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Physical Geography and Geoecology

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The influence of wind on treeline position – the question of summit syndrome

Vliv větru na polohu horní hranice lesa – otázka vrcholového fenoménu

Doctoral dissertation

Supervisor: Mgr. Václav Treml Ph.D.

Praha 2017

I declare that I wrote the thesis independently and that I cited all the information sources and literature. This work neither its part was not presented to obtain another academic degree or equivalent.

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Jakub Kašpar
In Prague, 15.6. 2017

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Title: The influence of wind on treeline position – the question of summit syndrome
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Abstract: Growing season temperatures drive treeline position on a global scale. However, environmental factors including wind action may critically modify the position of treeline ecotone on a regional or a local scale. The intensity of wind action increases with shortening of treeline-summit distance. High intensity of wind action may cause the presence of a summit syndrome. This results into the lowering of treeline below its potential limit given by temperature conditions. Alpine treeline ecotones occurring in 11 mountain ranges including the Harz Mts., the High Sudetes and the Carpathians represented the model areas for my research. These mountains are located at the 50th parallel and reflect an increase in the gradient of continentality. Moreover, the distance of treeline from the summit is highly variable among these mountains. These mountains are moreover characterized by differences in mass elevation effect and in the summit syndrome intensity. Treeline position in Central Europe is increasing its elevation about 94 m per 100 km towards the east, when reflecting rise of elevation isotherms due to increasing continentality. However, thermal conditions of the majority of these treelines do not differ significantly from each other as well as from similar positions in the Alps. Treelines in the Harz, Králický Sněžník, Hrubý Jeseník and Veľká Fatra are, however, an exception. These mountains showed higher radial and apical growth when compared to the rest of investigated treelines. We found that temperature conditions were strongly correlated to radial growth, correlations were lesser for height growth below 2 m and there was no correlation with height growth above 2 m. Results of xylogenesis indicated a potential influence of wind action on wood formation in high-elevation tree stands. Anyway, the high wind speeds were reflected in higher occurrence of clonal tree islands and irregular tree crowns reflecting prevailing wind direction in winter. Wind was able to limit only apical growth of trees after they exceed the height of 2 m. The approximate rate of this limitation was 0.65 cm per 1 m.s^{-1} of wind increment per year. Nevertheless, the overall wind-induced depression of highest treeline positions is probably low, even in windy mountain regions such as the mountainous regions of Central Europe, because even in the highest elevations, the wind-sheltered sites favourable for tree growth exist. Thus, overall effect of summit syndrome in mountains of Central Europe generally manifests in a difference in tree size between wind protected and wind affected sites. This might lead to slight treeline depression in mountain ranges such as the Králický Sněžník Mts. and Hrubý Jeseník Mts.

Keywords: treeline, summit syndrome, tree growth, wind influence, High Sudetes, Harz, Carpathians

Název: Vliv větru na polohu horní hranice lesa – otázka vrcholového fenoménu

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Abstrakt: Na globální úrovni je poloha horní hranice lesa daná izotermou teploty vegetační sezony. Na regionální úrovni, však může být její poloha modifikována dalšími environmentálními faktory, jako je například působení větru. Intenzita působení větru roste se zkracující se vzdáleností mezi ekotonem horní hrance lesa a vrcholovými oblastmi. Vysoká intenzita působení větru může vést k přítomnosti vrcholového fenoménu. Ten může vést ke snížení polohy horní hranice lesa pod její potenciální elevaci danou teplotními podmínkami. Ekoton horní hranice lesa vyskytující se v jedenácti pohořích Střední Evropy v Harzu, Vysokých Sudetech a Karpatech sloužil jako model pro můj výzkum. Tato pohoří kopírují 50. rovnoběžku a podél gradientu rostoucí kontinentality. Vzdálenost polohy horní hranice lesa od vrcholu je v těchto pohořích značně variabilní. Kromě toho se jednotlivá pohoří liší svou hmotnatostí a pravděpodobně také intenzitou vrcholového fenoménu. Poloha horní hranice lesa ve Střední Evropě roste o 94 m na 100 km směrem k východu, přičemž kopíruje nárůst nadmořské výšky izoterm v důsledku zvyšující se kontinentality a hmotnatosti pohoří. Teplotní podmínky na většině horních hranic lesa se vzájemně neliší. Stejně tak se neliší od podmínek na podobných stanovištích v Alpách. Výjimku tvoří Harz, Králický Sněžník Hrubý Jeseník a Veľká Fatra. V těchto pohořích byl rovněž zaznamenán vyšší radiální přírůst. Teplotní poměry silně korelovaly s radiálním růstem, ale pouze slabě s výškovým růstem stromů nižších než 2 m a vůbec s výškovým růstem stromů vyšších než 2 m. Také rozdíly v časování fenologických fází tvorby dřeva napříč ekotonem hranice lesa naznačily možný vliv větru na růst stromů v nejvyšších částech ekotonu. Vysoké rychlosti větru se odrazily ve vyšším výskytu klonálních stromových skupinek a nepravidelném tvaru korun kopírujícím převládající větrné proudění v zimních měsících. Navzdory tomu výsledky neprokázaly vliv větrem indukované ztráty biomasy na růst stromů ve zkoumaných pohořích. Vítr snižoval výškový přírůst stromu po dosažení výšky 2 m o 0.65 cm při nárůstu rychlosti větru o 1 m.s^{-1}. Přesto lze říci, že větrem způsobené snížení polohy horní hranice lesa je pravděpodobně malé i v větrných pohoří v rámci studované části střední Evropy. Vliv vrcholového fenoménu se v pohořích Střední Evropy projevuje pouze vytvářením rozdílu ve velikosti stromů mezi návětrnými a závětrnými polohami. Vrcholový efekt mohl tímto způsobem přispět ke snížení polohy horní hranice lesa v Králickém Sněžníku a Hrubém Jeseníku.

Klíčová slova: horní hranice lesa, vrcholový fenomén, růst stromů, Vysoké Sudety, Harz, Karpaty

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I. Introduction

1 Introduction

Treeline is a prominent vegetation boundary separating montane or subalpine forest from alpine zone (Körner 2012). In fact treeline is a transition zone (ecotone) of varying width. Across the treeline ecotone there is a considerable decline in tree size with increasing elevation. Steepness and position of this transition zone is controlled by the factors influencing tree growth, tree recruitment as well as by geomorphic or soil conditions (Holtmeier 2009).

The main driving factor of treeline position is an insufficient amount of heat during the growing season (Körner and Paulsen 2004). Low amount of heat does not allow to form tree stature. As a result, treelines are located at positions with very similar temperature conditions all over the world (mean air temperature 5 to 7 °C in the growing season, Körner and Paulsen 2004). Nevertheless, on a regional or local scales, treeline position may be considerably modified by other factors than temperature. This includes snow, wind, soil, and geomorphic conditions (Carlson et al 2011, Han et al. 2012a, Takahashi 2014).

Vegetation boundaries are often located below their potential limit given by temperature conditions. This is particularly true in mountains of limited extent or on isolated peaks, where vegetation transition zones are near to summits (Cogbill and White 1991, Carlson et al. 2011). This situation is in literature referred as a summit syndrome (Cogbill et al. 1997, Odland 2015). Besides of potentially limiting soil resources, the influence of wind seems to play a critical role in presence of summit syndrome (Carlson et al. 2011).

Treelines not reaching their temperature-limited potential positions were reported from Rocky Mountains (Holtmeier 1982), Appalachians (Leffler 1981, Cogbill and White 1991, Carlson et al. 2011), mountain regions of Central Japan (Takahashi 2014), Korean peninsula (Han et al. 2012a), Andes of Southern Ecuador (Wagemann et al. 2015), or from the Scandes (Kullman and Öberg 2009, Odland 2015). Treelines affected by the summit syndrome might represent source of uncertainty, when computing globally valid treeline temperature metrics (e.g. Körner and Paulsen 2004, Paulsen and Körner 2014) and when predicting responses of treelines to climate change (Cogbill and White 1991, Marcias-Fauria and Johnson 2013, Schickoff et al. 2015). However, the literature dealing with treelines influenced by summit syndrome or by intense wind action is relatively rare (e.g. Cogbill and White 1991, Cogbill et al. 1997, Holtmeier and Broll 2011, Odland 2015).

Moreover, the potential effect of wind action on treeline depression has not been sufficiently quantified.

Mountain ranges in Central Europe offer a possibility to study treelines differing in wind conditions as well as treelines located in varying distances from summits. Treelines might be depressed against their potential position due to the wind influence (Jeník 1961). The reasons of wind-induced treeline depression might be attributed to e.g. abrasion of stems and shoots by ice particles (Han et al. 2012a), weakening of hormonal signal due to partial loss of buds (Susiluoto et al 2010), apical breaks (Kajimoto et al 2002), or the need for production of reaction wood given, which demands a lot of resources (Du and Yamamoto 2007). To describe the influence of wind and summit syndrome on treeline the following goals were set:

i) To calculate temperature metrics for the highest treeline positions in mountain ranges of Central Europe and to compare these data among each other and with potential treeline temperature values published in literature.

ii) To compare relationship between growth and temperature metrics of the uppermost tree stands in Central Europe.

iii) To provide an analysis of the growth and morphology of trees growing along the wind speed gradient in the treeline ecotone.

iv) To evaluate differences in the timing of wood phenology at lower compared to the upper part of the treeline ecotone.

2 Literature review

This chapter reviews the current state of knowledge on (i) definition of treeline ecotone, (ii) hypotheses explaining limits of tree presence in cold environment, (iii) tree growth at treeline, (iv) supplementary factors influencing treeline position, and (v) recent treeline dynamics.

2.1 Treeline definition

According definitions of Holtmeier (2009) or Körner (2012), treeline ecotone can be delimited by three lines connecting tree species stands with the same or very similar characteristics (Figure 1): (i) **timberline**, the line connecting the uppermost margins of closed forest, (ii) **treeline**, the line connecting the uppermost stands of individuals fulfilling the definition of tree, which is usually a minimum height of 2 or 3 m and upright stem, and (iii) **tree species line** connecting upper limit of individuals represented by individuals of tree species lower than minimum height, by krummholz or seedlings.
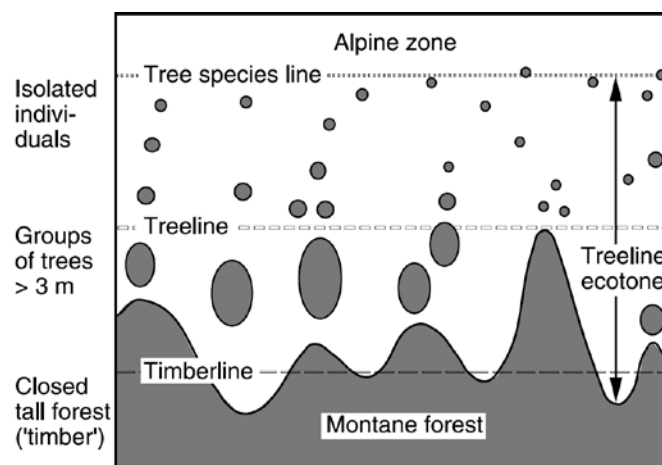
Figure 1: A schematic representation of treeline ecotone (Körner and Paulsen 2004)

The treeline ecotone is defined by minimum canopy cover and minimum tree size. The critical value for treeline delimitation according to criteria of canopy cover is variable in literature. For example, Roessler et al. (2008) used a threshold of 16 % of canopy cover for delimitation of isolated forest patches. Král (2009) defines treeline ecotone as an area with canopy cover from 26 to 50 %. On the other hand, Treml and Chuman (2015) define minimum canopy cover for treeline 50 % and Szerencsits (2012) applied threshold 60 % for delimitation the closed forest. The size of pixel, where the minimum canopy should be

achieved to form "forest" varies a lot among authors, usually reflecting data source they employed.

Many authors delimit the upper margin of treeline ecotone as a line connecting stands of trees with minimum tree height. Holtmeier (1963 in Holtmeier 2009) defined this value as an average height of snow pack. Recently the thresholds of 2 metres (Holtmeier and Broll 2010, Kullman 2010) or 3 m (Paulsen et al. 2000, Gehrig-Fasel et al. 2006, Körner 2012, Szerencsits 2012) are generally accepted. However, the more preferred threshold seems to be the tree height of 3 m. Moreover, height of 3 m corresponds very well with minimum size of trees recognizable on aerial images (Kašpar and Treml 2016).

2.2   Hypotheses explaining the formation of treeline

Since the times of pioneer treeline studies, several hypotheses explaining the treeline formation had been published. Hypotheses explaining the existence of treeline ecotone stem from two basic principles. The first can be described as a global-scale concept (Körner 1998), which is characterized by strong focus on ecophysiological perspective of tree growth (Körner 2012). Second concept is based on understanding of spatial and temporal patterns of trees, facilitation and competition (Holtmeier 2009). Körner (2012) summarized hypotheses into five major groups:

1. The stress hypothesis: tree growth is limited due to repeated damage given by frost desiccation, freezing or phototoxic effects.

2. The disturbance hypothesis: tree growth is limited by biomass loss caused by various factors such as mechanical damage by wind, ice blasting, snow breaks, avalanches, fungal infections. Trees are then not able to balance such biomass loses in longer time scale.

3. The reproduction hypothesis: pollination, seed development and seedling establishment may be limited at treelines due to several factors such as harsh meteorological or soil conditions.

4. The carbon balance hypothesis: either carbon uptake and carbon balance may be limiting factor of tree growth at treeline due to low intensity of photosynthesis at low temperature.

5. The growth limitation hypothesis: synthetic processes that lead from sugars and amino acids to the complex plant body may not be sufficient for growth or replacement of tissue that needs to be renewed.

Deviations of treeline position from potential value given by thermal conditions might be explained by stress and disturbance hypotheses (Case and Duncan 2014). However, some disturbances such as frost desiccation have less negative effect than was originally assumed (see review in Körner 2012).

High seedlings densities have been observed at many treelines, but these seedlings are not able to attain tree size (Wang et al. 2016). Successful seedling establishment and survival require several successive years with favourable conditions (i.e. sufficient warmth and moisture) together with a suitable microsite conditions (Barbeito et al. 2012). Many treeline tree species do not exclusively rely on sexual reproduction because of their capability to spread via clonal reproduction (Holtmeier and Broll 2017). Therefore, recruitment-limiting hypothesis does not allow to explain the treeline presence at a global scale and is probably supplementary to other hypotheses (Körner 2012).

Source limitation hypothesis is probably also not generally valid, because there was observed no difference in carbon uptake in comparison with trees growing in lower elevations (Hoch and Körner 2012).

According to sink limitation hypothesis, trees are not able to build new cells and finish their complete maturation due to low temperatures. Trees are still able to produce sugars and amino acids (Körner 1998) but they are not able to use them to build a new tissue. Hoch and Körner (2012). The growth limitation hypothesis relates low growth rates to inability of trees to build a new tissue because of too low temperature (Körner 1998). At low temperature, secondary growth is restricted despite of sufficient supply of carbohydrates (Hoch and Körner 2012). During the process of secondary growth the new tracheids are formed (Palardy 2008). Their amount is governed by the rate and duration of xylogenesis (Cuny et al. 2014), which is in cold climates controlled mainly by temperature conditions (Rossi et al. 2016). This assumption was confirmed by experiments of Gričar et al. (2006), during which heated trees produced more cells at locally heated parts of stem in comparison to untreated or cooled stems.

Recently, Petit et al. (2011) suggested that low efficiency of water conductive system limits tree growth at cold sites. To grow larger and taller, trees need to wide their conduit elements near to stem base (Anfodillo et al. 2006). However, low temperatures inhibit a formation of big conduits because the growing season is too short (Petit et al. 2011, Anfodillo et al. 2013). Consequently, high trees cannot maintain sufficient water supply during entire growing season.

On the basis of specific influence of climate factors or disturbances, following types of treeline ecotone can be distinguished (Harsch and Bader 2011): (i) **diffuse treeline**, characterized by the gradual transition of forest into alpine grasslands, which corresponds with gradual decrease in available heat with increasing altitude. (ii) **abrupt treelines**, characterized by a sharp boundary between forest and alpine zone Abrupt treelines emerge at places with strong establishment constraint (drought, strong competition with herbal layer, strong radiative cooling, Harsch and Bader 2011) (iii) **krummholz treelines**, characterized by presence of dwarfed and prostrate individuals above treeline and (iv) **islands treelines**, characterized by the presence of tree islands within the treeline ecotone.

Krummholz treelines are characteristic by the strong influence of other modifying factors than temperature such as precipitation regime (drought, high snow loads) and wind action. However, krummholtz tree form is a result of damage induced by wind actions (Harsch and Bader 2011). Island treelines are formed at places where facilitation is extremely important (intense wind action, radiative cooling) (Holtmeier and Broll 1992, Renard et al 2016). Abrupt, krummholz and island treelines have shown weaker response to recent temperature increase than diffuse treelines.

2.3 Tree growth as a main determinant of treeline position

2.3.1 Primary and secondary growth

Primary growth is represented by an apical growth and an elongation of shoots, whereas secondary growth is manifested in radial increment (Vaganov et al. 2006, Speer et al. 2012).

Shoots elongate as a result of bud opening and expansion of apical meristems (Pallardy 2008). Shoot elongation is a very organized process that involves cell division followed by cell expansion (Pallardy 2008). Meristematic activity in elongating shoots occurs near the shoot apex, the overall activity of apical meristems is correlated with duration and the rate of secondary growth (Pallardy 2008).

Radial increment is caused primarily by meristematic activity in the vascular cambium (Vaganov et al. 2006). Cambial zone is a layer of several flattened meristematic cells. Two types of cell division occur in cambial zone. Tangential division leads to production of new xylem and phloem cells. Multiplicative division leads to production of new cambial initials (Pallardy 2008). During the tangential division, cambial cells divide

towards the stem centre (to form xylem) and towards bark to form new phloem cells (Vaganov et al. 2006).

2.3.2 Anatomy of conifer wood

Conifer wood is composed of vertical (tracheids, parenchyma cells, resin ducts) and horizontal elements (radial rays). Vertical elements form about 90 % of the wood (Vaganov et al. 2006).

Vertical elements, namely tracheids, are dominant element of conifer woods. Their length varies usually from 1.5 to 5 mm and is particularly driven by the position within the stem. Their diameter varies by the position within the stem in the range from 20 to 80 microns.

Tracheids have two main functions: (i) they support tree stature and (ii) they supply leaves by water and nutrients. To do so, they are connected by pits in their walls. The overall efficiency of the entire system depends on the size of tracheids as well as on the size of pits in cell walls (Schulte 2012). New tracheids differentiate from cambial zone where cambial cells divide and form to their derivate - xylem and phloem. Following phases of xylem formation can be distinguished (Figure 2): cambial zone cells (CZ) characterized by thin cell walls and small radial diameters (Rossi et al. 2006a). During the period of dormancy, the cambial zone contains usually 4 to 6 cells, however, when cambium is reactivated at the beginning of growing season the amount of cells in cambial zone increase up to 40 cells within few weeks (Pallardy 2008). Enlarging cells (EN) develop from cambial zone cells by progressive extension of cell walls. (Rossi et al. 2007, Pallardy 2008). During this phase, the cell grows in length and diameter, while a very thin and plastic cell wall (primary cell wall) is created (Pallardy 2008). When cell is big enough, the wall thickening phase begins (WT). In this phase the lignin is being stored in cell walls and secondary cell wall is created (Pallardy 2008). Finally, each cell reaches maturity (MC) and terminates by its programmed death (Pallardy 2008, Gryc et al. 2012). As a result, tree stem is composed almost exclusively from dead cells that are predominantly responsible for transport of water and minerals from roots to leaves (Pallardy 2008).

Besides of dead parenchymatic cells, there are also living parenchyma cells in the stem, which predominantly serve to store reserves (Pallardy 2008). In response to change of stem strain or position caused by mass movements, landslides or long term wind pressure, trees start to produce reaction wood (Du and Yamamoto 2007, Tumajer and Treml

2013). By production of reaction wood trees compensate the outside pressure and try to restore previous stem position (Du and Yeamamoto 2007). In conifers, reaction wood is characterized by small cell lumens with thick cell walls of more circular diameters than normal wood (Du and Yeamamoto 2007). This is, however, compensated by low conductive capacity (Mayr et al. 2006).
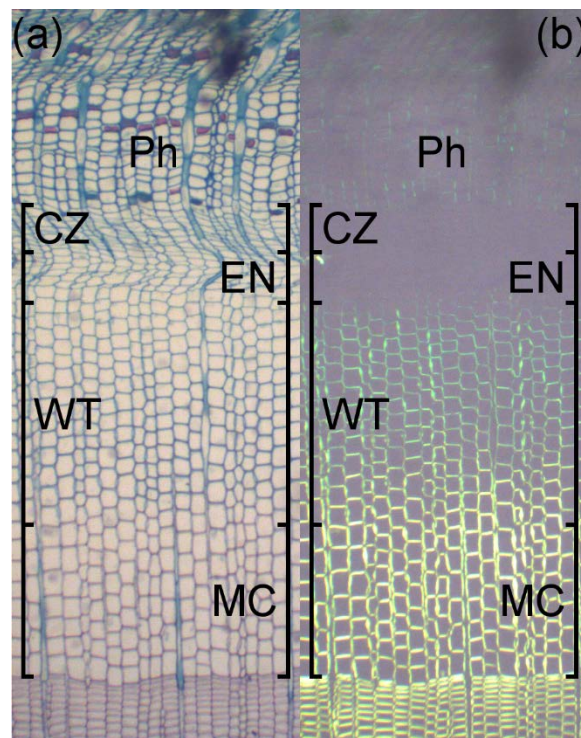
Figure 2: Microsection of Picea abies wood (cross-section) for analysis of intra-annual growth under normal (a) and polarized (b) light. The sample is magnified 400 times. Abbreviations: Ph – Phloem; CZ – cambial zone cells; EN – enlarging cells; WT – wall thickening cells; MC – mature cells.

