologies. The meteorological stations listed include low-elevation stations situated at the foothills of the given mountain range and were used for the calculation of lapse rates. Asterisks denote stations used for independent calculation of lapse rates. In cases where a meteorological station was not present in the given mountain range, distances to the nearest mountain meteorological stations are provided. Average wind speed refers to data from corresponding high-elevation meteorological stations for the period 1961–1990

Mountain range	Latitude, longitude	Highest peak elevation (m a.s.l.)	Published timberline elevation	Meteorological station (elevation, m a.s.l.; distance to nearest)	Mean lapse rate Jun–Sep (°C 100 m^{-1})	Average wind speed (m s^{-1})
Harz	51°48'N, 10°37'E	1141	1100 m (Hertel & Schöling 2011)	Brocken (1140 m), Wernigerode (240 m)	0.69	12.9
Krkonoše	50°44'N, 15°44'E	1603	1340 m (Treml & Migoń 2015)	Sněžka (1602 m), Pec pod Sněžkou (816 m) *Szrenicza (1332 m), *Vysoké nad Jizerou (693 m)	0.71	14.9
Králický Sněžník	50°12'N, 16°51'E	1424	1305 m (Treml & Migoń 2015)	Praděd (1492 m), Světlá hora (593 m)	0.65	–
Hrubý Jeseník	50°05'N, 17°14'E	1491	1405 m (Treml & Migoń 2015)	Praděd (1492), Světlá hora (593 m)	0.65	9
Babia Góra	49°35'N, 19°32'E	1725	1370 m (Czajka et al. 2015a)	Oravská Lesná (780 m, 31 km) Štrbské pleso (1322 m, 51 km) Chopok (2008 m, 65 km)	0.46 0.53 0.64	–
Malá Fatra	49°10'N, 19°00'E	1709	1450 m (Plesník 1999)	Chopok (2008 m, 45 km) Štrbské pleso (1322 m, 65 km) Oravská Lesná (780 m, 11 km)	0.64 0.53 0.46	–
Veľká Fatra	48°55'N, 19°04'E	1592	1510 m (Plesník 1999)	Chopok (2008 m, 33 km) Sliač (314 m, 34 km)	0.64 0.63	–
Nízké Tatry	48°57'N, 19°30'E	2043	1550 m (Plesník 1999)	Chopok (2008 m), Liptovský Hrádok (680 m)	0.64	8.6
Západné Tatry	49°12'N, 19°45'E	2248	1550 m (Švajda et al. 2011)	Štrbské pleso (1322 m) Liptovský Hrádok (680 m) Poprad (695 m)	0.53	–
Vysoké Tatry	49°08'N, 20°13'E	2655	1715 m (Plesník 1971)	Skalnaté pleso (1778 m), Štrbské pleso (1322 m), Poprad (680 m), Tatranská Lomnica (827 m) *Kasprow wierch (1989 m), *Tatranská Polianka (975 m)	0.52	3.8
Belianské Tatry	49°14'N, 20°13'E	2152	1475 m (Plesník 1978)	Skalnaté pleso (1778 m), Tatranská Lomnica (827 m)	0.55	7.3

Tatry Mountains), flysch areas of predominantly sandstone bedrock (Babia Góra Mountains) and crystalline massifs (the Vysoké and Západní Tatry Mountains, and the central part of the Nízké Tatry Mountains). Their topography ranges from true alpine mountain ranges (the Tatras) to mountains of moderate relief (the Babia Góra Mountains). The climate of all the areas is cold and humid, with annual precipitation totals ranging from ca. 1000 mm (the Hrubý Jeseník Mountains) to 2200 mm (the Vysoké Tatry Mountains: Migała 2005, Hlavatá et al. 2011). Soils of treeline ecotones are represented by podzols, acidic nutrient-poor cambisols and rankers (on acidic crystalline bedrock and flysch) (Tomášek 1995, Granec & Šurina 1999, Hertel & Schöling 2011). Rendzina soils are common where limestone bedrock is present (Granec & Šurina 1999).

The northernmost Central-European treeline ecotone is situated in the Harz Mountains (Hertel & Schölling 2011) (Table 1). East of the Harz, the Sudetes represent an area with well-developed treeline ecotones, namely in the Krkonoše, Králický Sněžník and Hrubý Jeseník Mountains (Fig. 1) (Jeník 1961). Besides low temperatures, high-elevation tree stands in all areas mentioned above are influenced by high wind speeds and past human interventions (Jeník 1961, Beug et al. 1999, Hertel & Schöling 2011, Šenfeldr & Maděra 2011, Treml & Chuman 2015). Further east, treelines are present on Mt. Babia Góra and Mt. Pilsko in the westernmost flysch Carpathians (Fig. 1) (Kozak 2003, Czajka et al. 2015a), in the Velká and Malá Fatra Mountains (Plesník 1999) and in the broader region of the Tatras (Plesník 1971). In the majority of Western Carpathian mountain ranges, the treeline ecotone has been seriously affected by long-term cattle grazing (Plesník 1971, Plesník 1978, Boltižiar 2007). However, undisturbed treelines occur on steep, inaccessible slopes and in areas where cattle grazing ceased several decades ago and tree stands advanced to their original position (Doležal & Šrůtek 2002, Boltižiar 2007).

Treeline ecotones are formed largely by Norway spruce (*Picea abies* [L.] Karst.). Swiss stone pine (*Pinus cembra*) occurs in the treeline ecotones of the Vysoké Tatry Mountains (Plesník 1971). Prostrate dwarf pine (*Pinus mugo*), either native or planted, is also common, often forming extensive closed stands (Wild & Winkler 2008, Švajda et al. 2011). Norway spruce in treeline ecotones occurs either as seed-based individuals or in the form of groups formed by vegetative reproduction (Šenfeldr et al. 2014). Agriculture, namely grazing, hay making and man-induced fires, depressed tree stands locally by several tens to hundreds of metres (Plesník 1978, Speranza et al. 2000, Novák et al. 2010). However, during the second half of the 20th century, tree stands in most treeline ecotones regenerated spontaneously due to the cessation of mountain agriculture and the establishment of protected areas (Kozak 2003, Boltižiar 2007, Solár & Janiga 2013, Treml & Chuman 2015).

2.2. Identification of uppermost tree groups

In each mountain range, tree groups at the uppermost position were identified by systematically surveying the slopes of the highest peaks with Google Earth. Google Earth was chosen for its convenient visualization capability and the availability of very high-resolution imagery for the entire region of Central Europe. In extensive mountain ranges (e.g. the Vysoké Tatry or Nízké Tatry Mountains), at least 4 regions with the highest peaks were surveyed. For each survey, the uppermost position of tree groups on each aspect was identified using the maximum available zoom level. A rough estimation of elevation for each identified tree group was obtained from the Google Earth terrain model. To obtain precise elevations, we used detailed digital terrain models (10 m resolution for the Czech Republic and Slovakia), georeferenced topographic maps with the original scale of 1:10 000 and 5 m contour intervals (Poland, Germany), or on-site GPS measurements. For each mountain range, the final treeline elevation was derived as a mean value for the highest tree groups on 3 slope aspects. This discarded lower elevation forest edges associated with long-laying snow patches and avalanches on leeward or north-facing slopes.

Based on field validation, the identified tree groups were composed of trees between 3 and 4 m tall, a height in the range of the trees in the treeline position (Körner 2012). Isolated tree groups possibly affected by the topographic shelter effect were not considered.

2.3. Climatic metrics

Temperature data represented by monthly temperature means from the nearest meteorological station (covering the reference period of 1961–1990; Table 1) were adjusted using environmental (i.e. near-surface) lapse rates to the location of the uppermost tree groups. The environmental lapse rates (Barry 2008) were computed based on pairs of meteorological stations (Table 1). If available, mean lapse rates computed from a set of meteorological stations were used. Climate stations with long-term data were not available for 3 mountain ranges (Malá Fatra, Velká Fatra and Babia Góra). In these cases, temperatures from the nearest 2 or 3 meteorological stations were lapse-rate-adjusted to the elevation of the uppermost tree groups and inverse-distance-weighted interpolation was used to estimate temperature in these areas. Precipitation data were also necessary for the computation of selected metrics. We used precipitation sums from meteorological stations situated in the vicinity of treeline ecotones (the Harz, Krkonoše, Hrubý Jeseník, Nízké Tatry and Vysoké Tatry Mountains). For the remaining areas, we used either data from the nearest high-elevation meteorological station (Králický Sněžník, Velká Fatra and Belianské Tatry, in each case within a radius of 15 km), or available interpolated precipitation data from the Landscape Atlas of the Slovak Republic (Babia Góra and Velká Fatra; Hrnčiarová 2002). The duration of snow cover was computed based on a degree-day model of snow accumulation and snow melt with the same parameters as those used by Paulsen & Körner (2014).