Horizontal elements are represented mainly by radial rays. These mostly parenchymatic cells are longer in radial than in vertical direction with considerably longer life than tracheids. Their presence along the stem is random but their total volume can represent up to 10 % of stem biomass. The main purpose of radial rays is a support of conductive system while radial rays connect the inside parts of the stem with cambial zone (Wilson and White 1986).

Wood anatomical properties are changing during the growing season. 'Earlywood' is produced at the beginning of the growing season, whereas later in the growing season trees start to produce so called 'Latewood' (Pallardy 2008). Earlywood has lower density and mechanical strength but higher water conductive potential and water storage capacity than latewood (Domec and Gärtner 2002). This is because earlywood tracheids have wider

cell lumens than latewood cells (Schulte 2012), a reflection of different demands on water supply during the growing season as well as the course of temperature conditions (Domec and Gärtner 2002, Pacheco et al. 2015, Castagneri et al. 2015 and 2017, Carrer et al. 2016, Ziaco et al. 2016). Latewood increases the mechanical strength of the stem (Vaganov 2001, Domec and Gärtner 2002, Pallardy 2008).

2.3.3   Climatic factors of tree growth at treeline

Temperature and growing season length

Tree growth lasts in temperate and boreal zones of the northern hemisphere from March to October with deviations reflecting temperature and moisture conditions (Rossi et al. 2016). Nevertheless, the highest intensity of cell production is observed around summer solstice (Rossi et al. 2006a). Rossi et al (2006a) explains the synchronization of maximum cell production with day length as an adaptation of trees, which ensures that all newly created cells reach maturity before the end of the growing season.

At treeline, temperature is the main controlling factor of tree growth (Körner 2012). Körner and Paulsen (2004) determined mean treeline growing season temperatures by direct measurements ranging from 5 to 7 °C. This theoretical concept was later supported by studies of intra-annual tree growth. Multiple studies proved that division of cells in vascular cambium proceeds when temperature exceed 5 °C (Rossi et al. 2007) and secondary cell wall thickening starts when average temperatures exceeds 6 – 8 °C (James et al. 1994, Rossi et al. 2006a, 2007).

However, cells need time to reach maturity. Therefore, the growing season length is important for tree growth as well. Common growing season lasts at treeline from 100 to 140 days (Rossi et al. 2016). The minimum growing season length is approximately 90 days as suggested by Körner (2012).

According to Moser et al. (2009) the growing season is shortened about 3 to 4 days with every 100 elevation meters due to decreasing temperature and later snowmelt. Similarly, Vaganov et al. (1999) observed shortening of the growing season due to late snowmelt at Siberia.

Snow cover

Snow cover has negative effect on tree growth via shortening of growing season, however, some snow-related effects positively influence tree existence at treeline (Holtmeier 2009). First, snow cover protects roots from deep soil freezing due to isolation

effect (Holtmeier 2009). Second, snow protects needles from frost desiccation and late frost periods at the beginning of the spring (Tranquillini 1979). Snow supplies the majority of soil moisture in continental areas (Hu et al. 2010). However, the occurrence of frost desiccation is higher at wind affected sites than at wind protected sites (Cairns 2001). For example, in average 8.68 % of canopy is destroyed in winter in krummholz (Cairns 2001).

Wind action

Since wind speed generally increases with elevation (Barry 2008), treeline trees are significantly affected by wind. Wind is primarily responsible for snow relocation (Jeník and Štursa 2003, Mamet and Kershaw 2013, Renard et al. 2016) and related irregular snow pack distribution. Snow and ice transported by wind abrades tree stems and shoots (Han et al. 2012a). In addition, wind accelerates heat exchange (Grace et al. 1989, Anten et al. 2010) and increases evaporative cooling (James et al. 1994). This eliminates the effect of radiative warming of the tree body during the daytime (James et al. 1994), which is less than 1 °C for stem and terminal shoots (Wilson et al. 1986, Wieser 2007) and about 2 °C for the canopy (Tranquillini 1963) when considered mean growing season temperatures.

At treeline trees, several consequences of intense winds wind action were described: (i) the change of growth form (e.g. presence of krummholz) (Plesník 1971, 1978, Wooldridge 1996, Harsch and Bader 2011); (ii) reduction of needle size (Han et al 2012a); (iii) discrepancy in length of branches between wind affected and wind protected side of tree (Plesník 1971, Han et al 2012a); (iv) change in biomass allocation in stem and branches (Watt et al. 2005); (v) stem eccentricity (Nicoll et al. 2008); (vi) presence of reaction wood in tree rings (Schweingruber 1996, Watt et al. 2005, Dean et al. 2013); (vii) reduction in tree height (Takahashi et al. 2012).

2.3.4   Internal factors of tree growth

The majority of treelines at the Northern hemisphere is composed of conifers, which are probably better adapted to cold treeline conditions (Holtmeier 2009). However, even at conifers, the obvious genetic variability was observed within a specific species. For example results of Zubizarretta-Gerendian et al. (2012) showed that seedlings from different climatic regions differ in growing strategy in early stage of their live as well as in their growth response to July temperatures. At the same localities, trees originated from northern areas showed higher primary and secondary growth as well as earlier bud break

than individuals originated from southern locations (Beuker 1994a and 1994b, Gömory et al. 2012, Westin et al. 2000).

Among internal growth factors, the effects of age and size play a crucial role (Pallardy 2008). Wood production of old trees starts later when compared to younger trees (Rossi et al 2007). Consequently, this leads to formation of narrower tree rings in old trees compared to juvenile individuals (Schweingruber 1996). The process of tree ageing is however not uniform and depends on site conditions. At sites with almost ideal conditions (sufficient amount of nutrients, precipitations and heat), the ageing process is considerably faster than at sites with restricted resources (Schweingruber 2007).

As trees are ageing, they also become larger. During the growth, trees are facing two major problems connected with water conductivity. First, they need to overcome increasing hydraulic resistance given by the friction of water with the cell walls and, second, they need to maintain sufficient supply of water to needles (Petit et al. 2011). To overcome hydraulic constrains, trees start to create lower amount of larger cells which are able to deliver higher amount of water to the apex (Carrer et al 2015). However, maturation of larger cells needs more time than the maturation of smaller cells (Anfodillo et al. 2013), therefore, big trees need longer period for cell maturation than small trees. As a consequence of cell size allowed by growing season length, tree height gradually decreases from timberline to tree-species line.

Besides direct environmental signal, division and differentiation of cells from cambial zone are controlled by activity of hormones from families of auxines, giberelines, cytokinins and ethylene (Pallardy 2008). Auxin is responsible for division of cells in vascular cambium (Pallardy 2008). Auxin is produced in terminal parts of stem (apex, shoots) and basipetaly transported towards the stem base (Friml 2003, Pallardy 2008). Its concentrations are affected mainly by photoperiod and ambient temperatures (Friml 2003, Rossi et al. 2007).

2.4 Supplementary factors influencing treeline position

2.4.1 Recruitment and seedling survival

Tree recruitment at treeline is either generative (seed-based reproduction) or vegetative (layering) (Holtmeier and Broll 2017). The both reproductive ways are affected by heavy losses of newly established individuals/ramets. Seedling mortality is generally very high, commonly between 60 and 90 % (Germino and Smith 1999). Mortality of

layering branches is about 36 % over 20 years (Vacek et al. 2012). At treeline, a fecundity and viability of seeds is sufficient (Hofgaard et al. 2009), the crucial bottleneck is represented by seedling survival (Camarero and Gutiérez 1999). Most conifer species require suitable establishment microsites (with bare ground or sparse herbal layer) (Batllori et al. 2009). On the other hand, for further seedling survival, facilitation of surrounding vegetation might be necessary (Smith et al. 2003). The optimal conditions for successful seedling establishment are species specific (Gaire et al. 2014), however the most important factors of seedling survival are snow cover and temperature regime (Camarero and Gutiérez 1999, Barbeito et al 2012). The relative importance of environmental factors differs with increasing age of individuals (Barbeito et al 2012). For example, the date of snow melt and overall radiation is important in early stages of tree life, whereas the influence of the other factors (such as wind) starts to be important when an individual reaches certain height (Barbeito et al 2012). The most favourable conditions for seedling survival are winters with sufficient snow cover preventing soil freeze, followed by early snowmelt together with relatively warmer springs and summers (Camarero and Gutiérez 1999, Barbeito et al 2012). Protective functions of surrounding tree stands may increase probability of seedling survival (Castanha et al. 2013).

Suitable conditions have to be met over several successive seasons, because all seedlings can be destroyed during only one winter or summer with unfavourable conditions (Smith et al. 2003). The occurrence of a long favourable period including several seasons is relatively rare though. Thus, tree establishment is not a continuous process. For example, many of tree islands in the Rocky Mts. were established in medieval climate optimum and then persisted via clonal reproduction (Holtmeier and Broll 2017). Regeneration pulses related to periods with favourable climate were observed across the majority of treelines (Camarero and Gutiérez 1999 and 2007, Wilmking et al. 2004, Dalen and Hofgard 2005, Treml et al. 2016).

2.4.2 Relief and topography

Local topography often plays significant role in modification of treeline position because of the influence on soil conditions and snow accumulation patterns (Germino and Smith 1999, 2000, Holtmeier 2009). This is particularly true for the long-laying or permanent snow fields, which usually depress local treeline (Holtmeier and Broll 2005).

Steep rock walls limit the occurrence of trees, slope curvature might affect treeline position as well through snow accumulation (concave slopes) or locally accelerated wind speed (convex slopes) (Holtmeier 2009, Treml and Chuman 2015). Patchiness of treeline ecotone often follows microtopography features such as solifluction risers, block fields, debris flow tracks, avalanche tracks etc. (Resler et al. 2005, Treml 2007, Holtmeier and Broll 2007, Hofgaard et al. 2009, Czajka et al. 2015a). Very shallow and undeveloped soils on resistant unweathered substrates can be limiting factors of treeline position as well (Holtmeier and Broll 2005).

2.4.3 The influence of mountain range size on treeline position

Treeline position generally decreases with increasing latitude, with exception of the tropics. Further, treeline position increases along maritime-continental gradients and towards the mountain range interiors (Han et al 2012b, Odland 2015, Zhao et al. 2015). The latter pattern leads to higher treeline positions in extensive mountain ranges than in small isolated massifs, called as the mass elevation effect, originally 'massenerhebung effect' (Brockmann-Jerosch 1919 in Wieser and Tausz 2007). The maritime-continental gradients occur, for instance, in central Scandinavia, where Kjällgren and Kullman (1998) reported an increase of the treeline elevation along the maritime-continental gradient between 100 to 150 m per 50 km of distance from the sea to inland. Around Tromsø at the coast (69 N, 19 E), the treeline is at 200 m ASL, while its elevation rises up to 700 m ASL in the Swedish Lapland (Holtmeier 2009); i.e. by ca 290 m per 100 km. Other examples of increasing treeline positions along continentality gradients are reported from south-eastern Tibet (Han et al 2012b – ca 150 m /100 km) or from north America, where the treeline in the Western Cascades is situated at 1500 – 1800 m and reaches 3000 m ASL in the Rocky Mountains; i.e. its elevation increases by ca 60 m per 100 km (Holtmeier 2009). Zhao et al. (2014) reports that continentality explains 11 % of the variation in timberline position in the western part of Eurasia. The low elevation of treelines in maritime regions results from high snow loads and intense wind action (Öberg and Kullman 2012; Takahashi 2014).

Concerning mass-elevation effect, mountains serve as elevated heat island, which makes them much warmer than free atmosphere in similar altitude leading to elevated treeline (Barry 2008). Central parts of mountain ranges receive more direct solar radiation because of less cloudiness compared to outer parts of mountains (Barry 2008). Mass elevation effect explains 52.2 % variability in global treeline elevation (Zhao et al. 2015).

2.4.4 Summit syndrome

Simultaneous influence of specific non-thermal factors occurring near to mountain ridges and summits can be described as a summit syndrome (Carlson et al. 2011, Körner 2012, Odland 2015). The expression 'summit syndrome' (or 'Gipfelphänomen' in German) was used first by Scharfeter in 1918 (Jeník 1961).

The summit syndrome manifests by abrupt change in several environmental characteristics at and in close vicinity of summits: (i) decrease in near the ground air temperature and soil temperature due to intense winds and low (or no) snow cover; (ii) low development of soils and (iii) abrupt change in vegetation reflected in locally depressed climatically-driven vegetation boundaries (Cogbil et al. 1997, Carlson et al 2011). Summit syndrome has been described from low elevated mountain ranges such as the Appalachians or High Sudetes (Jeník 1961, Leffler 1981, Cogbill et al. 1997) or from isolated peaks (Leuschner 1996).

In Appalachians, the patches of tundra ecotone are located in relatively low elevations at wind affected sites (Carlson et al. 2011). In addition, long lasting snow cover on leeward slopes depresses alpine tundra patches far below its climatic lower limit (Carlson et al. 2011). Consequently, treeline is depressed against its potential elevation up to 400 m (Cogbill et al. 1997), in southern part of Appalachians even about 1 000 m (Leffler 1981). In central Europe, the summit syndrome was reported from High Sudetes (Jeník 1961) and from isolated peaks of České Středohoří (Ložek 2011).

According to Dahl and Birks (2007) or Körner (2012), true climatic treeline cannot be formed in low elevated mountain ranges, since it requires several hundred meters of mountain terrain above treeline (Körner 2012, Körner et al. 2017). Grabherr et al. (2003) describe treeline in low mountains as pseudo-alpine or topographic timberline.

Isolated mountain massifs are often exposed to high wind speeds near summits (Barry 2008. Migała 2005). The acceleration of wind speed near isolated summits results from a low frictional effect of the surface on free air flow and from compression and subsequent release of air masses flowing over the mountain barrier (Barry 2008). Wind action is important particularly in winter, when wind transporting snow and ice abrades tree stems and leaves (Han et al. 2012a) and accumulates snow in leeward areas (Mamet and Kershaw 2013). Jeník (1961) described this phenomenon as a theory of anemo-orographic systems (A-O system). Even though, the presence of A-O system was described long time ago it was not sufficiently quantified. This also applies to entire summit syndrome, which is usually described as a binary factor which is just present or absent in given area.

2.4.5 Human interventions

Almost all European treelines have been developing under human pressure. The first evidence of human activities at treeline in the Alps were documented from the fifth millennium BC (Tinner and Theurilat 2003, Kaltenrieder et al 2005, Rey et al. 2013, Schwörer et al. 2014).

Even though, people were not able to reach the highest parts, the first evidence of pasture at treeline from the Alps are dated to 4 500 BC (Schworer et al. 2014). However, the first significant human interventions are dated from Southeastern Swiss Alps to 4 900 BC (Kaltenrieder et al. 2005), while from the Northwestern Swiss Alps from 1 000 BC (Schworer et al. 2014). First significant impacts (extensive erosion events) of mountain pasture on alpine landscape in Swiss Alps are dated to 12th century (Schworer et al. 2014). However, pasture in Swiss Alps receded considerably from the beginning of the 19th century (Gehrig-Fasel et al. 2007). In Italian Alps, grazing intensity peaked in the middle of the 19th century. In the first decades of the 20th century however, grazing was sharply reduced, first after the World War I (which included also the ban of goat pasture) and second after the World War II. The highest intensity of forest usage is dated to the 18th and 19th century (Motta et al. 2006).

In the Krkonoše Mts., the first significant human influences in the vicinity of treeline are dated to 1 000 AD (Malkiewicz et al. 2016) with substantial amplification of human impacts in 12th century (Speranza et al. 2000). Significant deforestation related to grazing and logging is dated to 15th and 16th century (Podrázský et al. 2007, Lokvenc 2007). In the Hrubý Jeseník and Králický Sněžník, the first human impacts were detected in 8th and 9th century, again with significant increase of human pressure from 14th century onwards (Novák et al. 2010, Dudová et al. 2013). In Carpathians, the first major human activities are dated to the era of Valach colonization, which lasted from 12th until 15th century (Plesník 1978, Fleischner and Chmiel 2010, Czajka et al 2015c). In High Tatras, treeline ecotone has been significantly affected by pasture and burning since 16th century (Obidowicz 1996, Plesník 1978). In 17th century, High Tatras hosted up to 200 000 sheep with the highest sheep density in the Belianské Tatry Mt. (up to 2 000 sheep per square km). Both in Sudetes and Western Carpathians, the intensity of mountain agriculture culminated in 18th and the first half of 19th centuries (Lokvenc 2007, Czajka et al. 2015c). Human activities in the past resulted in depression of treeline position about 200 or 300 m in Tatras (Plesník 1978) and in the same values are estimated from

several locations in High Sudetes (Lokvenc 2007). However, in extreme cases the treeline was lowered up to 700 m below its original position (Plesník 1978, Czajka et al. 2015c).

From the second half of 19th century, agricultural land abandonment started to be very important (Häufler 1955, Lokvenc 2007, Treml et al. 2016). Grazing and hay making in the vicinity of treeline ecotone was completely terminated in 1940s in the High Sudetes and in 1970s in Western Carpathians (Häufler 1955, Plesník 1978, Lokvenc 2007).

In the 1970s and 1980s, mountain forests in Sudetes and Western Carpathians underwent the period of high acid pollution load. Foliage loss and nutrient depletion from soils led to substantial growth depression (Kolář et al. 2015, Czajka et al. 2015c).

Despite the obvious human effect on treeline in the past, there is paleoecological evidence of naturally driven treeless area trough entire Holocene from the Krkonoše Mts. and from High and Low Tatra Mts. (Treml et al 2006, Novák et al. 2010, Obidowicz 1996). In the majority of remaining central-european mountains with treelines, alpine areas spontaneously developed in upper Holocene (Beug et al.1999, Novák et al. 2010, Kaczka et al. 2015), the latest. Since the middle of the 20th century, most treelines in Central European mountains have been developing spontaneously (Plesník 1978, Kozak 2003, Boltižiar 2007, Solár and Janiga 2013, Treml and Chuman 2015).

2.5   Recent treeline dynamics

In 20th century, increasing temperatures caused significant responses in temperature-limited ecosystems including treelines (Walther et al. 2002, Greenwood and Jump 2014). Most treelines revealed an increase in tree growth (Ponocná et al. 2016, Treml and Veblen 2017).

A few studies reported that treelines have been advancing about $0.3 - 0.43$ m.yr^{-1} in High Sudetes (Treml and Chuman 2015), $0.1 - 1$ m.yr^{-1} in Alaska (Dial et al. 2016), 1.15 m.yr^{-1} in the Alps (Leonelli et al. 2011), or even 3 m.yr^{-1} in Himalayas (Singh et al. 2011). On the other hand, some studies described stable treelines, for example Nagy et al. (2013) in the Cairngorn Mts. or Shrestha et al. (2015) from Nepal. Moreover, canopy densification rather than upward shift of trees has been frequently observed in various regions (Gehrig-Fasel et al. 2006, Danby et al. 2007, Singh et al. 2011, Pardo et al. 2013, Treml et al. 2016, Wang et al. 2016). This is supported by the study of Harsch et al. (2009) who reported that only 52 % of treeline had been advancing, whereas 1 % were retreating

and 47 % of treelines had not changed its position. Furthermore, 80 % of advancing treelines were classified as diffuse (Harsch et al. 2009).

Treeline position has been fluctuating troughout entire Holocene. The highest recorded treeline positions in Rocky Mountains were from 30 m (Carrara et al. 2015) up to 100 m (Morgan et al. 2014) higher than present treeline positions. Tinner and Theurilat (2003) and Heiri et al. (2006) reported Holocene treeline maxima to be 200 m higher compared to present treeline.

One of the possible reasons for ambiguous response of treeline to warming is a considerable time lag in treeline reaction (Körner 2012). Seedlings need some time to reach 'tree size'. Further, seedling establishment and survival is an episodic process (Camarero and Gutiérez 1999, Smith et al. 2003, Barbeito et al. 2012) and occurs mostly in regeneration waves (Körner 2012, Wilmking et al. 2004, Treml et al. 2016).

Plausible explanation of differences in treeline response to warming was offered by Harsch and Bader (2011) with their concept of treeline form (see above). Krummholz or abrupt treelines are relatively stable compared to diffuse treelines, because of other non-climate factors such as wind conditions, precipitation regime etc. (Harsch and Bader 2011). Furthermore, the response to changing climate can be species specific as well (Schwab et al. 2017, Treml and Veblen 2017).

3 Study area

Study area was represented by mountainous regions of Central Europe (from 48 to 51 °N and 10 to 20 °E) with palaeoecological evidence of climate driven forest free zones (Beug et al. 1999, Treml et al. 2006, Novák et al. 2010, Obidowicz 1996). Geographical position of the High Sudetes as well as Harz makes from these mountains the first major barrier for winds of north-western direction (Migała 2005). These mountains thus belong among the windiest mountain ranges in Europe (Migała 2005).

Most of the activities were conducted in the Krkonoše Mountains because of their good accessibility (study of xylogenesis). The Krkonoše Mts. belong to the windiest mountains in Europe (Migała 2005) and were therefore also suitable for studying the effect of wind on tree growth at treeline. The northernmost Central-European treeline ecotone is situated in the Harz Mountains (Hertel and Schölling 2011) (Table 1). Eastwards, the Sudetes represent an area with well-developed treeline ecotones (Krkonoše, Králický Sněžník and Hrubý Jeseník Mountains) (Jeník 1961). Further east, treelines are present on the Mt. Babia Góra and the Mt. Plisko in the westernmost flysch Carpathians (Figure.3) (Kozak 2003, Czajka et al. 2015b), in the Veľká and Malá Fatra Mountains (Plesník 1999) and in the Tatras (Plesník 1971).
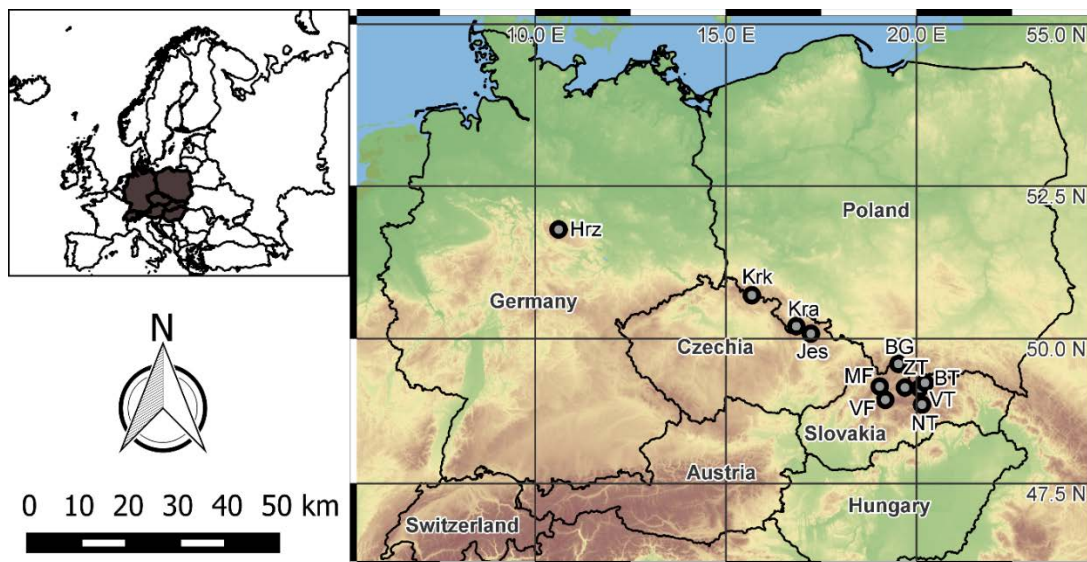

Figure 3: Location of the mountain ranges studied in Central Europe. Abbreviations in alphabetical order: (BG) Babia Góra and Pilsko; (BT) Belianské Tatry; (Jes) Hrubý Jeseník; (Kra) Králický Sněžník; (Krk) Krkonoše; (MF) Malá Fatra; (NT) Nízké Tatry; (VF) Veľká Fatra; (VT) Vysoké Tatry; (ZT) Západné Tatry.

The mountain ranges under study can be divided into two major groups. The Hercynian mountains (the Harz, Krkonoše, Králický Sněžník and Hrubý Jeseník Mountain) are lower elevated mountain ranges (from 1100 to 1600 m) composed mainly of acidic crystalline rocks characterized by flat summit surfaces and moderately steep slopes, with treelines located close to summits. The second group is represented by Western Carpatians, which vary in rock composition that includes limestone (Velká, Malá Fatra, Nízké and Belianské Tatry Mountains), flysh areas (Babia Góra Mountains) and crystalline massifs (the Vysoké and Západní Tatry Mountains, and the central part of the Nízké Tatry Mountains). In the Western Carpathians, there are mountains with moderate relief (Babia Gora or Veľká Fatra) or true alpine mountain ranges (the Vysoké or Západní Tatry Mountains). Treeline is located either close to summits at Babia Gora or Veľká Fatra Mts. or relatively far below summits (Vysoké Tatry, Západné Tatry).

The climate in all investigated areas is cold and humid with mean growing season temperatures from 9.4 °C (Harz Mts.) to 7.2 °C (Nízké Tatry Mts.) (Kašpar and Treml 2016) and annual precipitation from 1 200 mm (the Hrubý Jeseník Mountains) to 2 200 mm (the Vysoké Tatry Mountains: Migała 2005, Hlavatá et al. 2011). High-elevation tree stands are influenced by high wind speeds (Table 1).

The dominant treeline tree species is Norway spruce (*Picea abies* [L.] Karst.) (Treml and Banaš 2000, Hertel and Schöling 2011, Czajka et al. 2015b). In the Carpathians *Pinus cembra* and *Larix decidua* occur as well (Czajka et al. 2015b). Prostrate dwarf pine *Pinus mugo* either native or planted often forms extensive closed stands above timberline (Wild and Winkler 2008, Švajda et al. 2011). Treeline *Picea abies* occurs at treeline either as seed-based individuals or in the groups (tree islands) formed by vegetative reproduction (Šenfeldr et al. 2014).

The climate conditions together with vegetation and bedrock at Central European treelines determined development of soils, classified as podzols, dystric cambisols or rankers (on acidic crystalline bedrock and flysch) (Tomášek 1995, Granec and Šurina 1999, Hertel and Schöling 2011). Rendzinas are common in mountains composed of limestone (Granec and Šurina 1999).

Treelines in Central Europe have been for a long time under anthropogenic pressure. Most of the treelines was affected by long-term cattle grazing (Plesník 1971, Plesník 1978, Boltižiar 2007) or hay making (Lokvenc 2007). However, relatively undisturbed treelines remained on steep, inaccessible slopes. Furthermore, in areas where cattle grazing ceased several decades ago (Table 1), tree stands managed to attain their presumed original

position (Doležal and Šrůtek 2002, Boltižiar 2007). In the majority of the mountains under study, the protected areas were established after World War II and during the second half of the 20th century (Table 1). In the second half of 20th century and recently, treelines have been developing relatively spontaneously due to the cessation of mountain agriculture and nature protection (Kozak 2003, Boltižiar 2007, Solár and Janiga 2013, Treml and Chuman 2015).

Table 1: List of selected mountain ranges, with the highest peak elevation, treeline elevation and information about pasture abandonment and establishment of protected areas.

Mountain range	Latitude, longitude	Highest peak elevation (m a.s.l.)	Published timberline elevation	Pasture abandonment at the treeline eccotene	Time of establishment of protected area
Harz	51°48'N 10°37'E	1141	1100 m (Hertel and Schöling 2011)	Middle of the 19th century (Andreas Marten personal communication)	Eastern part in 1990, western part in 1994, Nationalpark Harz in 2006 (http://www.nationalpark-harz.de)
Krkonoše	50°44'N 15°44'E	1603	1340 m (Treml and Migoń 2015)	End of the 19th century, first half of 20th century (Lokvenc 2007)	Karkonoski Park Narodowy 1959 (Polish side), Krkonošský národní park 1963 (Czech side) (http://www.krnap.cz)
Králický Sněžník	50°12'N 16°51'E	1424	1305 m (Treml and Migoń 2015)	First half of 20th century (Treml et al. 2016)	National nature reservation Králický Sněžník 1990 (http://www.sneznik.cz)
Hrubý Jeseník	50°05'N 17°14'E	1491	1405 m (Treml and Migoń 2015)	First half of 20th century (Treml et al. 2016)	CHKO Jeseníky 1969 (http://jeseniky.ochranaprirody.cz)
Babia Góra	49°35'N 19°32'E	1725	1370 m (Czajka et al. 2015a)	Beginning of the 20th century (Kaczka et al. 2015b)	Babiogórski Park Narodowy 1994 (http://www.bgpn.pl/en)
Malá Fatra	49°10'N 19°00'E	1709	1450 m (Plesník 1978)	After 2nd World War (Plesník 1978)	CHKO Malá Fatra 1967 (http://www.npmalafatra.sk)
Veľká Fatra	48°55'N 19°04'E	1592	1510 m (Vestenický and Vološčuk 1983)	After 2nd World War (Plesník 1978)	CHKO Veľká Fatra 1973 (http://www.sopsr.sk/velkafatraweb/sk)
Nízké Tatry	48°57'N 19°30'E	2043	1550 m (Grodzińska el al. 2004)	After 2nd World War (Plesník 1978)	Národný park Nízke Tatry 1978 (http://www.napant.sk)
Západné Tatry	49°12'N 19°45'E	2248	1550 m (Švajda et al. 2011)	Some parts from the 1879, the rest of the area after 2nd World War (Plesník 1978)	Tatranský národný park 1948 (http://spravatanap.sk)
Vysoké Tatry	49°08'N 20°13'E	2655	1715 m (Plesník 1971)	Some parts from the 1879, the rest of the area after 2nd World War (Plesník 1978)	Tatranský národný park 1948 (http://spravatanap.sk)
Belianské Tatry	49°14'N 20°13'E	2152	1475 m (Plesník 1978)	Some parts from the 1879, the rest of the area after 2nd World War (Plesník 1978)	Tatranský národný park 1948 (http://spravatanap.sk)

4 Materials and Methods

Three different sets of methods of sample collection and processing were employed. First set of methods was used to calculate the thermal regime of treelines in Central Europe. Second set of methods was based on retrospective analysis of tree growth and morphometric measurements of selected trees. Last set of methods was related to monitoring and evaluation of xylogenesis. The number of sampled trees and sampling design differed according to the purpose of individual research tasks.

The comparison of treeline temperature regime was carried out at regional scale. Mountain ranges with climatically-driven treeless areas were selected based on literature survey (11 mountain ranges in total). Then, the highest positions of treeline were determined in each mountain range. To do so, we used Google Earth for availability of high-resolution satellite images. Available climate data from nearest mountain meteorological observatories (monthly temperature means and monthly sums of precipitation) were adjusted to the treeline position.

To compare thermal regime of treelines we computed mean temperature of the warmest month, mean Jun-Sep temperature and sum of temperatures above 0 °C. Further, mean growing season temperature and growing season length was calculated after Paulsen and Körner (2014). According this method, growing season length is shortened by the modelled duration of snow cover accumulated in the previous winter.

Retrospective analysis of tree growth was used in two studies monitoring interaction of tree growth with wind influence (in the Krkonoše Mts.) and other influencing factors (at regional scale). For the analysis of treeline position at regional scale, trees from the highest treeline positions in 10 mountain ranges were sampled. 15 trees in each highest treeline position were cored and measured for various growth parameters and variables describing biomass loss (about 150 trees in total). At a local scale, we randomly selected 70 plots in the Krkonoše Mts. At each plot, we sampled 3 individuals. For both studies, we measured tree height, stem girth, length of branches in four directions, we determined presence of apical breaks, stem abrasion, presence of multistems, layering branches and the number of trees in tree group. Two tree-ring cores were collected from each tree, at 50 cm and at 200 cm respectively. Obtained samples were used for analysis of radial growth and for calculation of average height increment. Tree ring cores were sanded and measured on

TimeTable using Past4 software (SCIEM 2009). The same software was consequently used for synchronization of tree ring series.

To identify the response of wood formation to temperatures in treeline ecotone, xylogenesis was analysed at two localities at upper (treeline) and lower (timberline) part of treeline ecotone. Both localities were located at southern slope of the Mt. Luční hora in the Krkonoše Mts. An altitudinal gradient between sites was about 140 m. From 6 to 10 trees were sampled during growing seasons 2010, 2011, 2012. Sampling has been continuing on another two sites in 2014 and 2015, however the results from these two sites are not published yet.

To analyse xylogenesis (intra-annual tree growth), microcores were collected each week using TREPHOR tool (Rossi et al. 2006b). Microcores were prepared (dehydrated and embedded into parafin) for sectioning following the procedure of Rossi et al. (2006b). Then, the samples were cut using microtome and attached to microslides (Gryc et al. 2012). Finally, the number of cells in each stage of development in three radial files was counted under 400x magnification.

Among statistical methods used in this dissertation, linear models (regression, correlation, ANOVA) or mixed-effect models were computed in R (R Development Cote Team 2015), multivariate statistics were performed in CANOCO 5 (Šmilauer and Lepš 2014).

5 Author's contribution to presented

Article	Author's contributions (%)	Primary responsibility	Further details and current status
Differences in intra-annual wood formation in *Picea abies* across the treeline ecotone, Giant Mountains, Czech Republic.	35 %	• data collection in 2011 and 2012, • sample preparation of samples from the half of vegetation season 2010 – 2012; • statistical evaluation,	Appendix 1 Published in 2015 in Trees
Thermal characteristics of alpine treelines in Central Europe north of the Alps.	60 %	• data collection and calculation • statistical evaluation • preparation of early version of manuscript	Published in 2016 in Climate research
The effect of wind on growth of treeline Norway spruce.	60 %	• sample collection and evaluation, • statistical evaluation, • manuscript preparation	Published in 2017 in Alpine Botany
Relation between tree growth and temperature explains formation of regional treelines. Journal of Biogeography, under review.	65 %	• sample collection and evaluation, • statistical evaluation, • manuscript preparation	Under review in Journal of Biogeography

II.   Article I

Differences in intra-annual wood formation in *Picea abies* across the treeline ecotone, Giant Mountains, Czech Republic

ORIGINAL PAPER

Differences in intra-annual wood formation in *Picea abies* across the treeline ecotone, Giant Mountains, Czech Republic

Václav Treml · Jakub Kašpar · Hana Kuželová · Vladimír Gryc

Abstract

Key message ***Picea abies* requires warming of both the above- and belowground parts of the tree for full resumption of cambial activity.**

Abstract Elevation-related decrease in growing season temperatures is a highly important factor in limiting tree growth in cold environments such as alpine treeline ecotones. In this study, we aimed to identify radial growth timing differences in *Picea abies* (L.) Karst. between the lower (timberline) and upper (treeline) parts of an alpine treeline ecotone. Over three growing seasons, soil and air temperatures were measured and phenology of wood formation was analyzed at two sites separated by 140 m of elevation in the Giant Mountains, Czech Republic. The results showed that there were two periods with significant differences in wood phenology between timberline and treeline. In the early part of the growing season, higher ambient temperatures at timberline led to higher number of cambial and enlarging cells here than at treeline. In the second part of the growing season, the bigger and/or more numerous tracheids at timberline than at treeline required more time for maturation. Significant delay in the beginning of wood formation at treeline in comparison to timberline was observed only in 2011, when soil was frozen markedly longer at treeline. We found that cambial activity significantly increased when soil temperature increased from near zero to a threshold temperature of 4–5 °C. We therefore suggest that for *P. abies* both the above- and belowground parts of the tree must be sufficiently warm for full resumption of cambial activity.

Keywords Cambium · Xylogenesis · Giant Mountains · Norway spruce · Tree ring · Elevation gradient

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Introduction

Growth of trees at their upper altitudinal limits is limited by available heat (Körner 2012a). Therefore, trees at climatic treelines are sensitive to temperature oscillations, with their reactions reflected in changes in radial growth, height growth or growth form (Holtmeier 2009). Two competing hypotheses have attempted to explain temperature limitation of tree occurrence in cold environments (Körner 1998; Wiley and Helliker 2012). The carbon balance hypothesis attributes low growth rates in cold environments to low rates of carbon assimilation ("source" limit); the growth limitation hypothesis, in contrast, explains low growth by temperature limitation of building new tissues ("growth" or "sink" limit; Körner 1998). Recently, the second seems to have received stronger support (Hoch and Körner 2012; Simard et al. 2013), but the exact description of low-temperature limitation of physiological processes is still missing.

The relationship between temperature and tree growth has been studied most frequently in terms of radial growth, both on inter-annual (e.g., Büntgen et al. 2007) and intra-annual time scales (e.g., Rossi et al. 2013).

Radial growth is realized mainly by mitotic activity of cambial cells and subsequent enlargement of cells differentiated from the cambial zone. Cambial activity is induced hormonally particularly by indole-3-acetic acid (IAA), whose production, in turn, is affected by photoperiod and ambient temperatures (Friml 2003; Rossi et al. 2007). Higher tissue temperatures promote cambial activity and cell enlargement (Gričar et al. 2006). These processes are not possible without stem rehydration, since the cambial water potential modulates cambial activity (Savidge 2000; Turcotte et al. 2009). Based on these considerations, complex climatic characteristics might, therefore, be expected to affect tree growth at treeline (e.g., Gorsuch and Oberbauer 2002).

Several studies have suggested that thermal limitation of tree growth at cold sites is closely coupled with tree architecture (Gruber et al. 2009; Petit et al. 2011; Anfodillo et al. 2012; Körner 2012b). Larger trees are usually exposed to lower ambient temperatures surrounding their tree tops, and their roots are also cooler due to soil shading by more extensive crowns (Gruber et al. 2009; Körner 2012a). Additionally, tree size and xylem conduit diameter are strongly, positively related (Anfodillo et al. 2012). Because tree stature decreases in the upslope direction across the treeline ecotone, the ambient temperatures and wood phenology of trees in this ecotone do not have simple, direct relationships with increasing altitude (Körner 2012a).

Published studies focused on intra-annual growth, conducted along altitudinal transects including treeline ecotones have been performed on *Pinus cembra* (Gruber et al. 2009) and *Larix decidua* (Moser et al. 2009). However, to our knowledge no data gathered from the altitudinal gradient in the treeline ecotone are available for Norway spruce [*Picea abies* (L.) Karst.]. Intra-annual wood formation of *P. abies* has been studied particularly in less extreme temperate environments (e.g., Gričar et al. 2014; Cuny et al. 2014).

Picea abies is an important treeline species in Central and Eastern Europe. In the treeline ecotone, the ring width of *P. abies* is governed mainly by positive responses to June–July temperatures (Büntgen et al. 2006; Savva et al. 2006; Büntgen et al. 2007; Hartl-Meier et al. 2014), but temperatures of the preceding autumn are also important (Treml et al. 2012). Across the treeline ecotone, the temperature-growth relationship might weaken with increasing elevation as a result of increasing climatic stress induced by wind action, irregular distribution of snow or frost-desiccation (Oberhuber 2004; Treml et al. 2012). One possible reason for changing climate–growth relations across the alpine treeline ecotone might be differences in wood phenology between the lower and upper parts of the ecotone, as different durations of wood-phenological phases imply different sensitivities to growing season temperatures.

In our study, we aimed to find the differences in phenology of wood formation between the lower part of the treeline ecotone (hereinafter called "timberline") and the upper part of the treeline ecotone ("treeline") in the Giant Mountains, Czech Republic. Our objective was to discern temporal differences in: (a) phenological phases and; (b) the number of cells within the individual phases. We assumed that the 140 m elevation difference between our sites should lead to significant delay in onset of wood formation at the colder, treeline site, which would also be characterized by significantly fewer formed cells in all phenological phases in comparison to the warmer timberline site. Treeline ecotones in our study area, aside from having low temperature, are affected by intense wind action as is rather common characteristic of treelines in a large number of mountain ranges in the world (Holtmeier 2009). We, therefore, aimed to also determine whether the temperature thresholds for the onset of wood formation at our sites are similar to those reported from typical alpine areas (e.g., Rossi et al. 2007).

To our knowledge, this study is the first examining the phenology of *P. abies* wood formation from an altitudinal transect across the treeline ecotone and, furthermore, expands the available information on the association between temperature and onset of wood formation in the treeline ecotone. In the present study, wood formation (or xylogenesis) is understood as a suite of phenological phases beginning with cambial cell division and followed by cell differentiation (Chaffey 2002).

Materials and methods

Study area

The Giant Mountains in the Czech Republic, with highest peak Mt. Sněžka (1602 m), are characterized by high precipitation (approximately 1,400–1,600 mm per year) and mean annual temperature of 0.3 °C in the uppermost locations (1901–1995; Glowicki 1998). Strong west winds (mean wind velocity ca. 10 m s⁻¹ at Mt. Sněžka) are responsible for irregularly distributed snow pack, with its minimum depths at summits and maximum depths in the alpine timberline zone (Štursa et al. 1973; Tolasz et al. 2007). The forests of the upper montane belt and treeline ecotone are composed of *P. abies* [L.] Karst. Graminoids and prostrate dwarf pine (*Pinus mugo*) stands dominate alpine and subalpine communities. The treeline ecotone is situated at altitudes ranging from 1,250 to 1,450 m.

Our two study sites are located along an altitudinal gradient on the south-facing slope of Mt. Luční Hora

(1,555 m). Stands at the "timberline" site (1,310 m, 50°43′19″N, 15°40′19″E) comprise *P. abies* with maximum height about 8–9 m and canopy cover 30 %. The "treeline" site (1,450 m, 50°43′27″N, 15°40′42″E) is represented by open *P. abies* stands (canopy cover ca. 10 %) commonly consisting of clonally formed tree groups. The maximum tree height at the latter site is about 4 m. Soils at both sites are podzols.

Temperature measurements

At each site, air temperatures at the tree top (1 measuring point) and soil temperatures in the root zone (−10 cm, four measurement points) were recorded. Temperatures were measured and stored in 1-h intervals using EMS MicroLog (soil) and EMS Minikin (air, in radiation shield) loggers (http://www.emsbrno.cz). The temperature sensors have ±0.2 °C accuracy. Daily temperature means and daily maximum and minimum air and soil temperatures were used in subsequent comparisons and analysis.