Using climatological data, we calculated a set of thermal metrics selected based on previous studies on treeline climatology (Schmitt et al. 2004, Rossi et al. 2007, Gehrig-Fasel et al. 2008, Körner et al. 2011, Paulsen & Körner 2014). The individual metrics were strongly correlated, so we applied cluster analysis and selected only one metric to represent each cluster (Fig. 2). Metrics that correlated less with metrics representing other clusters were preferred. The second selection criterion was the degree of uncertainty related to the computation of a given metric. The following climatic metrics were finally used: annual number of days with temperatures above 0.9°C without snow cover (Days > 0.9S), degree-days above 0°C (DD0) and average temperature in the June–September period ($T_{JUN–SEP}$). Daily temperature values were necessary to compute the mean temperature of the continuous period with air temperature higher than 0.9°C and no snow cover (*T*-Days > 0.9S), Days > 0.9S and DD0. We obtained them by cubic spline interpolation of monthly temperature means.

Although representing one cluster group (Fig. 2), degree-days above 5°C showed high uncertainty related to spline-interpolated daily temperatures. This metric was therefore discarded from further analysis. On average, degree-days above 5°C computed from observed daily mean temperatures differed by 19% from daily temperatures derived from a spline function. We also conducted a similar evaluation of uncertainty for the remaining metrics. Because values of individual metrics (i.e. mean temperatures, degree-days, number of days) differed greatly, we scaled them to have a range from 0 to 100. Values derived from observed daily temperatures were assigned the percentage of 100, and 0 was assigned to the minimum possible value of a given metric (i.e. 0 days, 0 degree-days [°D] and 0°C for mean temperatures). For mean growing season temperatures, the biologically meaningful temperature of 0°C was chosen because trees do not grow and exhibit almost no metabolic activity below this point (Rossi et al. 2008, Körner 2012).

For comparative purposes, the average temperature of the warmest month (T_{WARM}) was used as a traditional thermal treeline indicator. The metric *T*-Days > 0.9S, as the metric probably best matching treeline position, is also presented (Paulsen & Körner 2014).

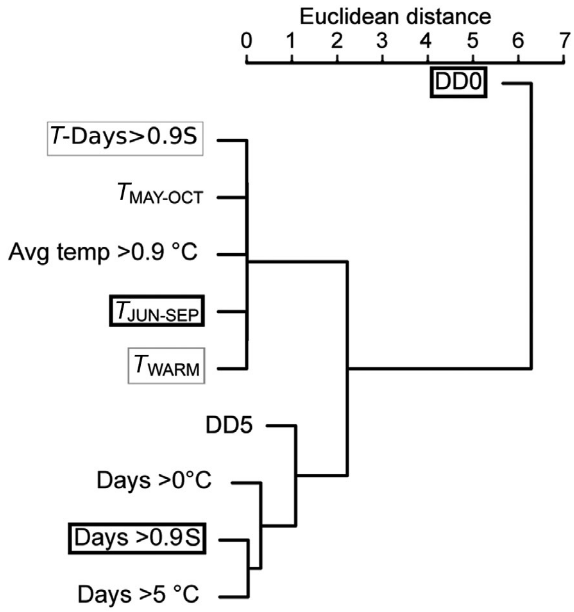

Fig. 2. Dendrogram expressing the relationships among calculated thermal metrics. The Ward method based on Euclidean distances was applied. Metrics selected for our study are highlighted by a black frame (cluster representatives entering into all analyses) or a grey frame (metrics used only for comparisons). Abbreviations: DD0 (DD5): degree-days above 0°C (5°C); *T*-Days>0.9S: average temperature of continuous period with air temperature higher than 0.9°C and no snow cover; $T_{JUN–SEP}$ ($T_{MAY–OCT}$): average air temperature from June to September (May to October); Avg temp>0.9: average air temperature of continuous period with air temperature higher than 0.9°C; Days>0 (5): number of days with mean air temperature higher than 0°C (5°C); Days>0.9S: number of days with mean air temperature higher than 0.9°C and no snow cover; T_{WARM}: mean temperature of the warmest month

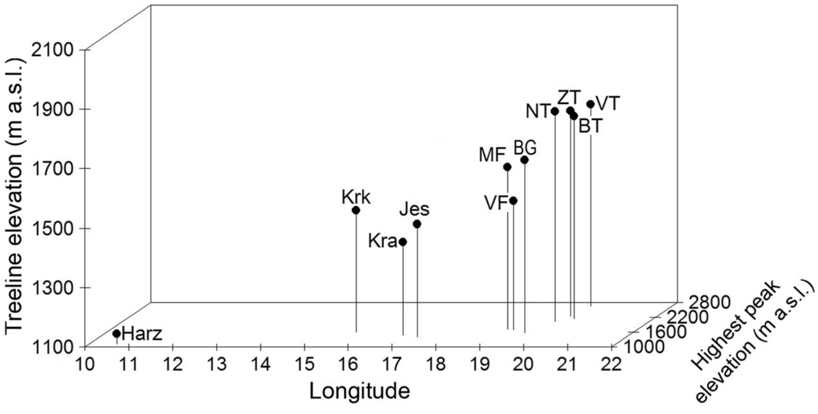

Fig. 3. Relationship among the elevation of uppermost tree groups, highest peak elevation and longitude. BG: Babia Góra and Pilsko; BT: Belianské Tatry; Jes: Hrubý Jeseník; Kra: Králický Sněžník; Krk: Krkonoše; MF: Malá Fatra; NT: Nízké Tatry; VF: Velká Fatra; VT: Vysoké Tatry; ZT: Západné Tatry

2.4. Statistical analysis

To compare treelines based on climatic metrics ($T_{JUN–SEP}$, DD0, Days>0.9S, T_{WARM}, T-Days>0.9S), each metric was z-transformed (i.e. the mean was equalized to 0 and the standard deviation was set to 1). For each metric, the mean value and confidence interval were computed based on a 1-sample t-test.

Applying linear models, we further explained treeline temperature metrics (only these representing clusters from Fig. 2: Days>0.9S, DD0 and $T_{JUN–SEP}$) using longitude and the elevation drop between treeline and the highest summits. A vertical elevation drop between the treeline and the highest summit is indicative of the summit syndrome. In Central Europe, longitude — besides a having positive relationship with thermic continentality (Plesník 2002, Mikolášková 2009) — is also negatively correlated with average wind speed (Table 1) and rime load (Błaś et al. 2002). Both of these climatic characteristics might preclude trees from growing at their temperature limit. Because wind speed and rime data were not available for all mountain ranges under study, longitude was used as a surrogate for wind speed and rime load. We used multiple linear regression within the framework of hierarchical partitioning (Chevan & Sutherland 1991, Walsh & Mac Nally 2004). All statistical analyses were performed using R statistical software (R Development Core Team 2015).

3. RESULTS

Treelines represented by the highest positions of tree groups in the Tatras were located between 1777 m (the Nízké Tatry Mountains) and 1806 m above sea level in the Západné Tatry Mountains (Fig. 3, Table 2). In the remaining Carpathian ranges (the Malá Fatra, Velká Fatra and Babia Góra Mountains), the elevations of the uppermost tree groups ranged from 1532 m in the Velká Fatra to 1679 m in the Babia Góra Mountains. The uppermost position of tree groups in the Sudetes ranged from 1412 m in the Králický Sněžník Mountains to 1508 m in the

Table 2. Temperature metrics characterizing the highest treeline positions in Central European mountain ranges north of the Alps