Wood sampling and evaluation

Wood formation of eight (2010), ten (2011) and six (2012) *P. abies* individuals from each site was assessed (see Table 1 for the overall tree characteristics by site and year). The average ages of monitored individuals were 72 years at timberline and 70 years at treeline. Between-site differences in age were not statistically significant (Mann–Whitney *U* test, $p > 0.05$). Differences in age were, however, statistically significant between the trees sampled in different years. Mean tree heights were 8.3 m at timberline and 3.8 m at treeline. Between-site differences in tree height were significant in each year of monitoring (*t* test, $p < 0.05$).

Wood microcores were sampled using a Trephor puncher (Rossi et al. 2006). The distance between adjacent sampling points on a stem was always larger than 3 cm. Microcores were sampled at stem height 1 ± 0.2 m. Sampling intervals ranged from 7 to 8 days at the beginning of the growing season to 10 days in the second half of

the growing season. Sampling was conducted from April (or May, in 2010) to the end of September or the beginning of October. Immediately after sampling, the microcores were immersed in formaldehyde-ethanol-acetic acid fixative (FAA) and transported in Eppendorf microtubes to the laboratory. Laboratory procedures followed Gryc et al. (2012). Microcores were dehydrated using successive series of ethanol and xylol and embedded in paraffin; then, using a sliding microtome, 20-μm thick cross sections were created. Paraffin was removed using successive series of xylol and ethanol-solutions with descending ethanol concentration. Cross sections were then stained with safranin and astra blue, and mounted on permanent slides using Canada balsam.

For each cross section, the number of cells in each phenological phase was counted under 400–500× magnification. The following phases were distinguished: cells in the cambial zone (CZ), enlarging cells (EN), wall-thickening cells (WT) and mature cells (MT). Cambial cells were radially flattened, with thin cell walls. Enlarging cells had only primary walls and cell protoplast and ratios of tangential:radial size smaller than 2. Wall-thickening cells were characterized by glistening cell walls under polarized light and the presence of cell protoplast. Mature cells showed empty cell lumina and red cell walls. The number of cells in three radial files was counted, and the mean value from these three files was considered in further analysis. The number of cells in each cell phase (except cells in the cambial zone) was standardized for possible differences attributable to sample position on the stem (height, eccentricity) using the number of cells in the preceding year's tree ring (Rossi et al. 2003).

For each tree, the date (day of the year—DOY) of the onset of cambial activity was determined as indicated by the number of cambial cells first being higher than that in the dormant cambium at the end of the growing season plus its standard deviation (SD) (Rossi et al. 2007). The end of cambial activity was indicated by the decrease in the number of cells in the cambial zone below the mean number of cells in the dormant cambial zone plus SD. The onset of cell enlargement was indicated by the occurrence

Table 1 Basic characteristics of studied trees

Year	Site	Age (years)	Height (m)	Diameter at breast height (cm)	Radial size of tracheids (μm)	Tree ring width (mm)
2010	Timberline	56 ± 10	7.2 ± 0.6	27.2 ± 5	28.3 ± 8	1.60 ± 0.62
	Treeline	49 ± 13	3.5 ± 0.4	12.6 ± 2	21.4 ± 3	1.42 ± 0.72
2011	Timberline	68 ± 21	7.7 ± 0.7	28.9 ± 6	30.8 ± 5	2.17 ± 0.90
	Treeline	72 ± 24	3.6 ± 0.4	12.7 ± 2	25.2 ± 10	1.00 ± 0.74
2012	Timberline	92 ± 26	9.9 ± 0.9	39.1 ± 5	46.3 ± 26	2.21 ± 1.17
	Treeline	89 ± 22	4.2 ± 0.5	13.3 ± 2	15.9 ± 5	1.44 ± 1.15

Tracheid sizes and tree ring widths are from rings formed in the listed year (i.e., 2010, 2011 or 2012). Mean values and standard deviations are shown

of the first row of enlarging cells, the beginning of cell wall thickening by the first row of wall-thickening cells, and cell maturation by the first row of mature cells. The duration of cell differentiation was defined as the period between the appearance of the first enlarging cells and the achievement of the full development of all cells in the growth ring. For the onset and termination of each cell phase, the differences in DOY between sites and between years were tested using a Mann–Whitney U test. In addition, for each sampling date, between-site differences in the number of cells in individual cell phases were tested, again using a Mann–Whitney U test.

Radial tracheid size (i.e., the diameter of cell lumen and cell wall) was measured at three files of tracheids per tree ring from microcores collected at the end of the last sampling interval (i.e., when all tracheids were mature). Measurement was done using WinCell software (Régent Instruments 2011). Between-site differences in cell sizes were tested with t test.

Temperature characteristics of the onset of wood formation

For each season and each site, the average, maximum and minimum daily air and soil temperatures were computed. Additionally, to identify longer warm or cold periods affecting wood formation (Begum et al. 2013), 6-day backward means of average, maximum and minimum daily temperatures were computed.

Because temperature data were collected at the site level, the onset of wood formation had to also be defined at the site level, i.e., one date determined to characterize the onset of each phenological phase for all the trees at the site. For this purpose, the site level date of the onset of cambial activity was determined as the day when the mean number of cells in the cambial zone of all trees, minus half the standard deviation (SD), exceeded the mean number of cells in the dormant cambial zone (Rossi et al. 2007). The onset of cell enlargement at the site level was indicated by the mean number of enlarging cells being greater than 1 (after subtracting half the SD). Because, we were also interested in the first significant and pronounced reaction of the cambial zone to temperature at site level, we also distinguished statistically significant differences in the number of cambial cells between two consecutive observations (hereinafter called "significant increase in cambial activity"). Differences between two consecutive observations were tested using the Wilcoxon signed rank test.

We assumed that temperature thresholds of the onset of wood formation should display low variability among the sites and seasons. Furthermore, if a temperature threshold is first reached in spring, trees should display a clear and consistent growth reaction across sites and sampling years
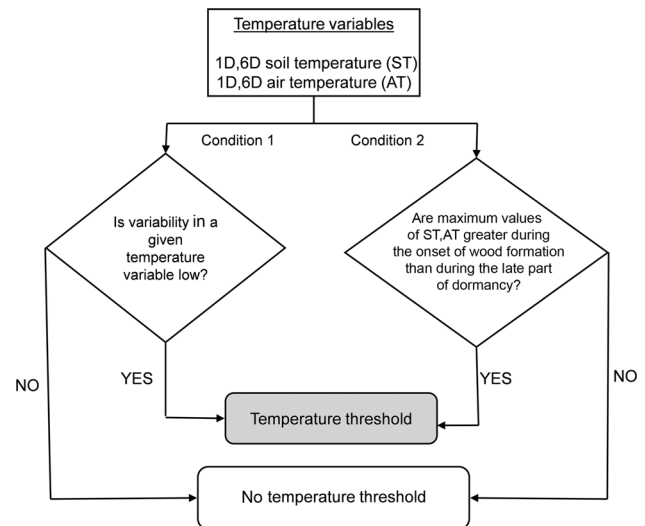

Fig. 1 Scheme describing the procedure of temperature threshold selection. *1D* daily temperatures, *6D* 6-day backward temperature means

(Fig. 1). For each sampling interval in which one of the early phenological phases of wood formation was recorded for the first time, we would identify the highest value of each temperature variable during that interval. The variability in these highest temperature values across sites and years was measured using standard deviations.

Additionally, we examined whether the studied temperature variables actually could have triggered individual early phenological phases of wood formation (Fig. 1), by testing whether maximum temperatures (both daily and 6-day air and soil temperatures) were greater during each given sampling interval in which an early phenological phase of wood formation was recorded for the first time than in the late part of dormancy that preceded it. Temperature data from the beginning of April were available for each year, therefore the period from the beginning of April to the last week preceding the onset of a given phenological phase was used for computation of maximum temperature variables values shown in late dormancy. The Wilcoxon signed rank test was used to statistically analyze differences between temperatures characterizing the phase onset and the late part of dormancy.

Results

Site temperatures

Mean growing season temperatures, expressed as the average temperature over the May–September period, ranged from 8.2 °C for air and 6.9 °C for soil at the treeline site to 10.6 °C (air) and 8.6 °C (soil) at the
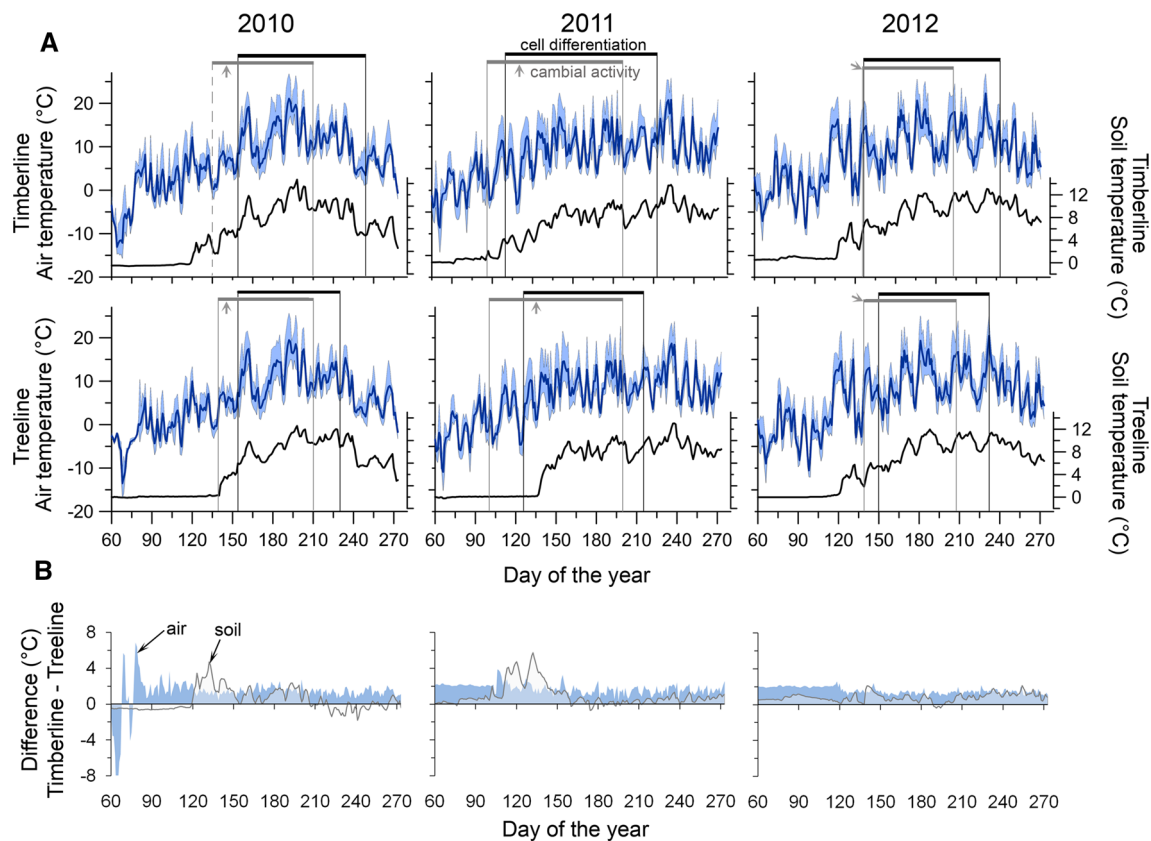
Fig. 2 a Daily means of air and soil temperatures during growing seasons 2010, 2011 and 2012. Air temperatures are buffered by daily minima and maxima. *Horizontal gray* and *black stripes* indicate duration of cambial activity and cell differentiation, respectively. *Arrows* denote first significant increase in the number of cambial cells. **b** Between-site ($T_{\text{TIMBERLINE}} - T_{\text{TREELINE}}$) differences in daily air and soil temperature means

timberline site (Fig. 2a). The warmest growing season was in 2012, whereas the coldest was the 2010 season. The warmest month of the year was always July both in terms of air and soil temperatures. Averaging across all three growing seasons, soil temperatures were lower at treeline than at timberline by 0.8 °C, and air temperatures were lower by 1.4 °C. The vertical temperature gradients were thus approximately 0.5 °C/100 m for soil temperatures and 0.9 °C/100 m for air temperatures. The highest between-site differences were recorded in May for soil temperatures and in April for air temperatures (Fig. 2b).

Mean temperatures for the period between the onset of cambial activity and the end of cell differentiation were 11.1 ± 0.6 °C for air and 8.7 ± 0.6 °C for soil at timberline and 9.9 ± 0.5 °C for air and 8.1 ± 0.6 °C for soil at treeline. Between-site differences during the period of cambial activity and cell differentiation were thus smaller by 0.2 °C for both air and soil temperatures than differences computed over the May–September period.

The abrupt spring increase in soil temperatures from near-zero temperatures indicating snow melt and/or soil thawing were simultaneous across the two sites in 2012, occurring between May 3 and May 5 (Fig. 2a). In 2010, snow melt and/or soil thawing was delayed by 20 days at treeline compared with timberline; however, increase in soil temperature at timberline was slow, with several oscillations back to about 2 °C. In 2011, abrupt soil warming was delayed at treeline in comparison to timberline by about 20 days.

Between-site differences in wood formation

The onsets of individual phenological phases of wood formation tended to be earlier at the timberline site than at the treeline site (Fig. 3). In contrast, the ending of cell enlargement and wall thickening was earlier at the treeline site than at the timberline site (Figs. 2a, 3). However, statistically significant delays in the onsets of both cambial activity and cell enlargement at treeline in comparison to timberline were recorded only in 2011, and significantly delayed wall thickening at timberline against treeline site was observed only in 2010 (Mann–Whitney *U* test, $p < 0.05$). Remaining differences in DOY of onset and

Fig. 3 Differences in dates (day of the year) of the onset and termination of individual phases of wood formation. *Middle points* denote means, *whiskers* indicate standard deviations. *CZ* cambial activity, *EN* enlarging cells, *WT* wall-thickening cells, *M* mature cells
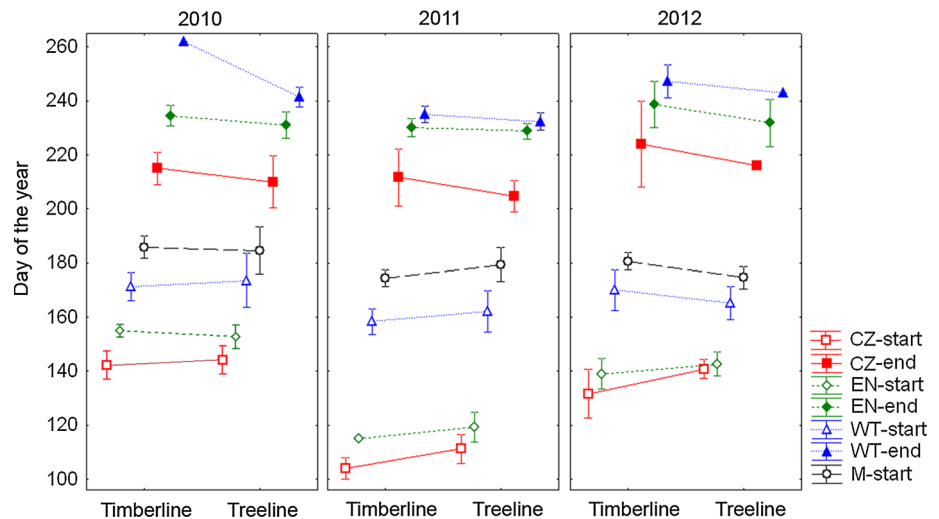
termination of individual phases of xylogenesis were not statistically significant (Mann–Whitney U test, $p > 0.05$).

Between-site differences in the number of cells found in each phase of wood formation (Fig. 4) were characterized particularly by higher number of cambial and enlarging cells at timberline in comparison to treeline during the first half of the growing season. Moreover, higher number of cells in the cell-enlargement and wall-thickening phases at timberline than at treeline was observed in August, i.e., at the end of these phases. In 2010 and 2012, greater number of mature cells was observed at treeline than timberline at the beginning of cell maturation. In 2011, this difference was reversed at the end of the growing season, when timberline trees had significantly more mature cells than did the treeline trees.

At the site level, the onset of cambial activity was observed in 2011 and 2012 on the same sampling date at both sites (Table 2). In 2010, cambial activity of most trees at timberline had started immediately before the first sampling date (Figs. 2a, 4). The first significant increase in the number of cambial cells occurred at both sites at the same time in 2010 and 2012. In 2011, this increase in cambial activity was delayed at treeline by 1 week compared to timberline. The first enlarging cells at the site level (i.e., the date when the mean number of enlarging cells for all trees was bigger than 1) occurred earlier at the timberline site in 2011 and 2012, whereas in 2010 it happened at both localities at the same time (Table 2; Fig. 4). The beginning of cell enlargement occurred approximately 2 weeks after the onset of cambial activity.

The duration of cell differentiation ranged from 96 to 121 days at the timberline site and 83–102 days at the treeline site, and it was always longer at the timberline site than at the treeline site (Table 2). The between-site differences in number of mature cells at the end of the

growing season were statistically significant only in 2011, with timberline trees forming more cells than treeline trees. Average radial sizes of tracheids were 33 ± 17 and 21 ± 9 μm at timberline and treeline, respectively, with significant differences in each year ($p < 0.05$) (Table 1). In each growing season, tree ring widths were significantly greater at timberline than at treeline (timberline mean = 1.9 mm, treeline mean = 1.1 mm, t test, $p < 0.05$).

Temperature ranges characterizing onsets of cambial activity and cell enlargement

The lowest variability among temperature variables characterizing the onset of cambial activity at the site level (Table 3) was in 6-day minimum air temperatures (3.7 °C mean $\pm$ 1.9 °C SD). During both the first significant increase in the number of cambial cells and the beginning of cell enlargement, the lowest variability was again in 6-day minimum air temperatures (4.9 ± 0.9 and 5.2 ± 1.3 °C, respectively). Daily mean and maximum air temperatures showed greater variability, whereas the standard deviations of soil temperatures were generally smaller than those of air temperatures except for air minima (Table 3).

Soil temperatures (4.6 °C for daily and 3.6 °C for 6-day means) during the first pronounced increase in cambial activity were significantly higher than those prior to this period ($p < 0.05$, Wilcoxon signed rank test) (Table 3). During the onset of cell enlargement, the 6-day soil temperatures were also significantly higher than those before this period ($p < 0.05$, Wilcoxon signed rank test). Neither the temperature variables characterizing the onset of cambial activity nor the remaining variables (particularly air temperatures) associated with the periods of significant
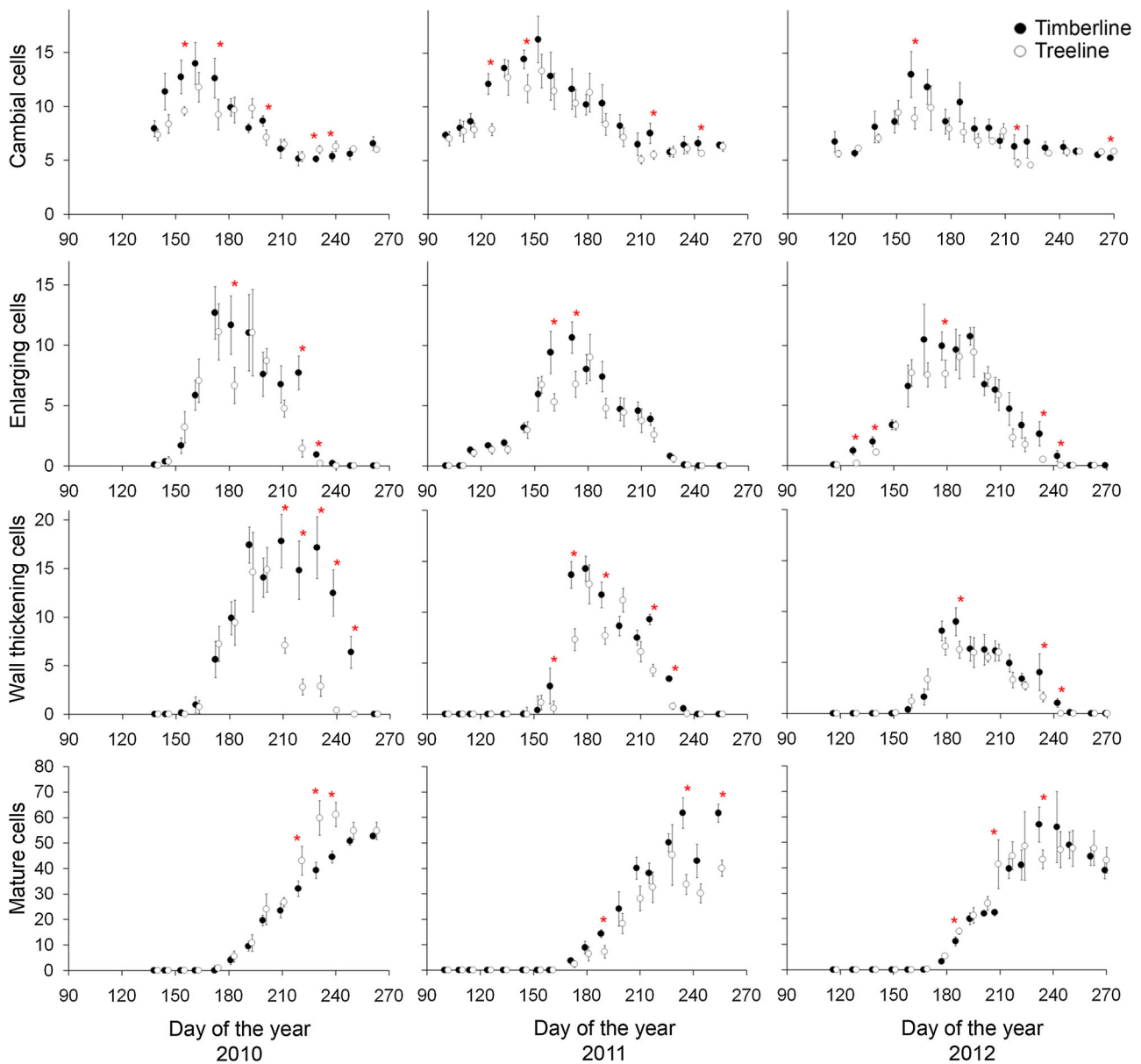
Fig. 4 The number of cells in individual phases of xylogenesis. *Middle points* indicate means, *whiskers* indicate standard deviations. *Asterisks* indicate significant differences in the number of cells between timberline and treeline based on Mann–Whitney *U* test (*p* < 0.05). *Black circles* denote timberline, *white circles* denote treeline

increase in cambial activity and cell enlargement were significantly higher than those in the periods preceding the given phenological phases of wood formation (Table 3).