Mountain range	Highest tree-group elevation (m)	Standard deviation of highest positions at three different slope aspects (m)	Jun–Sep mean temperature (°C)	Sum of temperatures >0°C (°D)	Number of days with mean temperatures >0.9°C without snow cover	Temperature of warmest month (°C)	Mean temperature over the period with temperatures >0.9°C without snow cover (°C)
Harz	1134	2.6	9.4	1495	139	10.6	7.4
Krkonoše	1508	2.3	7.7	1136	127	8.9	6.4
Králický Sněžník	1412	1.6	8.8	1336	142	9.9	7.4
Hrubý Jeseník	1478	1.2	8.3	1252	144	9.5	7.1
Babia Góra	1679	27.4	8.5	1293	130	9.7	6.6
Malá Fatra	1645	19.7	8.2	1245	137	9.4	6.4
Velká Fatra	1532	2.6	8.7	1338	141	10.0	7.0
Nízké Tatry	1777	17.9	7.2	1038	121	8.3	6.1
ZápadnéTatry	1806	13.9	8.6	1317	132	9.8	6.4
Vysoké Tatry	1790	10.2	8.5	1302	133	9.6	6.8
Belianské Tatry	1780	14.7	8.2	1237	130	9.3	6.8

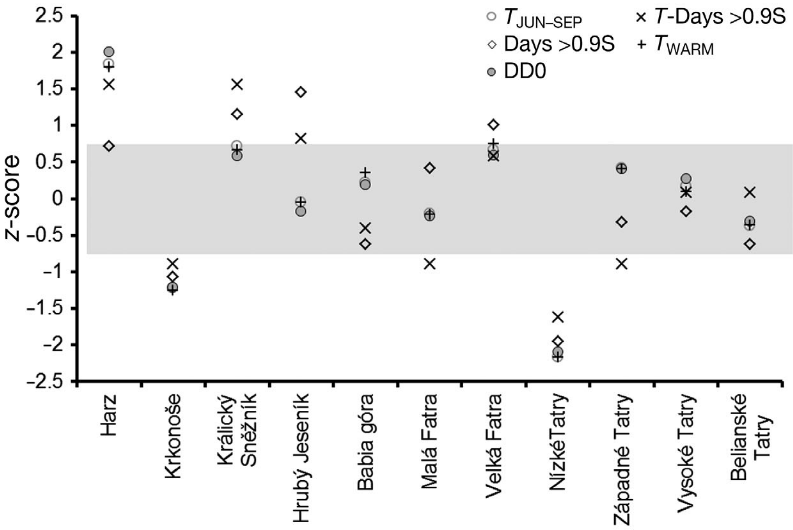

Fig. 4. Treeline temperature characteristics based on standardized metrics (DD0: degree-days above 0°C; Days>0.9S: number of days with temperature above 0.9°C without snow cover; $T_{JUN–SEP}$: average temperature in the June–September period; T-Days>0.9S: average temperature of the continuous period with air temperature higher than 0.9°C and no snow cover; T_{WARM}: mean temperature of the warmest month). All metrics have a mean value of 0 and standard deviation of 1. The grey band denotes the confidence interval of mean values derived from a 1-sample *t*-test

Krkonoše Mountains. The uppermost position of tree groups in the Harz Mountains was 1134 m. Identified highest positions of tree groups show low variability across aspects (Table 2), and their elevation is thus representative of the given mountain area. There is a clear increasing trend in treeline elevation along the longitudinal gradient (r = 0.93) and with increasing elevation (r = 0.88) of the mountain ranges under study (Fig. 3).

$T_{JUN–SEP}$ at treeline was 8.4°C ±0.5 (±SD) in all the mountain ranges in the study (Table 2). Days>0.9S was 134±6, and *T*-Days>0.9S over this period was 6.7 ± 0.4°C. DD0 was 1272 ± 112°D, and T_{WARM} was 9.5 ± 0.5°C.

Based on all climatic variables, the warmest treeline is located in the Harz Mountains (Fig. 4), where the growing season temperatures ($T_{JUN–SEP}$, *T*-Days>0.9S) and DD0 exceed the confidence interval of the CENA mean. Moreover, the treelines in the Hrubý Jeseník, Králický Sněžník and Velká Fatra Mountains are significantly warmer than the mean for CENA in the context of Days>0.9S and growing season temperatures represented by *T*-Days>0.9S (the Hrubý Jeseník and Králický Sněžník Mountains only). The coldest treeline positions were found in the Nízké Tatry and Krkonoše Mountains: both exhibited low values for all temperature variables that exceeded the confidence interval of the CENA mean.

Within the framework of hierarchical partitioning, linear models explaining the dependence of temperature variables (Days>0.9S, DD0 and $T_{JUN–SEP}$) on longitude and vertical drop between treeline and highest summit were not statistically significant. The independent effects of longitude and vertical drop to highest summit were not significant either. However, the highest values of $T_{JUN–SEP}$ and *T*-Days>0.9S were recorded for the 4 mountain ranges with the lowest vertical drop between the treeline and the summit (Harz, Králický Sněžník, Hrubý Jeseník and Velká Fatra).

Computed thermal variables depend on the lapse rates applied. The average elevation difference between a meteorological station and the nearest treeline was 292 m. The estimated error of lapse rates derived from a comparison with independent station data (Table 1) showed that the mean difference in lapse rates was 0.05°C per 100 m in the Krkonoše Mountains and 0.02°C in the Tatras for the June–September period. The mean estimated error of $T_{JUN–SEP}$ for all mountain ranges was therefore 0.05–0.14°C, with the maximum value in the Velká Fatra Mountains (0.17–0.42°C). The lowest error was in the Harz and Belianské Tatry Mountains, where meteorological stations are situated at the treeline elevation.

Additional uncertainty is associated with the use of daily temperatures derived from spline interpolation of monthly temperature means to compute the Days>0.9S, DD0 and *T*-Days>0.9S metrics. Based on 3 treeline regions with available measured daily data (stations Brocken, Chopok and Säntis; for their location, see Tables 1, 3), metrics based on observed and interpolated daily data differed by 7 and 9% for Days>0.9S and DD0, respectively, and 13% for the *T*-Days>0.9S.

5. DISCUSSION

Although several studies have been published on timberlines (i.e. the upper limits of closed forest) in CENA (e.g. Plesník 1971, Czajka et al. 2015b), our study presents the first comprehensive overview of thermal characteristics of the highest treeline po-

Table 3. Growing season temperature characteristics of treelines in the Alps and Central European mountain ranges north of the Alps (CENA) mean (±SD) values. Temperatures from climatic stations come from the NOAA climate database. Missing values were filled in using regressions against the Climatic Research Unit time series dataset (Harris et al. 2014). Mean daily temperature values for climatic stations were obtained using spline interpolation of monthly temperature data. Temperature metrics were not available for empty cells

Region	Period	Average Jun–Sep temperature (°C)	Sum of temperatures >0°C (°D)	Mean temperature of warmest month (°C)	Period with temperatures >0.9°C without snow cover (d)	Mean temperature over the period with temperatures >0.9°C without snow cover (°C)	Source
Alps – several locations	2004–2005	8.0±0.6 (mid-May–mid-Nov)					Gehrig-Fasel et al. (2008)
Dolomites 46°N,12°E	2002–2004	9.8–10.0					Rossi et al. (2007)
Mt. Patscherkofel 47°N,11°E	2000	8.2 treeline (end May–1 Oct)					Körner & Paulsen (2004)
	2006, 2007	8.8 timberline					Gruber et al. (2009)
Mt. Patscherkofel 47°N,11°E Treeline 2070 m	1961–1990	7.7	1115	9.0	153	6.8	Climate station
Villacher Alps 47°N,13°E Treeline 2050 m	1961–1990	8.1	1193	9.3	138	7.3	Climate station
Andermatt/Gütsch Treeline 2200 m	1961–1990	6.8	934	8.2	106	6.3	Climate station
Säntis 47°N,9°E Treeline 1900 m	1961–1990	7.3	1146	8.4	123	6.7	Climate station
CENA	1961–1990	8.4 ± 0.5	1272 ± 112	9.5 ± 0.6	134 ± 7	6.7 ± 0.4	Present study

sitions in Central Europe north of the Alps. The highest-elevated treelines are less affected by the second-order drivers of treeline position and thus are more suitable for comparative studies than timberlines (Körner 2012, Treml & Chuman 2015).