Discussion

Given the 140 m altitudinal gradient, we expected differences between sites in the onset of cambial activity and cell enlargement. However, the onsets (in early May) of both cambial activity and cell enlargement were only slightly delayed at treeline compared to timberline, with only

1 year showing statistically significant differences at the weekly sampling resolution. That year was 2011, when the between-site temperature differences, particularly in soil temperatures, were the greatest. If there was any delay in cambial reactivation and/or in onset of cell enlargement in the remaining years, it would have to have been shorter than 1 week. Indeed, such short delays were reported by Moser et al. (2009), who found that cambial reactivation of larch was delayed about 3–4 days per 100 m of elevation.

Later (in the second half of May and in June), we observed that the between-site differences in the number of cells were, however, pronounced, with more cells in the

Table 2 Basic characteristics of wood formation at the site level: onset and duration of cambial activity and cell-enlargement phases, duration of cell differentiation

Year	Site	Onset of cambial activity	Significant increase in cambial activity	Duration of cambial activity (days)	First enlarging cell	End of cell differentiation	Duration of cell differentiation
2010	Timberline	Before 19 May	25 May	More than 71	3 Jun	6 Sep	95
	Treeline	19 May	25 May	71	3 Jun	27 Aug	85
2011	Timberline	10 Apr	5 May	98	25 Apr	15 Aug	112
	Treeline	10 Apr	14 May	98	4 May	4 Aug	91
2012	Timberline	18 May	18 May	69	18 May	30 Aug	104
	Treeline	18 May	18 May	69	29 May	20 Aug	83

Table 3 Average values and standard deviations of temperature variables characterizing early stages of wood phenology

Variable	Onset of cambial activity (°C)	First significant increase in cambial activity (°C)	First enlarging cells (°C)
Air temperatures			
1 day mean	8.3 ± 3.7	11.3 ± 3.3	10.4 ± 3.6
1 day max	12.5 ± 4.1	16.1 ± 3.3	15.1 ± 4.2
1 day min	5.7 ± 3.3	8.3 ± 2.9	7.8 ± 3.2
6 day mean	5.1 ± 1.8	8.0 ± 1.0	8.3 ± 1.7
6 day max	8.7 ± 2.2	12.1 ± 2.1	12.4 ± 2.7
6 day min	2.4 ± 1.6	4.9 ± 1.0	5.3 ± 1.3
Soil temperatures			
1 day mean	1.6 ± 2.1	$4.6 \pm 2.2*$	4.6 ± 2.2
1 day max	1.9 ± 2.3	$4.9 \pm 2.4*$	5.0 ± 2.4
1 day min	1.4 ± 2.0	$4.2 \pm 2.0*$	4.3 ± 2.1
6 day mean	1.3 ± 1.6	$3.6 \pm 1.8*$	$3.8 \pm 1.9*$
6 day max	1.5 ± 1.8	$4.1 \pm 2.0*$	$4.2 \pm 2.1*$
6 day min	1.1 ± 1.4	$3.2 \pm 1.6*$	$3.5 \pm 0.9*$

Asterisks mark that temperatures were significantly higher during the sampling interval of the given phase's onset than in the preceding period of late dormancy ($p < 0.05$)

cambial zone and more enlarging cells found at timberline than at the treeline site. Thus, after the onset of cambial activity, the number of cambial zone cells and enlarging cells probably react to ambient temperatures more directly than does the onset of cambial activity itself. A similarly clear reaction of cambial activity and the number of enlarging cells to warmer ambient temperatures have been documented in other studies (e.g., Gričar et al. 2006; Lenz et al. 2013).

We observed that, during the growing season, cell differentiation phases usually finished later at timberline, lead to longer duration of wood formation there. The differences in the number of cells between timberline and treeline at the end of cell enlargement and wall thickening were even more pronounced than the differences in the early

phenological phases of wood formation. This delay is in accordance with significantly bigger diameters of tracheids at timberline requiring more time for their enlargement (Anfodillo et al. 2012). Our data suggest that the difference in the number of cells achieved at the end of cell enlargement is probably retained or even increased during the wall-thickening phase. Delay in finishing the cell-enlargement and wall-thickening phases is also in line with the possible integrative effect of growing season temperatures on the completion of cell maturation (Rossi et al. 2013). In comparison to treeline, the timberline site showed more intensive cambial activity, followed by production of greater number and/or larger sizes of enlarging cells which then needed more time for maturation (Lupi et al. 2010; Cuny et al. 2014).

Similar dates for the onset and differing dates for the completion of the enlargement and wall-thickening phases contrast with the findings of Moser et al. (2009) on larch. They found that whereas onsets were delayed at higher elevations, the termination of cell differentiation was simultaneous. We suggest that this disparity between spruce and larch might be attributed to the differences in responses between evergreen and deciduous conifers (Oribe and Kubo 1997). Size-related differences in the duration of cell differentiation for larch might be smaller than in spruce leading to termination of cell differentiation at about the same time at high-elevation site (small trees) and low-elevation site (big trees).

At our sites, the onset of cambial activity was observed approximately 2 weeks before the significant increase in cambial activity. This initial, slight increase in cambial activity was frequently detected while the soil was still frozen, but air temperatures were high (6-day mean = 5.2 °C, maximum daily mean = 12.5 °C), in accordance with observations by Lenz et al. (2013). However, air temperatures at our sites prior to the onset of cambial activity were even higher, but without any observed reaction in the cambial zone. It is thus questionable whether they can trigger the onset of cambial

activity. Moreover, temperatures (both air and soil) characterizing the period of the onset of cambial activity showed relatively large variability. This variation might stem from the relatively early cambial reactivation sometimes confronting other extrinsic limits of the onset of wood formation, such as photoperiod (Körner 2012a). Therefore, if high ambient temperatures are achieved prior to the potential photoperiod signal, they might not induce any reaction in the cambial zone.

Whereas the onset of cambial activity at our sites was not associated with a clear temperature threshold, soil temperature did seem to present a threshold for the first significant increase in the number of cells in the cambial zone. The number of cells in the cambial zone significantly increased when soils heated rapidly from near-zero temperatures to 4–5 °C (6-day mean = 3.6 °C). Slightly higher temperature values (6-day mean = 3.8 °C) were thresholds for cell enlargement at our sites. Air and soil temperatures associated with the onset of cell enlargement were within the ranges suggested by Rossi et al. (2007, 2008a, i.e., mean air temperatures of 5.6–8.5 °C, stem temperatures of 7.2–9 °C, and soil temperatures from 2.6 to 7.5 °C).

Considering the abovementioned findings, our data indicate that significant increase in cambial activity followed by cell enlargement is probably associated with the thawing and warming of soils, as suggested by, e.g., Kirdyanov et al. (2003), Moser et al. (2009), Gruber et al. 2009 and Alvarez-Uria and Körner (2007). Once both the above- and belowground parts of a tree are sufficiently warm, root activity is resumed, cambial cells are rehydrated, and mitotic activity abruptly increases (Savidge 2000). The increase of activity is not only due to rehydration but also due to stimulation by cytokinins produced in the root apices, which increases the responsiveness of cambium to IAA (Friml 2003; Fonti et al. 2007; Ursache et al. 2013). Moreover, the synthesis of cytokinins is probably affected by temperature (Aloni et al. 2006). Körner and Hoch (2006) also argue for decisive effects of soil temperature on tree growth, based on a natural experiment at a site with cold soils and warm ambient air. However, exceptions to the general relationships between growth onset and both soil temperature (Lupi et al. 2011) and plant rehydration (Turcotte et al. 2009) have been found, showing the overall picture to be more complicated. Our finding that soil temperatures, but not air temperatures served as thresholds suggests that either: (1) for full resumption of cambial activity in the stem, both below- and aboveground parts of trees must be sufficiently warm; or (2) due to their inertia, soil temperatures might be a surrogate for accumulation of heat at the site, similar to, e.g., degree-day sums. The second of these interpretations has, however, been questioned by Seo et al. (2008).

Because we compared treeline and timberline trees, our sites differed in tree size. Both size and age of trees probably affect the onset and duration of wood formation (Rossi et al. 2008b). Smaller trees might be more responsive to ambient temperatures both due to closer coupling of stem temperatures with air temperatures (Mayr et al. 2006) and shorter distances between stems and shoots, where IAA is produced (Larson 1969). Therefore, the smaller size of trees at treeline might decrease their delay in xylogenesis onset relative to timberline trees. As reported by Anfodillo et al. (2012), the effect of tree size on duration of cell differentiation is even more pronounced than that on the onset of wood formation. In the cold and unpredictable environment of treeline, one could infer that small tree stature is advantageous, since small trees are capable finishing radial growth earlier than the big ones. Furthermore, size-related effect on the period of cell enlargement might explain the relatively weaker tree ring width-based climate–growth responses of generally smaller treeline trees in comparison to timberline trees, as derived by standard dendrochronological methods (Vittoz et al. 2008; Treml et al. 2012). The short period of cell enlargement for treeline trees might encompass only a limited interval during the growing season, with high temporal variability among growing seasons, i.e., occurring over different parts of May, June or July. Therefore, despite the strong temperature limitation of treeline trees, their ring widths, closely related to the period of cell enlargement (Cuny et al. 2014), may not respond tightly to simple temperature variables such as June or July means.

Because the Giant Mountains are among the windiest locations in European mountain regions (Migala 2005), a comparison of temperatures measured at our wind-affected treeline ecotone with typical temperature-limited treelines might reveal the extent to which strong winds depress treeline position. For example, timberline sites in the Dolomites, studied by Rossi et al. (2007) between 2002 and 2004, revealed similar June–September soil and air temperatures to those of our sites (soil temperatures from 9.3 to 11.1 °C on south-facing slope in the Dolomites and from 8.4 to 9.6 °C in the Giant Mountains, air temperatures from 8.9 to 11.4 °C in the Dolomites and from 9.2 to 10.9 °C in the Giant Mountains). However, a comparison between the growing season soil temperatures reported by Körner and Paulsen (2004) from treeline in the eastern and central Alps with identically defined temperatures measured at our treeline site (mean temperature of continuous period with soil temperatures above 3.2 °C, not shown) reveals that the Giant Mountains treeline site was 1 °C warmer than similar locations in the eastern and central Alps (8.4 °C in the Giant Mountains treeline and 7.4 °C in the warmest location in the eastern Alps). The net temperature difference between treelines in the eastern Alps and the Giant Mountains is, however, smaller, because, in both regions,

summer air temperatures have been increasing since the 1980s with the slope of regression curve being 0.04 (based on CRU TS data set; Mitchell and Jones 2005, updated). The estimated growing season temperature rise between 1997 and 2001 (when the data of Körner and Paulsen (2004) were collected) and 2010–2012 was about 0.4 °C based on CRU TS data set, which is in agreement with data from climatic stations (Barbosa et al. 2011; Ceppi et al. 2012). Our treeline site in the Giant Mountains was, therefore, about 0.6 °C warmer than similar sites in the eastern or central Alps, which could likely be attributed to the effect of wind. Energy losses due to the formation of wind-induced reaction wood, repair of browsed or broken shoots, and weak hormonal stimulation of growth from damaged apical shoots hamper tree growth at wind-affected locations (Holtmeier 2009).

Conclusions

The results of our study show that across the alpine treeline ecotone, differences in seasonal resumption of cambial activity and onset of individual phases of wood formation of *P. abies* were significant only in cases of several weeks delay in soil warming at the treeline versus the timberline site. Otherwise, the between-site differences in onsets of individual wood formation phases were smaller than our weekly sampling resolution. The first pronounced increase in cambial activity was associated with the first warming of the soil from near-zero temperatures to 4–5 °C in the spring. This might indicate that, in this species, full resumption of cambial activity at the basal part of the stem requires all parts of the tree to be sufficiently warm. Irrespective of simultaneous or shifted onset of cambial activity at our study sites, significantly more cambial and enlarging cells were observed at the warmer, timberline location than at the colder, treeline site during the early part of the growing season. Whereas differences in the number of cells at the beginning of the growing season were likely due to temperature, timberline trees also displayed greater duration of the cell-enlargement and wall-thickening phases, associated with more prolonged enlargement of the larger tracheids there. Therefore, we suggest that for *P. abies*, both temperature and size effects govern differences in wood phenology across the treeline ecotone.

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III.   Article II

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

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

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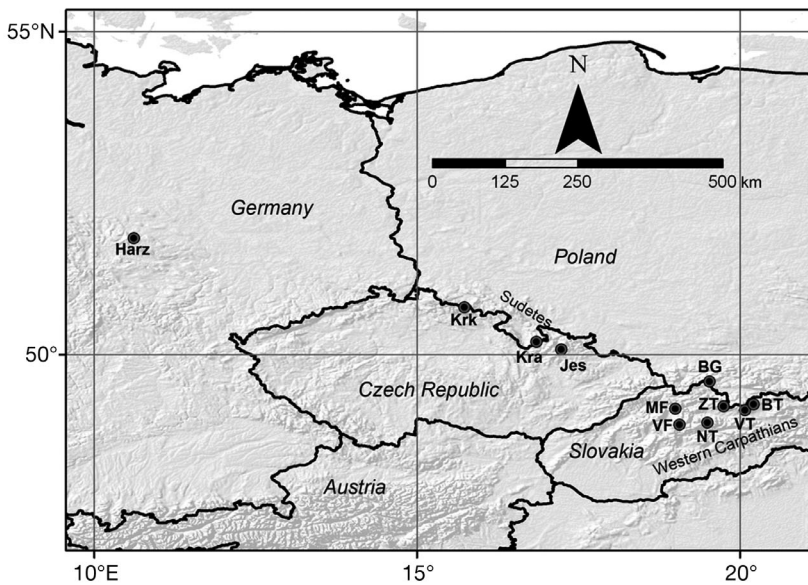
Fig. 1. Location of the mountain ranges studied in Central Europe. BG: Babia góra and Pilsko; BT: Belianské Tatry; Jes: Hrubý Jeseník; Kra: Králický Sněžník; Krk: Krkonoše; MF: Malá Fatra; NT: Nízké Tatry; VF: Velká Fatra; VT: Vysoké Tatry; ZT: Západné Tatry

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).

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)

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 un-
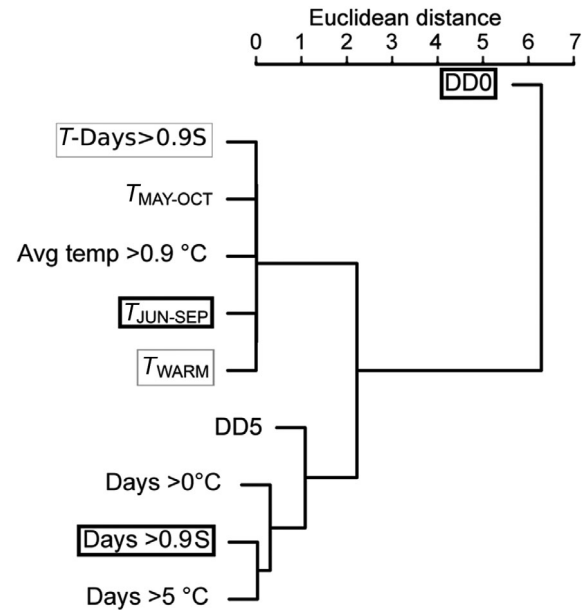

Fig. 2. Dendrogram expressing the relationships among calculated thermal metrics. The Ward method based on Euclidean distances was applied. Metrics selected for our study are highlighted by a black frame (cluster representatives entering into all analyses) or a grey frame (metrics used only for comparisons). 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

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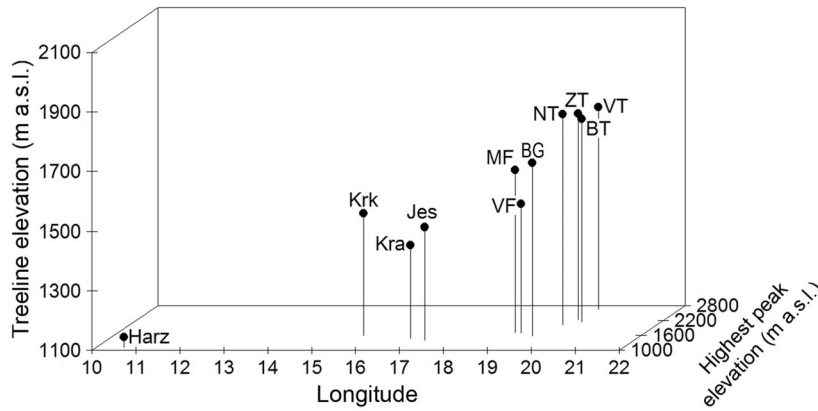
Fig. 3. Relationship among the elevation of uppermost tree groups, highest peak elevation and longitude. BG: Babia Góra and Pilsko; BT: Belianské Tatry; Jes: Hrubý Jeseník; Kra: Králický Sněžník; Krk: Krkonoše; MF: Malá Fatra; NT: Nízke Tatry; VF: Velká Fatra; VT: Vysoké Tatry; ZT: Západné Tatry

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, longi-

tude — 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 Nízke 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

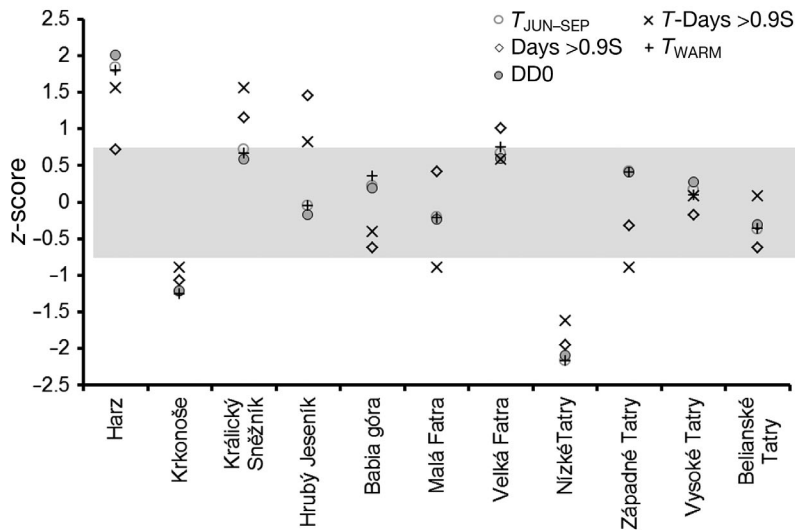| Mountain range	Highest tree-group elevation (m)	Standard deviation of highest positions at three different slope aspects (m)	Jun–Sep mean temperature (°C)	Sum of temperatures >0°C (°D)	Number of days with mean temperatures >0.9°C without snow cover	Temperature of warmest month (°C)	Mean temperature 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
Nízke 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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IV.   Article III

How wind affects growth in treeline *Picea abies*

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ORIGINAL ARTICLE

How wind affects growth in treeline *Picea abies*

Jakub Kašpar[1] · **Jiří Hošek**[2] · **Václav Treml**[1]

Abstract   Globally, treeline position is driven by temperatures during the growing season. Nevertheless, at regional scales, the position of uppermost tree stands also reflects other climatic factors, including wind action. It remains uncertain, however, how much do intense winds depress the treeline below its potential position. Our objective was to quantify the effect of wind speed on the possible depression of upper forest margins below the potential treeline in a windy mountain range with the treeline located close to summit areas. In the Giant Mountains, Czech Republic, growth parameters and symptoms of wind-induced loss of biomass were determined for Norway spruce (*Picea abies* [L] Karst.) in 70 plots distributed along a gradient of wind speed within the treeline ecotone. Wind speed was modelled for each plot. General linear models were applied to discern the effect of wind on tree growth. Our results show that high wind speeds are reflected in the presence of clonal tree islands and irregular tree crowns. Despite evident wind-induced biomass loss, radial growth was not significantly affected, and the effect of wind on height increment was limited only to parts of the stem from 2 m above ground. Considering that the height growth was substantially reduced by wind in about half of the treeline area, and

wind was able to limit only growth of trees taller than 2 m, the overall wind-induced depression of highest treeline positions is probably low, even in windy mountain regions.

Keywords   Height increment · *Picea abies* · Radial growth · Thigmomorphogenesis · Tree rings

Introduction

On a global scale, treeline position is determined by minimum available heat during the growing season and minimum growing season length still enabling the formation of a tree (Paulsen and Körner 2014; Rossi et al. 2016). However, at local to regional scales, there are plenty of examples of uppermost forest margins that are depressed below the potential growth-limited position as a result of high seedling mortality or dieback induced by secondary climatic factors (Harsch and Bader 2011). Among these factors, wind has been frequently reported to suppress tree growth and seedling establishment in the treeline ecotone (Holtmeier and Broll 2010; Takahashi 2014; McIntire et al. 2016). Nevertheless, the importance of wind action as a factor limiting the tree life form in the treeline ecotone is uncertain. If wind is a significant agent limiting tree growth and establishment, then the effect of the recent temperature increase on upward expansion of trees will be weaker than expected under consideration of temperatures alone.