We documented that the maximum treeline elevation in CENA increased by approximately 94 m per 100 km between 10 and 20°E. This increase in treeline elevations with longitude is associated with rising isotherms of growing season temperatures towards the east (Quitt 1971, Květoň 2001), a reflection of both increasing continentality (Mikolášková 2009) and the mass elevation effect of mountain ranges. Considering only the effect of the continentality and the reference period 1961–1990, July–September temperatures at 1000 m elevation level along 49.5°N were 11.6°C at 13°E and 12.3°C at 18°E, which means an increase of 0.16°C per 100 km (Květoň 2001). The effect of mass elevation is evidenced by the rising elevation of CENA mountain ranges (correlated with their extent) between the Harz Mountains and the Tatras (see Fig. 3).

A majority of the treelines studied exhibited similar values for each temperature metric, an indication that treeline positions experience similar climatic forcing. However, the values of treeline thermal metrics in CENA are mostly higher than the minimum values necessary for tree growth derived from the global dataset of treeline locations compiled by Paulsen & Körner (2014) (minimum Days>0.9S = 94; *T*-Days>0.9S = 6.4°C). Purely temperature-based metrics showed that except for the Nízké Tatry and Krkonoše Mountains, the CENA treelines are warmer than treelines in the Alps by ca. 1°C when considering regional mean values (Table 3). If the growing season is delimited by snowmelt, growing season length and growing season mean temperatures in the CENA and Alps are similar (Tables 2, 3). Therefore, in agreement with a previous study (Paulsen & Körner 2014), we found that the thermal metrics computed over the period defined by the real start of the growing season correlate well with treeline position.

We also suggest that some differences in treeline temperature metrics between CENA and the Alps might be explained by different mesoclimatic settings of each of these regions. In comparison with the Alps, the CENA mountain ranges are relatively small and thus largely affected by intense wind action, cloudiness and orographic precipitation (Barry 2008), which decrease radiative heating of the ground (Treml & Banaš 2008). This is important, because radiative heating has a fundamental effect on the ground temperatures in open treeline stands, and low ground temperatures limit tree growth (Körner & Hoch 2006, Treml et al. 2015). Physiologically important temperatures such as ground or tree tissue temperatures thus might differ between CENA and the Alps less than was shown in our analysis.

Four regional treelines (Harz, Králický Sněžník, Hrubý Jeseník and Velká Fatra) were significantly warmer than the mean values derived from the entire CENA area. We observed that: (1) these treelines were located near summits, suggesting a possible influence of the summit syndrome; and (2) most of these mountain ranges were situated in the western half of CENA (Harz, Králický Sněžník and Hrubý Jeseník). However, neither the effect of vertical distance between the treeline and the highest summit (i.e. the summit syndrome) nor longitude (a proxy for wind speed and rime load) significantly influenced treeline temperatures in our study. The small number of regions examined may be why we did not detect statistically significant effects. Previous studies have shown that areas situated in the western half of CENA exhibit a high frequency of fog and rime (Błaś & Sobik 2000, Błaś et al. 2002). Additionally, mean wind speed tends to be higher towards the west ($r = 0.79$; Table 1). Rime and strong winds are responsible for breaks of apical shoots and abrasion of foliar cuticula (Hertel & Schöling 2011, Han et al. 2012). Hormonal signals stimulating radial and height growth of damaged trees are then weaker as a consequence of broken shoots (Cairns 2001). One possible explanation for the location of the uppermost tree stands that exist below the potential, i.e. temperature-related, tree limit may be attributed to large biomass loss and related low growth rates due to sheer forces of wind at such summits. However, it still remains unclear whether the uppermost tree stands in the Harz, Králický Sněžník, Hrubý Jeseník and Velká Fatra Mountains are exclusively climate-driven and related to the summit syndrome and/or maritime influences, or whether past human interventions played a decisive role here (Beug et al. 1999, Novák et al. 2010). Potential upward advance of tree stands in the Harz or Králický Sněžník Mountains is, however, also restricted by their very close location to summit areas, meaning that they have nowhere to expand.

Comparison between directly measured short-term treeline temperatures from the Alps (Körner & Paulsen 2004, Rossi et al. 2007, Gehrig-Fasel et al. 2008) and from CENA (Treml & Banaš 2008, Hertel & Schöling 2011, Treml et al. 2015) reveals ambiguous differences between both regions (Table 3). For example, growing season treeline ground temperature (defined by the 3.2°C threshold; Körner & Paulsen 2004) in the Krkonoše Mountains was 0.5°C warmer than the same temperature at the maximum treeline position in the Alps (Treml et al. 2015). This was not true for the Harz Mountains, where growing season ground temperature was 6.7°C (2005–2006, season with slightly above-average air temperatures; Hertel & Schöling 2011) and matched well with treeline temperatures derived from the worldwide dataset of Körner & Paulsen (2004). In our study, the Harz treeline was the warmest among the studied mountain ranges, except the metrics deriving the growing season length from the snow melt threshold. However, according to soil temperature measurements conducted in the Harz Mountains by Hertel & Schöling (2011), the growing season was rather long (180 days) so it also comprised long periods with low soil temperatures slightly exceeding the threshold of 3.2°C. This could explain the overall low mean growing season temperature. Similar climatic conditions observed at the treeline in the Harz Mountains have been reported from natural wind-affected treelines in Central Japan (Takahashi et al. 2012, Takahashi 2014).

Besides areas included in our CENA dataset, there are several other mountain ranges in this part of Europe that have been reported to be at or approaching the upper forest limit (e.g. Grosser Arber in the Bavarian Forest, Mt. Fichtelberg in the Erzgebirge Mountains and Mt. Lysá hora in the Beskydy Mountains; Jeník 1961). Their temperature metrics were the following: 157–168 days of the growing season with a mean temperature between 7.8 and 8.4°C, a mean temperature of 9.6–10.1°C in the June–September period and 1569 to 1599°D above 0°C. Computed thermal metrics thus revealed that these areas are substantially warmer than the analysed

CENA dataset, and therefore far below the climatic tree limit.

Our analysis revealed that the various commonly employed temperature metrics have different predictive power for treeline position. They all depend on reliable lapse rates, unless temperatures are measured right at the tree limit in a proper way. In our study, however, the estimated uncertainty attributed to lapse rates was rather low — 0.14°C (0.42°C at maximum) — for simple temperature metrics based exclusively on monthly temperature means. Additionally, temperature metrics based on daily means are derived from mean monthly trends as provided by climate databases by spline approximation, which is a substantial simplification (Zimmermann & Kienast 1999, Paulsen & Körner 2014). DD0, season length and *T*-Days > 0.9S showed relatively low deviations from computations based on observed daily values (between 7 and 13 %). Deviations of the traditionally used metric, degree-days above 5°C, were high (19 %), thus challenging the derivation of this metric from monthly temperature means.

6. CONCLUSIONS

Our study presents the first compilation of thermal treeline indicators in 11 mountain ranges in Central Europe north of the Alps. Treeline elevation increases along the 50th parallel from 1100 m at 10° E to 1800 m at 20° E in response to rising growing season isotherms associated with increasing thermic continentality and the mass elevation effect. The treelines we studied exhibited temperatures similar to those of treelines in the adjacent Alps when temperature metrics for growing season were defined by absence of snow pack and minimum temperature. However, temperatures were higher when growing season was only defined by commonly employed temperature metrics computed over a fixed period or based only on minimum temperatures. We identified 4 mountain ranges (Harz, Králický Sněžník, Hrubý Jeseník and Velká Fatra Mountains) where the uppermost tree stands are likely influenced by their proximity to mountain summits and are located below the potential treeline elevation. Summit areas in these mountain ranges are affected by intense winds and high rime loads, which cause large biomass loss and prevent the establishment of fully grown trees. The comparison of various ways of expressing temperatures for treelines in CENA and the Alps revealed a better agreement if growing season definition takes into consideration snow pack constraint of season length. Such all-season metrics match the position of the treeline irrespective of the regional degree of continentality.

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