Besides coastal regions, areas with high wind speeds occur near mountain summits of isolated mountain massifs, where wind speed is accelerated because of (1) a low frictional effect of the surface on free air flow and (2) compression and subsequent release of air masses flowing over the mountain barrier (Barry 2008). Wind has been suggested to affect the position and shape of the upper forest margins

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in the Rocky Mountains (Holtmeier 1982), the mountain regions of Central Japan (Takahashi 2014), the Andes of Southern Ecuador (Wagemann et al. 2015), the Scandes (Kullman and Öberg 2009), the Cairngorm Mts. (Wilson et al. 1987) or in the Sudetes in Central Europe (Jeník and Štursa 2003).

In many cases, the above-mentioned list contains mountain ranges with treelines located close to their summit parts. A prominent example of a mountain range where the uppermost forest margins are located close to gently rolling summits are the Appalachian Mts., where local krummholz treelines exist in conditions of relatively high growing season temperatures but under the influence of strong winds (Cogbill and White 1991). Lowering of treelines in the vicinity of mountain summits is known as the so-called summit syndrome (Körner 2012). However, not only "warm" treelines, but also some treelines existing within temperature range characterizing highest zonal treeline positions (e.g. 7 °C for growing season soil temperature in the Alps, Körner 2012; 6.3–7.3 °C for growing season air temperature; Kašpar and Treml 2016), occur close to summits (Kašpar and Treml 2016). Therefore, the summit syndrome, which is largely related to accelerated wind speed, is assumed to affect true temperature-limited treelines as well.

The main challenge for treeline trees is to sustain sufficient growth (Smith et al. 2003). Stem growth is affected by meristem temperature (Körner 2012; Hoch and Körner 2012), but also by biomass loss (Harsch and Bader 2011). Accelerated air flow cools meristems and needles due to enhanced heat exchange (Grace et al. 1989; Anten et al. 2010). Intense winds are supposed to increase evaporative cooling of meristems and needles wetted by rain or fog (James et al. 1994). Meristem cooling has a direct effect on growth suppression (Gričar et al. 2006; Lenz et al. 2013). Indirect effects of wind are often connected with the redistribution of snow (Weisberg and Baker 1995). Snow is usually deposited on the leeward side of trees or inside tree islands. Accumulated snow shortens the growing season due to delayed snowmelt (Vaganov et al. 1999) and increases seedling mortality caused by snow fungi (Senn 1999). On the other hand, seedling survival is enhanced in snow-accumulation patches in the regions heavily affected by strong winds (Renard et al. 2016). Windy treelines are characterized by the occurrence of tree islands that are slowly shifting towards their leeward side because of reduced dieback and enhanced seedling survival (Alftine and Malanson 2004).

Wind generates mechanical stress due to stem bending (Gardiner et al. 2016). Trees generally tend to counteract mechanical stress by reducing their apical growth in favour of radial growth (Bonnesoeur et al. 2016). Stem radial growth reflects drag forces affecting the tree crown

with the growth reaction varying along the stem (Niklas and Spatz 2000). Permanent wind stress finally leads to increased stem taper (Ennos 1997; Bonnesoeur et al. 2016). Furthermore, wind-transported snow and ice particles abrade tree stems and needles at wind velocities greater than 7 m s^{-1} (Mamet and Kershaw 2013). Needles are consequently either destroyed or their cuticula is damaged, and needles become vulnerable to winter desiccation (Tranquillini 1979), though this mechanism is not generally responsible for limiting tree growth at the treeline (Grace 1990; Körner 1998). High and irregular foliage loss and meristem damage may result in an asymmetric shape of the tree crown, reflecting the prevailing wind direction (Mamet and Kershaw 2013). Moreover, browsing on terminal parts is also expected to weaken hormonal signalling which controls tree growth and biomass allocation (e.g. Hertel and Schöling 2011; Susiluoto et al. 2010).

So far, studies dealing with the effect of wind on treeline position have reported biomass loss to be the most important agent depressing the position of upper forest margins below the potential treeline (e.g. Kullman and Öberg 2009; Takahashi 2014). High biomass loss can ultimately result in the krummholz growth form of tree species (Harsch and Bader 2011). Wind action has also been shown to be severely affecting seedling mortality, and thus contributing to the formation of island treelines (Harsch and Bader 2011; Renard et al. 2016). Most of the studies mentioned above assessed the effect of wind assuming that wind speed increases with elevation (Takahashi 2014), did not relate modelled wind speed to tree growth (Wagemann et al. 2015) or arbitrarily defined leeward and windward sites (Resler 2006; Han et al. 2012). However, these assumptions might not apply to complex terrain with wind fields heavily affected by topography (Barry 2008). As far as we know, the response of tree growth characteristics to a gradient of quantified wind speed (be it modelled or measured) has not been studied in the treeline ecotone, although this step is necessary to estimate the effect of wind speed on the anticipated "treeline depression". In this study, we hypothesized that along wind-affected treelines situated near summit areas, the variance in tree growth metrics not attributable to elevation and tree age should be possible to explain by the degree to which the sites under study were exposed to wind. Our objective was to test the effect of wind speed on various growth metrics and to quantify the effect of wind speed on the possible depression of upper forest margins below the potential treeline. To address this question, we collected data on growth characteristics of treeline trees in a treeline ecotone located 50 to 200 m of elevation below summits in the Giant Mountains, a part of the Sudetes mountain chain (Czech Republic, Poland).

Materials and methods

Study area

The Giant Mts. (Fig. 1) are among the windiest mountain ranges in Europe (Migała 2005) with dominant westerly winds, the mean wind velocity being 12 m s^{-1} on the highest peak Mt Sněžka, 1603 m ASL (Fig. 2a; Metelka et al. 2007). Due to their pronounced relief, rising above the surrounding lowlands by ~1200 m, the Giant Mts. represent the first barrier to westerlies flowing from the North Sea. Westerly winds in combination with the longitudinal orientation of main ridges are responsible for significant differences between windward and leeward sites in terms of vegetation composition and irregular distribution of snow cover (Jeník and Štursa 2003). The Giant Mts. are characterized by high precipitation (approximately 1400–1600 mm per year) and a mean annual temperature of 0.5 °C at the uppermost locations (Migała et al. 2016). There are about 180 days of continuous snowpack above the timberline (Metelka et al. 2007). Snow depth varies depending on the topography; however, disregarding cirques and nivation hollows, local maxima are usually achieved at the timberline; from the timberline towards summit areas, snow depth decreases (Štursa et al. 1973). Mean maximum snowpack depth on plateaus above the timberline was 1.8 m (Labská bouda station, 1961–1990). The highest situated trees are growing around the 1500 m elevation contour, along which the growing season lasts 127 days on average (Kašpar and Treml 2016). The measured mean growing season ground temperature (following the methodology of Körner and Paulsen 2004) is 7.1 °C based on six treeline sites and growing seasons from 2006 to 2012 (unpublished data of V. Treml). The treeline ecotone is situated approximately
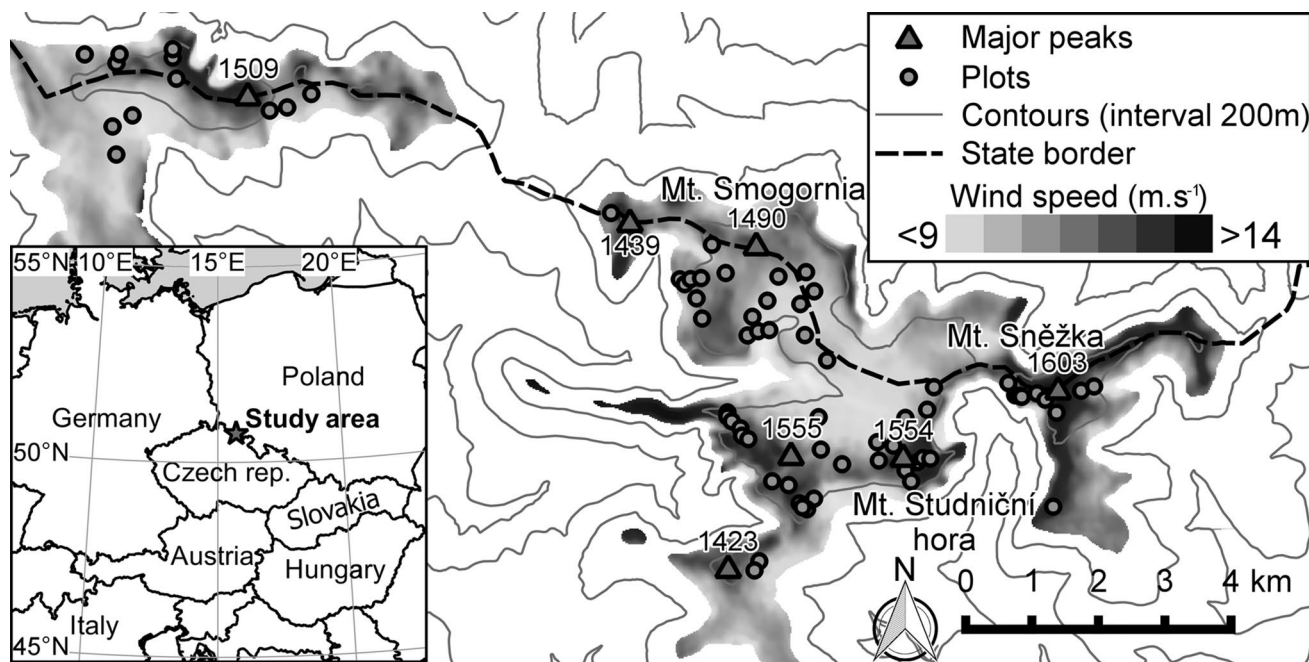
Fig. 1 The Giant Mountains with locations of sampling plots and modelled wind speeds in the treeline ecotone. The ecotone is represented by the area covered by trees of heights ranging from 2 to 5 m

Fig. 2 **a** Histogram of wind speeds (based on 3 h measurement intervals) at Mt Sniezka (2004–2005); **b** verification of modelled wind speeds by wind speeds measured at four climatic stations. Abbreviations for climatic stations: *Lab* Labská bouda; *Pec* Pec pod Sněžkou; *Sne* Sniezka; *Szre* Szrenicza
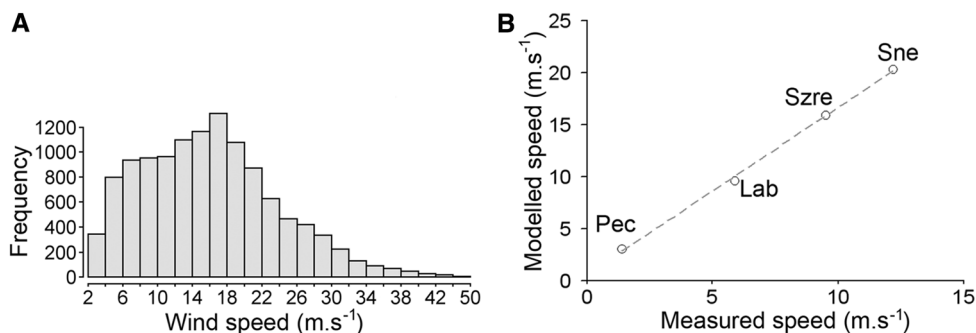
between 1300 m (the upper limit of closed forest) and 1500 m (Treml and Chuman 2015). Norway spruce (*Picea abies* [L] Karst.) is the dominant treeline tree species. Trees with flag-like crowns are common; low spruce mats (lower than 0.5 m) occur in locations exposed to strong winds (Treml and Migoń 2015). The prostrate shrub dwarf pine (*Pinus mugo*) is also widespread in the treeline ecotone. The position of the treeline had been affected by cattle grazing and mowing of grass, particularly in the eighteenth and nineteenth centuries; however, human impact on the treeline gradually decreased in the twentieth century, and since the 1940s, the treeline ecotone has been developing spontaneously (Lokvenc 1995).

Data collection and processing

We selected 70 plots in the treeline ecotone by stratified random sampling with respect to the proportional distribution of plots at different elevation levels and on slopes of eastern (leeward) and western (windward) aspect. Initially, the plots were placed randomly along transects across the treeline ecotone using GIS. Additional plots were subsequently generated in under-represented aspect-elevation categories. The plots were then identified in the field, and some of them (located inside of fully closed dwarf pine stands) were moved to the nearest accessible position. The plots covered an elevation range between 1330 and 1540 m a.s.l. The average nearest neighbour plot distance was 263 m; the shortest distance between two plots was 40 m. Within each plot, three randomly selected patches represented by individual trees or tree islands were sampled. Only individuals taller than 2 m were considered. For each patch, we determined whether it was represented by an individual tree or a tree island. Tree islands were mostly formed by ramets with upright stems, but some trees in each island originated from seeds. For each individual or the tallest specimen of a tree-island, we identified the presence/absence of apical breaks, presence/absence of layering branches (for isolated individuals or trees at margins of tree islands) and stem splitting. Not only contemporary, but also all earlier apical breaks were determined in the stem section above the lower increment core, based on a candelabra-like stem morphology (Schweingruber 1996). We measured tree height, stem girth, length of the longest and shortest stem axis (at 1 m stem height). Furthermore, lengths of branches were determined in four directions (north, south, west and east) at 2 m above the ground (i.e. approximately above the average maximum height of the snowpack). In tree islands, maximum branch lengths were measured for trees growing at the margins of tree islands. For each patch, distance to the nearest barrier (other trees, tree islands, rocks, *Pinus mugo* stands, etc.) in three directions was measured. Two perpendicular tree-ring cores were sampled

from each tree (or from the tallest tree of a tree island) at ~0.5 m stem height to obtain tree-ring widths (TRW), tree age and the number of missing rings. An additional core (or cross-section) was sampled from approximately 2 m stem height to compute height increment and to ascertain the proportion of reaction wood. To compute height increment, the exact distance of each core from the stem base and the highest internode was measured. The tree-ring cores were sanded, ring widths were measured on a positioning table and cross-dated (Speer 2012). In cases of off-pith cores, the number of missing rings was estimated using a pith-locator according to Batllori and Gutiérrez (2008).

For each tree, we computed parameters describing allometry, such as crown shape (length of the shortest/longest branch) and stem taper (girth divided by tree height). Height increment was calculated as (1) height increment between 0.5 and 2 m (the number of tree rings at ~0.5 m minus the number of tree rings at ~2 m divided by the exact distance between cores), and (2) height increment above 2 m (stem length above the upper core divided by the age of the tree at the height of the upper core, current growing season increment was not considered). Height increments were computed both for the entire sample set and for the samples free of apical breaks. The proportion of tree rings with reaction wood was determined in the first 15 tree rings of the upper core.

Wind speed and other environmental variables

For each plot, we calculated the following variables based on a digital terrain model with 10-m resolution: elevation, curvature, slope, heat load (combination of slope and aspect, McCune and Keon 2002) using ArcGIS software. Wind fields were computed using the WAsP Engineering system version 3 (Mann et al. 2002), which is based on the linear model LINCOM (Astrup et al. 1997). It is broadly used for estimating wind speed in windy areas (Rathmann et al. 1999; Larsen and Mann 2009). The LINCOM model simulates neutrally stable flow over hilly terrain using linearized mass and momentum equations. Its outcome yields a perturbation of wind speed and pressure that is induced by varied terrain in comparison to flat terrain conditions with uniform roughness. Without perturbation the model produces a logarithmic profile of wind speed. For the purpose of this study, the model was run in the selected domain at 20-m horizontal resolution. The wind fields were simulated for the generalized wind speed of 7 m s^{-1} corresponding to the height of 10 metres above flat terrain with a uniform roughness of 0.1 m. The resulting wind fields were derived as average model outputs for input wind directions of 210, 240. 270, 300 and 330°, hence corresponding to prevailing westerly winds in the Giant Mountains.

The averaged outputs of the model were verified using measured mean wind speed from meteorological stations representative of major landforms—two summit stations (Sniezka and Szrenicza), one climatic station located on a flat high-elevated plateau (Labská bouda) and a deep valley station (Pec pod Sněžkou). The measured wind speeds are averages from 3-h measurements in the period 2004–2005. Since the modelled and measured data matched very well (Fig. 2b), we considered the modelled data suitable for further analysis. The simulations provided wind speeds comparable with wind speeds measured directly at the local meteorological station Sniezka (Fig. 2a), considering the 75th percentile of wind speed distribution. The 75th percentile was selected because only high wind speeds efficiently limit tree growth (Bonnesoeur et al. 2016).

Statistical analysis

Growth metrics for each plot were represented either by average values (height increment between 0.5 and 2 m, height increment above 2 m, proportion of reaction wood, age of trees, number of missing tree rings, crown shape and stem shape, stem taper) or by sums (presence of tree islands, number of apical breaks, layering branches). Prior to the averaging, the effects of age and elevation on growth metrics were removed for tree height, stem girth and TRW. This effect was removed using multiple linear regression where the response variable was the growth metric and where tree age and elevation were explanatory variables. Residuals from the regression models were used in further analyses. These variables are hereafter called tree height, girth and TRW residuals.

All variables (except count or semi-categorical metrics) were visually checked for normality and transformed, if necessary, by applying a logarithmic transformation (height increment, tree age, distance from the nearest barrier and heat load index), square root transformation (elevation) or exponential function (stem shape). Finally, all the above-mentioned metrics were transformed to unit variance and zero mean. Basic descriptive analysis of relationships among the response variables (growth metrics) and explanatory variables was done using Pearson correlations or ANOVA. To identify whether values of growth metrics were spatially clustered, we calculated spatial autocorrelations. Autocorrelation was measured using Moran's I as implemented in ArcGIS (Wong and Lee 2005).

The growth metrics were correlated, so redundancy analysis (RDA) was performed to examine the relationships among all variables and to determine the variance in growth metrics explained by environmental variables (Šmilauer and Lepš 2014). To explain the effect of environmental variables on each growth metric, we applied general linear models assuming a Gaussian distribution of response

metrics (tree height residuals, girth residuals, TRW residuals, height increment below and above 2 m, proportion of reaction wood, taper, crown shape). For height increments, the environmental variables were supplemented by tree height and the presence of apical breaks. Tree age entered among environmental variables in all cases, except for TRW, stem height and girth residuals. A generalized linear model with a Poisson distribution of semi-categorical response metrics was applied to the presence of tree islands and the numbers of layering branches and apical breaks. Due to a high proportion of zero values in our samples, the same model with negative binomial distribution of the response variable was used for the number of missing tree rings (Legendre and Legendre 2012). The quality of model fit was evaluated using R^2. The independent explanatory power of each environmental variable was estimated using hierarchical partitioning (Chevan and Sutherland 1991; Walsh and McNally 2013).

In addition, interactions of wind speed and other variables were alternatively considered in all models, which led to an increase in the overall number of explanatory variables. To determine the importance of variables, including interactions, we generated a set of models with all explanatory variable combinations. The models were ranked according to the Akaike information criterion (AIC) (Burnham and Anderson 2004). For each explanatory variable and interaction entering to the best model, we further estimated its AIC-weighted importance, a unitless metric indicating summed AIC across all models in which the variable appears. This importance ranges from 0 (variable with no explanatory weight) to 1 (variable in all top models) (R package MuMIn, Bartoń 2015). All statistical analyses were performed in R (R Development Core Team 2008) and CANOCO (RDA analysis, Šmilauer and Lepš 2014).

Results

We collected growth data for 210 trees growing in 70 plots. Almost 67% of the trees were found in tree islands. Average tree height was 366 ± 50 (SD) cm, and average girth was 34 ± 7.5 cm. Average estimated age was 58 ± 11 years, mean TRW being 1.04 ± 0.16 mm. At least one missing tree ring was recorded in 60 trees (nearly 30% of all trees). The average height increment was 7.3 ± 1.2 and 11.1 ± 2.1 cm year^{-1} below and above 2 m, respectively. Considering only trees without detected apical breaks, the height increment was 7.5 ± 2.1 (below 2 m) and 11.5 ± 3.0 (above 2 m). Apical breaks were found in 49% of the trees.

Certain growth metrics were strongly related to elevation and tree age. Tree height decreased with increasing elevation ($r = -0.42$) and with decreasing age ($r = 0.27$). Significant correlations with age ($r = 0.46$) and elevation

($r=-0.43$) were determined for stem girth as well. TRW correlated with age and elevation ($r=-0.52$ and -0.22, respectively). Height increment to 2 m was significantly correlated only with tree age ($r=-0.49$), but not with elevation ($r=-0.05$), and height increment above 2 m decreased with increasing age ($r=-0.51$) as well. Linear models explaining tree height, girth and TRW (response variables) by tree age and elevation (explanatory variables) were statistically significant ($p<0.01$), as was the effect of both explanatory variables. The models explained 21, 29 and 35% variability in tree height, girth and TRW, respectively. To discern the effect of wind on tree height, stem girth and TRW, we used residuals from these models in further analysis.

Growth metrics, such as the proportion of reaction wood and height increment below 2 m, did not show any trend along the gradient of increasing wind speed (Fig. 3b, c). On the other hand, TRW and tree height residuals decreased with increasing wind speed with the exception of the highest wind speed interval (Fig. 3a, d). Values of the remaining metrics, namely height increment above 2 m, stem taper and crown shape, decrease from sites with low wind exposure to highly wind-exposed sites. The steepest decreasing slope was observed in the middle of the modelled wind speed range (from 9 to 12 m s^{-1}, Fig. 3f, g). The influence of wind on crown shape was also obvious, as indicated by the length of branches categorized by their aspect. On average, western branches (length$=44\pm20$ cm) were about 30 cm shorter than eastern branches (length$=78\pm22$ cm) and about 20 cm shorter than southern and northern branches (length$=65\pm23$ cm, Fig. 3h). As regards the spatial distribution of growth metrics (Table 1), the strongest tendency towards clustering was observed for mean tree age, occurrence of apical breaks and the proportion of reaction wood.

The ordination plot (Fig. 4) indicates that high wind speed is reflected in an increased frequency of tree islands and trees with irregular crowns. At the same time, large trees growing at sites influenced by high wind speeds tend to have lower average height increments. It is also obvious that older trees were predominantly situated on southwest-facing steep slopes (i.e. sites with a high heat load), and these trees were characterized by more frequent apical breaks. The first four RDA axes explain 15% of variance in growth variables, of which 92% is captured by environmental variables.

Environmental variables, supplemented in relevant cases by tree age, tree height and presence of apical breaks, successfully predicted the following growth metrics (Table 2): height increment below 2 m, height increment above 2 m, proportion of reaction wood, crown shape, presence of apical breaks, presence of layering branches and occurrence of tree islands. Models for the remaining response variables (TRW residuals, taper, tree height residuals and girth residuals) were not statistically significant. Wind speed entered with a significant negative effect into models explaining height increment of trees above 2 m (regression coefficient -0.65, interactions of wind speed and heat load were important as well), crown shape (together with age, interactions of wind speed and elevation and curvature were important), presence of layering branches (together with distance from the nearest barrier) (Table 2). Wind speed positively affected the presence of clonal groups. Height increment below 2 m was explained only by age. The proportion of reaction wood depended on the elevation. The presence of apical breaks had a low explanatory power in models for radial and height increment. Apical breaks were common for old and rather low trees growing on steep slopes (Table 2).

Discussion

In this study, we exemplify that only certain growth metrics are affected by wind action in treeline ecotones. This is especially true for the presence of tree islands and flag-like tree crowns at wind-exposed sites. The occurrence of tree islands, maintained mostly by clonal reproduction, is an efficient way to occupy a position at wind-exposed sites, where generative regeneration is sparse and occasional (Alftine and Malanson 2004; Holtmeier and Broll 2010). As regards flag-like crowns, we expected the evident loss of biomass caused by wind browsing to result in decreased radial growth due to the need to compensate for biomass loss in branches related to defoliation (e.g. Handa et al. 2006; Susiluoto et al. 2010). However, there was no straightforward linear trend of TRW decrease along the gradient of wind speed. We observed a decrease of TRW in the modelled wind speed range of 9 to 14 m s^{-1}; however, at the highest wind speeds (14 m s^{-1} and more), tree rings again become wider. We suggest that the observed trend of TRW along the wind speed gradient results from interference between two types of physiological processes. First, processes causing decreased growth, such as limited radiative warming of meristems in windy conditions (James et al. 1994) and weak hormonal signalling from damaged buds and foliage (Pallardy 2008; Han et al. 2012) or, alternatively, changes in biomass allocation in trees subjected to foliage loss (Handa et al. 2006), probably dominate under lower wind speeds. Second, under the highest wind speeds, thigmomorphogenesis should be considered (Bonnesoeur et al. 2016), because trees under intense mechanical stress tend to increase their radial growth. The increasing representation of tree islands towards sites most exposed to wind probably does not influence TRW, because when

Fig. 3 Distribution of growth variables along the gradient of wind speed. Means and standard deviations are presented. **a** Tree ring width residuals; **b** proportion of reaction wood in the first 15 tree rings at 2 m above the ground; **c** height increment between 0.5 and 2.0 m (*full circles* denote complete dataset, *empty circles* are used for dataset free of apical breaks); **d** height increment above 2 m (*full* and *empty circles* are used in the same way as in **c**); **e** tree height residuals; **f** stem taper; **g** tree-crown shape; **i** average length of branches in four aspects
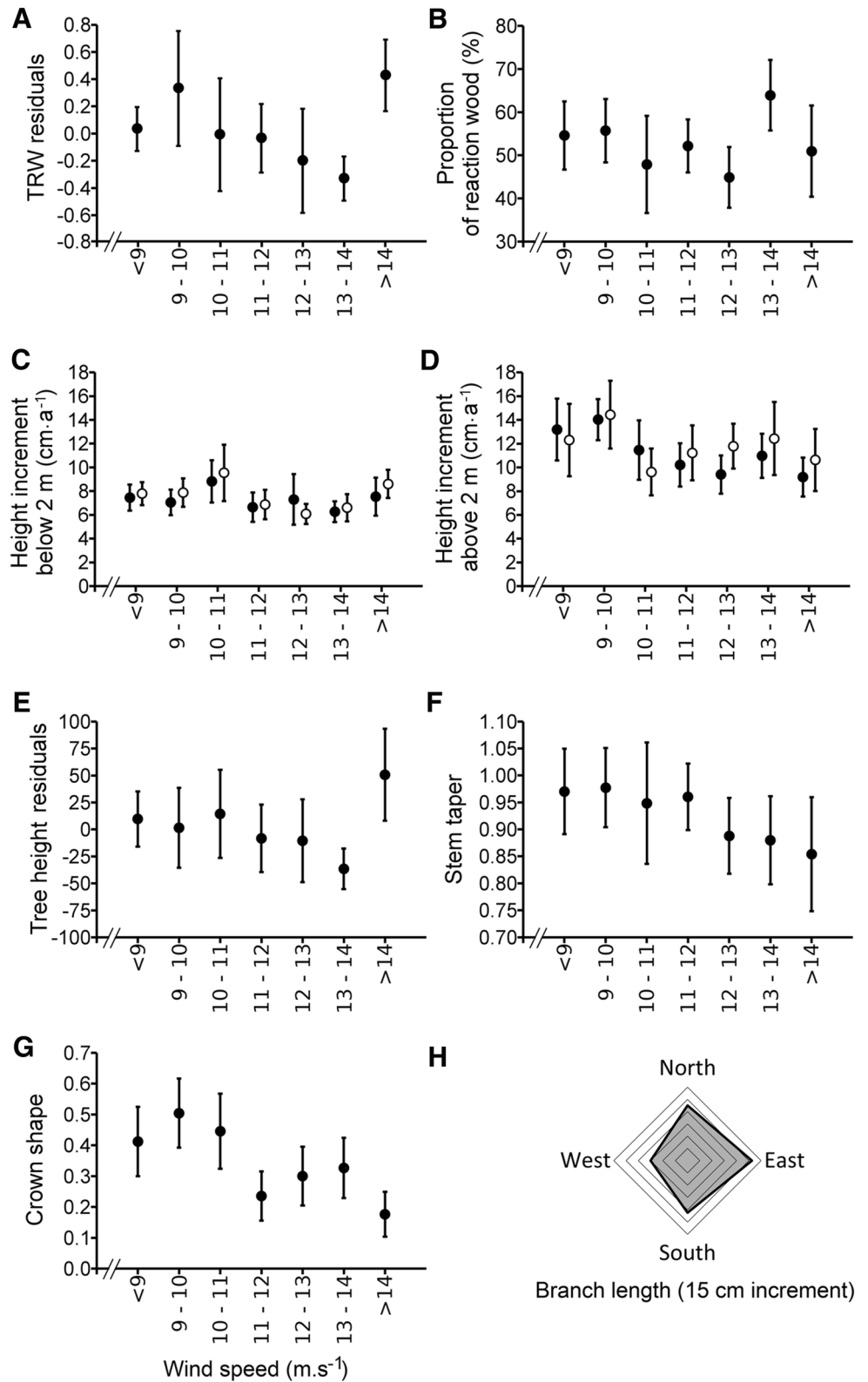
considering exclusively solitary trees, the trend in TRW is similar to the trend in the dataset containing all trees (Appendix 1).

The limited reaction of radial growth to loss of branch biomass attributable to wind abrasion means that trees have sufficient reserves in their photosynthetic capacity and

Table 1 Spatial autocorrelation of growth metrics

Metric	Moran's I	z score
TRW residuals	0.15*	2.10
Height increment between 0.5 and 2 m	−0.07	−0.75
Height increment above 2 m	0.09	1.39
Proportion of reaction wood	0.22**	3.12
Number of missing rings	0.12*	2.07
Age	0.36***	4.88
Tree height residuals	0.09	-0.94
Girth residuals	0.09	1.31
Stem taper	0.08	1.26
Crown shape	0.04	0.76
Tree islands	0.04	0.71
Apical breaks	0.21**	2.97
Layering branches	0.05	0.83

Moran's I and z scores are listed. Asterisks denote the statistical significance of Moran's I as follows: $p < 0.001$ (***), $p < 0.01$ (**) and $p < 0.05$ (*)
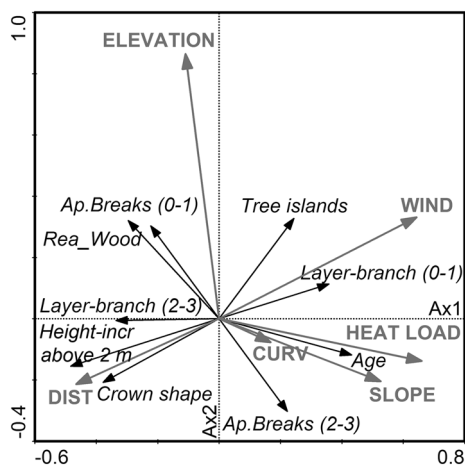

Fig. 4 RDA analysis of growth metrics and environmental variables for plots distributed along the gradient of wind speed. Only variables with higher fit than 10% on Axis 1 and Axis 2 are depicted. Environmental variables are marked in grey capitals, growth metrics are in italics. *Age* age of trees; *Ap.Breaks(0–1)* 0–1 tree with apical breaks on a plot; *Ap.Breaks(2–3)* 2–3 trees with apical breaks on a plot; *tree islands* all trees on a plot grow within tree islands; *height-incr above 2 m* height increment above 2 m; *layer-branch (0–1)* 0–1 tree with layering branches on a plot; *layer-branch (2–3)* 2–3 trees with layering branches on a plot; *Rea_Wood* proportion of reaction wood; *CURV* terrain curvature; *DIST* distance from the nearest barrier; *ELEV* plot elevation; *HEAT* heat load index; *SLOPE* slope; *WIND* modelled wind speed

that the loss of even a substantial proportion of branches and needles is not significant. Some studies, however, have reported decreases in radial growth after defoliation, depending on its extent, from 37 to 84% (Li et al. 2002; Susiluoto et al. 2010; Puri et al. 2015). On the other hand,

if the defoliation was less extensive, a situation probably typical of treeline habitats, radial growth was not affected (Puri et al. 2015). Moreover, it is worth mentioning that the average length of the growing season at the treeline in the Giant Mts. is 127 days (Kašpar and Treml 2016), which is about 30 days more than the minimum growing season length necessary for sustainable growth of trees at the treeline (Paulsen and Körner 2014).

Along the gradient of modelled wind speed, there was no trend in height increment below 2 m. Similar to TRW, height increment to 2 m was greater at the highest modelled wind speed (more than $14 \ m \cdot s^{-1}$) than in the preceding wind speed interval ($13–14 \ m \cdot s^{-1}$); however, this difference was substantially smaller than in the case of TRW. This ambiguous course of height increment below 2 m results from interfering effects of wind speed and tree age. At most wind-exposed (and often high-elevated) sites, juvenile specimens with relatively high growth rates prevail. In addition, wind-exposed trees usually have extremely wind-shaped crowns resulting from asymmetric foliage loss and bud damage on the windward side of the tree. Debudding and foliage loss (if not applied to the apical bud) might enhance the growth of unaffected shoots (Polák et al. 2006; Susiluoto et al. 2010). Additionally to the effect of age, this mechanism, together with the protective effect of tree islands (Šenfeldr et al. 2014; 82% of trees at most wind-exposed sites grew within tree islands), might explain the slight increase in height growth at extremely wind-exposed sites.

Once a tree top sufficiently protrudes above the snow surface and the tree is tall enough (in our case taller than 2 m), wind action becomes an important limiting factor of height growth. Based on regression coefficients, we found that in the modelled wind speed range of $7–14 \ m \cdot s^{-1}$, annual height growth is depressed by about 0.65 cm per $1 \ m \cdot s^{-1}$ of wind increment, assuming a linear response. However, towards the highest modelled wind speed, the uncertainty of our modelled growth reduction increases due to a low available number of observations and a high proportion of tree islands, which have a facilitative effect on tree growth. That the reduction of height increment is limited to the stem section above 2 m can most probably be ascribed to the absence of a protective effect of the snow-pack against ice and snow blasting above the snow surface (Holtmeier 2009; Holtmeier and Broll 2010) and also to increasing wind pressure with increasing distance above the ground (Aulitzky 1961). The reduced height increment at wind-exposed sites corroborates observations of Han et al. (2012) for *Picea jezoensis* in Korea, indicating that it is a general phenomenon. As the mechanism responsible for the wind-induced depression of height growth, we suggest direct growth limitation through cooling of apical meristems. Windy conditions eliminate the effect of daytime

Table 2 Relationship between growth metrics and environmental variables supplemented in relevant cases by tree age and tree height

Response variable	R²	Age	Elevation	Wind speed	Distance from barriers	Heat load index	Slope	Curvature	Apical breaks	Tree height	Variable importance-interactions with wind speed
TRW residuals	0.04			33.8 (−0.09)	2.3	7.2	39.0	9.3	8.4		
Height increment below 2 m	**0.39**	**80.4** (−)	7.4	2.4 (+0.06)	0.8	2.5	0.7	0.5	2.4	3.0	
Height increment above 2 m	**0.43**	**40.8** (−)	2.4	**18.4** (**−0.65**)	1.4	**18.7** (−)	4.8	8.5	0.9	4.2	Heat load (0.65)
Proportion of reaction wood	**0.23**	2.5	**51.3** (+)	12.0 (−0.46)	3.4	21.4	5.8	3.6			
Tree height residuals	0.02			9.9 (−0.10)	24.8	53.4	10.2	1.7			
Stem girth residuals	0.03			40.7 (−0.18)	8.1	30.5	11.8	9.0			
Stem taper	0.18	2.1	3.6	23.6 (−0.47)	**28.7** (−)	**32.7** (−)	5.9	3.4			
Crown shape	**0.27**	**30.7**	10.4	**21.4** (**−0.27**)	16.4	2.4	8.1	10.7			Elevation (0.31), curvature (0.34)
Presence of tree islands	**0.15**	5.0	**50.7** (+)	**33.0** (**+0.1**)	1.8	0.9	3.3	5.5			
Number of missing tree rings	**0.29**	**69.6** (+)	13.1	2.9 (−0.08)	2.9	6.8	3.7	1.0			
Apical breaks	**0.27**	**15.5** (+)	12.8	2.9 (−0.03)	0.5	6.4	**28.0** (+)	0.8		**33.1** (−)	
Layering branches	**0.19**	8.0	5.7	**32.8** (**−0.27**)	**35.2** (+)	4.8	4.8	8.6			

R^2 values of statistically significant models ($p < 0.05$) are in bold. The proportion of explained variability (%) is listed for each variable; numbers in bold mark a significant effect ($p < 0.05$) indicated by hierarchical partitioning. Plus or minus signs denote the direction of the given effect. In the wind speed column, regression coefficients for wind influence are in brackets. Results of general linear models are provided for TRW residuals, stem girth residuals, height increment below and above 2 m, proportion of reaction wood, stem taper and crown shape. Generalized linear models are presented for the number of missing rings, apical breaks, layering branches and presence of tree islands. Variable importance for interactions with wind speed is listed in the last column (values higher than 0.3 are showed only)

radiative warming of the canopy and meristems (James et al. 1994). This warming is estimated to be about 2 K for the canopy (Tranquillini 1963) but less than 1 K for stem or terminal shoots (Wilson et al. 1987; Wieser 2007), if mean seasonal temperature is considered. The effect of apical breaks can probably be excluded because their presence was independent of wind speed.

The reported depression of uppermost tree stands in wind-affected mountains ranges from 100 m in the boreal central Scandes in Sweden (Kullman and Öberg 2009) to about 50 m in the tropical Andes of Equador (Wagemann et al. 2015). The results of our study, however, indicate that conservative estimates of wind-induced treeline depression are probably more realistic. In the Giant Mountains, areas with modelled wind speeds greater than $10 \text{ m} \cdot \text{s}^{-1}$ (which substantially affect height growth) represent 48% of the treeline ecotone. We estimate that the wind-induced reduction of height growth in these areas ranges from a few per cent to up to 37% of the average height increment of stem sections above 2 m. Still, however, more than 50% of the treeline ecotone is not affected by wind, allowing the treeline to locally reach its potential position.

In a previous study at the Sudetes treeline, Treml et al. (2012) documented a substantial increase in radial growth since the 1980s associated with climatic warming. Here, we found that height increment below 2 m negatively correlates with tree age. Therefore, similar to ring width, past height increments were substantially lower than contemporary height growth. Once trees exceed the height of 2 m, the effect of climatic warming is, however, counterbalanced by wind action. This could explain the recent advance of average treeline position but not of maximum treeline position in the Giant Mts. (Treml and Chuman 2015).

Our results also show that high wind speeds are reflected in the frequent occurrence of clonal tree islands. This means that wind action suppresses generative establishment in favour of vegetative spreading (Tranquillini 1979; Šenfeldr et al. 2014 and references therein). On the other hand, we observed fewer layering branches at wind-exposed sites than in leeward areas. Still, germination in open stands distant from tree islands is substantially less probable at wind-exposed sites than establishment of new seedlings or ramets next to tree island margins. In wind-affected environments, tree establishment is extremely contingent on facilitation by neighbouring trees (Resler et al. 2005; McIntire et al. 2016), and vegetative reproduction is successful despite the negative influence of wind (Šenfeldr and Maděra 2011).

The wind speeds modelled in this study correspond with values measured at four climate stations. Therefore, modelled wind speeds probably well capture topographically driven differences. For the sake of simplicity,

modelled wind speeds were represented by mean values, which emphasize more intense winds (approximately corresponding to the 75th percentile of measured wind speed distribution). We, however, cannot draw an exact conclusion as to which part of the wind speed distribution is actually effective at limiting tree growth. In addition, wind gusts that might be effective at removing entire trees or part of their biomass (Gardiner et al. 2016) were not considered. We simply assumed that wind-exposed sites are more probably affected by wind gusts in comparison with wind-protected sites.

To summarize, in the Giant Mountains at one of the windiest treelines in Europe, topographically accelerated wind speed is manifested in the presence of tree islands and flag-like tree crowns. However, the evident loss of branch and needle biomass at wind-exposed sites is not linked directly to a decrease in radial growth. We suggest that an interplay between wind-induced meristem cooling, reduced radial growth in response to foliage loss and bud damage, thigmomorphogenesis and the protective effect of tree islands result in indistinct trends in radial growth along the wind-speed gradient. In contrast to radial growth, the effect of wind is significant for height increment in trees taller than 2 m, that is, trees sufficiently tall to be exposed to wind. About half of the treeline ecotone area is subjected to wind speeds reducing height increment. Small trees under 2 m in height exhibited a rapid increase in height growth in the last decades; however, when these trees grew over 2 m tall, their height increments became limited by wind at wind-exposed sites. The observed treeline advance could therefore be limited by wind action in exposed mountain massifs of restricted elevation. However, considering that wind velocities effectively limiting height growth are reached only in about half of the treeline area in the Giant Mountains and that wind is able to limit growth only of trees taller than 2 m, we propose that the overall wind-induced depression of the treeline is relatively low even in windy mountain regions.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Declaration of authorship VT and JK conceived and designed the project. JK collected and analyzed the data. JH modelled wind speeds. JK, VT and JH wrote the manuscript.

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V. Article IV

Relation between tree growth and temperature explains formation of regional treelines

Relation between tree growth and temperature explains formation of regional treelines

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Abstract (276 slov)
In temperate and boreal zone, treeline growing season temperatures should be ideally the same, because of identically temperature-limited tree growth. However at regional scales, reported treeline temperatures and growth performances vary a lot suggesting either additional limiting factors or differential sensitivity of treelines to ongoing warming. Here we present a comparison of tree growth parameters and treeline temperatures across ten mountain ranges in Central Europe north of the Alps (51-48°N, 10-20°E). We test if tree growth is approximately same across all treelines and less limiting temperatures at warm treelines are counterbalanced by other limiting factors, or, if growth varies exclusively as a consequence of temperature variability. In all treeline regions, approximately 3 m high *Picea abies* were sampled to measure radial and height growth and to determine symptoms of biomass loss. Tree ring width, height increment below 2 m and the height increment above 2 m of stem height were modelled using treeline temperature metrics, symptoms of biomass loss, reaction wood presence, and site properties. We found that radial growth, height growth to 2 m and height growth above 2 m showed high, weak, or almost no correlation with temperature, respectively. Certain warm treelines with high radial growth rates were characterized by high proportion of reaction wood, frequent symptoms of biomass loss and high stem taper. However, the others revealed a limited evidence of biomass loss or reaction wood presence indicating that they are either a remnant of past disturbances or their response to recent temperature increase is lagged due to anthropogenic land-use. We propose that the comparison of growth, temperature metrics and symptoms of biomass loss is particularly helpful to discern formation of regional treelines.

Introduction
Treeline is a prominent vegetation boundary reflecting elevation-driven temperature gradient. Above treeline, woody plants are not able to form tree stature because of too low temperature of plant body during the growing season and/or due to too short growing season (Körner 2012, Rossi et al. 2016). Treeline position is thus driven by air temperature, which influences plant body temperature. As a result, treeline positions in seasonal climates are characterized by similar temperatures in the growing season irrespective of bioclimatic region (Körner and Paulsen 2004, Paulsen and Körner 2014) and treeline positions can be used as climatic markers indicating ongoing or past temperature changes (e.g., Tinner and Theurillat 2003, Heiri et al. 2006). However, in contrast to assumed uniform temperatures across treelines, the ranges of treeline temperature metrics are relatively high even on regional scale as has been reported from the Alps (Körner and Paulsen 2004, Gehrig-Fasel et al. 2008) or from mountain ranges north of the Alps in Central Europe (Kašpar and Treml 2016). There are plenty of possible explanations ranging from measurement errors, microclimatic variability or varying deviances of plant body temperature from measured air or soil temperature. In addition, not only treelines in equilibrium with their temperature conditions (i.e. potential treelines) but also "depressed" treelines have been probably included in global or regional comparisons.

Although the ultimate limit of tree existence at its upper distributional margin is low growth (Körner 1998), the uppermost tree stands often occur below potential treeline because of other limiting factors such as establishment constraints or biomass loss (Harsch and Bader 2011). Such uppermost tree stands (hereafter also called "treelines") thus exist in warmer environments than potential treelines and the less negative effect of temperature on tree

growth is compensated by, e.g. drought-limited seedling survival (Batllori et al. 2009, Gill et al. 2015), competition-driven exclusion of seedlings in dense herbal plant communities (Tingstad et al. 2015) or high biomass loss in areas with high wind speeds and/or high snow pack (Kajimoto et al. 2003, Han et al. 2012, Takahashi 2014). In addition, recent studies from warm-temperate mountain ranges suggest drought-limited growth supplementary to the temperature-limited growth at some treelines (Gonzáles de Andrés 2015, Piper et al. 2016).

At European temperate treelines, the reported mean growing season ground temperatures vary from 6.7 to 8.8 °C (Körner and Paulsen 2004, Gehrig-Fasel et al. 2008, Hertel and Schöling 2011, Treml et al. 2015a). The growing season length at European treelines indicated by wood formation ranges between 83 and 137 days considering Picea abies, Pinus cembra and Larix decidua in the Alps and the Sudetes Mts. (Rossi et al. 2006, 2007, 2008, Moser et al. 2009, Treml et al. 2015a), however growing season as long as 150 (Rossi et al. 2008) or 170 days (Gruber et al. 2009) was observed as well. Modelled growing season lengths derived from climatic data span from 106 to 144 days in the broader region of Central Europe and the Alps (Kašpar and Treml 2016).

Similarly to treeline temperature metrics, the broad range has been observed also for growth parameters of treeline trees. For example, taking into account single tree species – *Picea abies* – the reported mean tree-ring widths from European treeline areas vary from 0.6 to 1.9 mm (Bednarz et al. 1998-1999, Paulsen et al.2000, King et al. 2013, Sidor et al. 2015, Ponocná et al. 2016). Great variability in TRW is obviously driven by age trends, site effects and different sampling positions across treeline ecotones. However, some TRW variability might be also ascribed to varying temperature conditions among treelines.

Since the tree growth is temperature-limited at treeline, the growth should be approximately the same at treelines with the same tree species. However, as shown above, there is rather a broad range of temperatures and growth parameters reported from treelines, even within one macroclimatic region such as temperate zone of Europe. Besides of difficulties to capture treeline temperature metrics correctly, another source of uncertainty lies in limited knowledge of various factors depressing the uppermost tree stands bellow the potential treeline. Within the temperature range characterizing treeline regions, two growth patterns might by theoretically possible. First, tree growth will be approximately the same across all treeline regions, and higher treeline temperatures will be counterbalanced by the influence of other growth-limiting factors (e.g. biomass loss). Second possibility is that the warmer the treeline is, the higher tree growth is. In that case, the low and warm position of uppermost tree stands might result from the effect of occasionally acting factors like past disturbances or from the lag of treeline position behind the recent temperature increase. Our goals therefore were: (i) to compare growth parameters with treeline temperature metrics, (ii) to compare parameters indicative for biomass loss among treelines, and (ii) to identify treeline regions with unusually high tree growth suggesting that these treelines are situated below potential treeline.

Materials and methods
Study Area

Study area was represented by ten mountain ranges located at 48-51°N and 10-20°E in Central Europe north of the Alps (hereafter CENA; Figure 1) stretching between the Harz Mts. in the west and the Vysoké Tatry Mts. in the east. In all mountain ranges there is a paleoecological evidence of climate-driven treelines during the upper Holocene (Beug et al. 1999, Treml et al. 2006, Novák et al. 2010). Some of these mountain ranges (Harz, Krkonoše, Králický Sněžník and Hrubý Jeseník) are represented by a medium relief mountains exaggerated against foothills by 800-1000 m, eastern part of the CENA has

pronounced alpine relief exaggerated against foothills by more than 1200 m. Lithologies range from acidic nutrient poor bedrock (prevailing in the west) to flysch and limestone lithologies prevailing in the east.

Dominant treeline tree species is Norway spruce (*Picea abies* L. Karst). In West Carpathians (Babia Gora, Malá and Veľká Fatra Mts. the Tatras) also European larch (*Larix decidua*) and Swiss stone pine (*Pinus cembra*) occur (the latter only in the Vysoké Tatry Mts.). Except the Harz, Hrubý Jeseník and Králický Sněžník Mts., a shrubby dwarf pine (*Pinus mugo*) is widespread in the treeline ecotones. Treeline elevations range from 1100 m a.s.l. in Harz to 1770 m a.s.l. in Tatras (Table 1). The length of the growing season varies in CENA from 127 to 144 days and average growing season temperatures range from 6.1 to 7.4 °C (Kašpar and Treml 2016, Table 1). Precipitation sums range from 1200 mm (Hrubý Jeseník Mts.) to 2200 mm in the Vysoké Tatry Mts. (Hlavatá et al. 2011). Precipitation in the same elevation generally increases toward the west, however there are also pronounced gradients of increasing precipitation along elevation. Mean wind speed in summit regions tends to increase toward the west (Kašpar and Treml 2016). Treelines in the majority of studied mountain ranges had been locally affected by human action in the past, particularly by cattle grazing and hay making (Beug et al. 1999, Plesník 1978, Speranza et al. 2000, Novák et al.2010). However, since the 1950s in the west and 1970s in the east, treeline ecotones have been developing spontaneously without extensive direct human impacts (Kozak 2003, Boltižiar 2007, Solár and Janiga 2013, Treml et al. 2016).

Data sampling and preparation

In each mountain range we collected growth parameters along the highest local treeline elevations identified by Kašpar and Treml (2016). At each local treeline, ~ 15 trees or tree-islands were sampled in the upper part of treeline ecotone along an elevation contour connecting uppermost positions of 3 m high trees in each aspect and in stands having a minimum canopy 0.1. Tree height of 3 m did not apply to the Harz Mts. and Velká Fatra Mts., where upper limit of tree stands was formed by trees of 4-5 m height and no trees higher than 3 m were found above this line. Elevation contour was divided into 15 regular sections and the nearest tree or tree island to each section node was sampled. Trees (or tree islands) were thus regularly distributed in all aspects in each area (Table 1).

For each sampling point we determined whether it was represented by individual tree or clonal tree island. In case of tree-island, we recorded number of trees within the tree-island. Presence of apical breaks was determined as well. Not only contemporary, but also earlier apical breaks were determined based on candelabra-like stems (Schweingruber 1996). Following parameters were further measured for the single highest tree at each sampling point: tree height, stem girth (all in 1 m height), lengths of branches at four directions (north, south, west and east) at approximately 2 m above the stem base (i.e. approximately above the maximum height of snow pack) and a distance to the nearest barrier protecting trees against wind (other tree-groups, rock formations, *Pinus mugo* stands etc.) considering mean value of three directions. Tree-ring cores were sampled using Pressler borer from each tree (or from the highest tree within tree island). Two cores were extracted at 0.5 m of stem height to obtain tree-ring widths (TRW) and tree age. Third core (or cross-section) was taken at approximately 2 m stem height to compute mean height increment and to detect proportion of reaction wood. In order to compute the height increment, exact distance of each core to the stem base and to the uppermost internode was measured.

Tree-ring cores were sanded, ring widths were measured and cross-dated (Speer 2012). For a few tree-ring cores without pith, the number of missing tree-rings was estimated according to Batllori and Gutiérrez (2008). Two parameters describing tree allometry were computed: crown shape (length of the shortest/longest branch), and stem taper (girth

divided by tree height). We calculated two variants of height increments: (i) average height increment between 0.5 m and 2 m (number of tree rings at ~0.5 m minus number of tree rings at ~2 m divided by exact distance between cores) and (ii) the average height increment above 2 m (distance between the upper core and uppermost internode divided by the number of rings except the ring from contemporary growing season). Proportion of reaction wood was determined as a number of tree-rings with presence of reaction wood in first 15 tree-rings of the upper core (in 2 m height).

Treeline temperature metrics
Treeline temperature metrics for each region was computed according to the study of Kašpar and Treml (2016) (Table 1). Following temperature metrics was used: mean air temperature over June – September period, mean temperature of the period with mean daily temperature > 0.9 °C and no snow cover (hereafter called "mean growing season temperature", Paulsen and Körner 2014), length of the growing season delimited by 0.9 °C daily temperature threshold and no snow pack (further called as "length of the growing season", Paulsen and Körner 2014), and sum of daily temperatures exceeding 0°C (hereafter called as a "degree days above 0°C"). Average temperature metrics were computed specifically for each tree considering the period of radial growth or height growth. For example, if height growth below 2 m was realized by a given tree in the period 1970-1985, the temperature metrics were computed over this period. Source temperature and precipitation data came from nearest meteorological stations considering local lapse rates. Detailed description of computation of treeline temperature metrics is described in Kašpar and Treml (2016).

Statistical analysis
For each tree we determined its elevation, heat load (a combination of aspect and slope, McCune and Keon 2004) and slope from digital elevation model with 30 m resolution using ArcGIS software (ESRI 2014). Further, elevation difference between nearest summit and the location of a tree was calculated (hereafter called as "peak distance"). Prior to statistical analysis, all continuous variables were visually checked for normality and transformed, if necessary, applying logarithmic or square root transformation. Finally, all continuous variables were z-transformed to have unit variance and zero mean.
At first step, we looked for the basic pattern in data. Pearson correlations were computed to test for possible relations between tree age and field-derived variables describing growth and shape of trees in each treeline region. Analysis of variance including Tukey post-hoc test was performed in order to determine possible differences in all growth parameters among treeline regions. Then, at the level of all treeline regions, the relationship of treeline temperature metrics with growth parameters (TRW, both variants of height increment) was analyzed using linear regression.
Second, to explain variance in each growth parameter considering intra-regional variability (tree height, girth and taper, TRW and height increment under and above 2 m), linear mixed effect models were applied (R package lme4, Bates et al. 2015, and LmerTest, Kuznetsova et al. 2015). Explanatory variables were represented by treeline temperature metrics (alternatively Jun-Sep temperature, growing season temperature, length of growing season, degree days above 0°C), tree age, peak distance, distance from nearest barrier, number of trees in tree island, heat load index and parameters indicative for wind-induced bending and biomass loss (presence of apical breaks, crown shape and proportion of reaction wood). Models for each response variable were computed four times with four different temperature metrics. Mountain range was designed as a random variable. We generated a set of models with all explanatory variable combinations. The models were ranked by

Akaike information criterion (AIC) (Burnham and Anderson 2002). For each explanatory variable, we further estimated AIC-weighted importance, a unitless metric indicating summed Akaike information across all models in which the variable appears. Importance ranges from 0 (variable with no explanatory weight) to 1 (variable in all top models) (R package MuMIn, Barton 2015). The coefficient of determination (marginal R2) was computed for the full model as a measure of each model's explained variance (Nakagawa and Schielzeth 2013). All statistical analyses were performed in R (R Development Core Team 2016).

Results

The entire data contains 152 trees with average tree age 49 years. Tree age did not significantly differ among the regions (p=0.19). The oldest trees were found in the Harz Mts. and in the Hrubý Jeseník Mts. and the youngest in the Nízké Tatry Mts. (Figure 2A). Average TRW was 1.1 mm. Trees in the Harz Mts. had significantly wider tree rings than trees in the remaining mountain ranges except the Veľká Fatra and Západné Tatry Mts. (p=0.00, Figure 2B). The narrowest tree-rings were determined in the Nízké Tatry Mts. Average height increment below 2 m was 7.0 cm. Variance in height increment below 2 m was usually greater within a given region than between regions with an exception of difference between the Harz Mts. (the highest height increment) and the Západné Tatry Mts. (the lowest height increment) (p<0.05, Figure 2C). Height increment above 2 m attained 11.0 cm in average. No statistically significant differences in height increment above 2 m were recorded (p=0.84), nevertheless the highest height increment above 2 m was found in the Veľká Fatra Mts. and the smallest in the Vysoké Tatry Mts. (Figure 2D). Trees in the Harz Mts. and the Veľká Fatra Mts. were significantly higher (p<0.05) than trees in the remaining mountains (Figure 2G). The average tree height was 359 cm Trees with the greatest girth were found in the Harz, Hrubý Jeseník and in the Veľká Fatra Mts., the smallest girth had trees in the Vysoké Tatry Mts. Similar pattern as for girth was observed for stem taper (Figure 2I). Trees with the lowest proportion of reaction wood came from the Krkonoše Mts. On the other hand, the highest proportion of reaction wood occurred in the Nízké Tatry Mts. and in the Králický Sněžník Mts. (Figure 2F). The most symmetric tree crowns characterized trees in the Veľká Fatra Mts. (Figure 2J), significantly more symmetric than in the Babia Gora, Hrubý Jeseník and Nízké Tatry Mts. and in the Králický Sněžník Mts. (p<0.05). Tree islands in the Babia Góra Mts. were formed by the highest number of trees, significantly more than in the remaining mountain ranges except Hrubý Jeseník Mts. (p<0.05, Figure 2E).

Within single regions, TRW correlated negatively with tree age in the Hrubý Jeseník Mts., the Babia Gora Mts. and the Západné Tatry Mts. (p<0.1, Figure 3). Height increment to 2 m was negatively correlated with tree age in all mountain ranges (p<0.1). Significant correlation between tree age and height increment above 2 m was found only in the Nízké Tatry Mts. (p<0.1) (Figure 3).

Considering all regions together, TRW significantly correlated with each temperature metrics (Figure 4A). Correlations ranged from 0.31 (growing season temperature) to 0.43 (degree day temperatures). Height increment below 2m revealed significant correlations (p<0.05) with temperature metrics between 0.24 (growing season length) and 0.47 (June-September temperature) (Figure 4B). Correlations between temperature metrics and height increment above 2m were weak (Figure 4C). The only significant relation was found between height increment and mean June-September temperature.

Linear mixed effect models explained successfully all growth parameters but height increment above 2 m (Figure 5, Appendix S1). Temperature metrics had important predictive effect for stem girth, TRW and, to some extent, also for height increment below

2 m and tree height. The effect of temperature was always positive. Tree age was important to predict tree height, stem girth, stem taper and height increment to 2 m (positive effect). Distance to peak was important for taper (negative effect). Distance to barriers affected tree height - trees growing close to barriers were more probably smaller. More reaction wood occurred at smaller trees with tiny TRW (important negative effects on tree height, stem girth and TRW). Apical breaks frequently entered into the models explaining tree taper with a positive effect (more apical breaks occurred at trees with higher taper). The effects of remaining explanatory variables (heat load index, size of tree island and crown shape) were relatively less important.

Focusing exclusively on temperature metrics, the highest explanatory power for tree height revealed growing season temperature and degree days above 0°C (Figure 5, Appendix S1). June-September temperature, degree days and growing season length entered into top models explaining stem girth and TRW. For height increment below 2 m, only growing season temperature and June-September temperature had a significant effect in a part of best models (Appendix S1). June-September temperature frequently entered in best models explaining height growth above 2m, however the marginal R^2 of the full model was very low (Appendix S1).

Discussion

This study introduces the first attempt to link growth parameters and temperature metrics for treeline trees in different treeline regions. We assumed two possible scenarios. First, the basic growth parameters will be approximately the same in all mountain ranges and higher treeline temperatures will be counterbalanced by higher presence of symptoms of biomass loss, or, second, that varying temperatures among treelines will be reflected in varying growth and growth will be correlated with temperature. Our results showed that a combination of both above-mentioned hypotheses is closest to be true.

Among the growth parameters used in this study (radial growth, height growth to 2 m, height increment above 2 m), radial growth represented by TRW revealed the closest link to treeline temperature metrics. Warmer treelines were therefore characterized by wider tree rings of treeline trees. TRW is probably less affected than height increment by facilitation (Šenfeldr et al. 2014) and by environmental factors other than temperature (e.g., wind action) and thus retains stronger temperature signal. This finding contrasts to the studies of Jalkanen and Tuovinen (2001), McCarrol et al (2003) or Salminen et al. (2009), who found better correlations of height rather than radial growth with climate. However, these studies were conducted far below the treeline. As opposed to lower elevations, the height growth at treeline is much more subjected to biomass loss due to snow loads, wind-induced abrasion (Autio and Colpaert 2005, Han et al. 2012, Mamet and Kershaw 2013) or wind-induced cooling below temperature thresholds allowing growth (James et al. 1994).

Radial increment and stem girth were closely correlated with all temperature metrics except mean growing season temperature. Concerning June-September temperature and growing season degree days, the weight of peak growing season conditions is relatively higher than for temperature metrics capturing entire growing season. The June-July period is the most influential part of the growing season for radial growth at treelines in temperate and boreal Europe (Linderholm 2002, Frank and Esper 2005, Ponocná et al. 2016). The importance of growing season length can be probably attributed to the spring timing of growth onset – the earlier wood formation is started the more wood is formed during the growing season (Rossi et al. 2006). Poor performance of mean growing season temperature for prediction of radial growth might be explained by the fact that the entire growing season delimited by the 0.9 °C threshold and absence of snow includes long period from August to October without direct influence on tree ring width (Rossi et al. 2006, Cuny et al. 2014).

As opposite to TRW, height growth below 2 m was correlated the best with the mean growing season temperature. Warmer growing seasons led to higher height increment to 2 m of tree height. However, the effect of mean growing season temperature can be indirect. High entire growing season temperature could be the consequence of late growing season start (straight away with high air temperature) because of delayed snow melt in areas with high snow pack. High snow pack is protective against ice and snow blasting above snow surface (Mamet and Kershaw 2013). Alternatively, sufficiently high temperature over the entire growing season enables intense formation of reserves in autumnal periods with no sink activity (i.e. no growth) and these reserves can be utilized at the beginning of subsequent growing season. Similarly, Gamache and Payette (2004) showed that height growth of treeline *Picea mariana* was correlated to temperature of preceding growing season. Reserves might be necessary for height growth to repair meristems damaged from various agents effective in winter like wind action, rime and snow loads (e.g., Hertel and Schölling 2011).

Considering height growth above 2 m, we found only very weak relation with temperature metrics. At the same time, the intra-regional variability in height growth was high suggesting that site-specific effects are important. We propose that factors other than temperature such as facilitation within tree islands, wind abrasion, snow and rime load might be responsible for not determined relation of height growth above 2 m to temperature (Kašpar et al. 2016). Once trees sufficiently protrude above the snowpack, various abrasion-causing factors become important. Furthermore, higher trees are also exposed to stronger wind pressure leading to decrease in height growth (Gamache and Payette 2004, Kharuk et al 2010, Barbeito et al. 2012). However, none of our explanatory variables indicative for wind-induced abrasion or biomass-loss explained any variability in height growth above 2 m.

While we observed stratification of some treeline growth parameters according temperature metrics, there were also treeline regions with obvious symptoms of biomass loss. For example, we found a gradual decrease in stem taper from the westernmost area (the Harz Mts.) to the east. At the same time, stem taper was explained by treeline distance to the nearest peak - the shorter distance, the more pronounced taper. Distance of treeline to peak is generally increasing toward the east indicating that western treelines are more prone to be affected by summit effect (sensu Aulitzky 1967). Stem tapering is a result of limitation of apical growth, while radial growth remains more or less the same (Bonnesoeur et al. 2016). Additionally, apical breaks also increased stem taper. As a consequence, basal stem diameters of trees growing in windy areas near summits become after some time much wider than expected according to tree height. In investigated treelines, TRW well correlated with treeline temperature, while the relation between apical growth of stems above 2 m and temperature was weak. This combination finally resulted in higher stem taper in warmer than in colder treelines. The observation of tapered trees at warm treelines might indicate the retarded advance of local treelines, because of summit climatic conditions preventing unambiguous response of trees to warming (Gamache and Payette 2004, Kašpar et al. 2016).

As an indicator of mechanical effect of wind on stems, we used the proportion of reaction wood at 2 m stem height. We believe that reaction wood in stem sections distant from the base is indicative for stem bending triggered by wind action rather than bending from creeping snow as typical at stem base (Schweingruber 1996). Formation of the reaction wood is demanding particularly for lignin deposited in thick secondary cell walls (Du and Yamamoto 2007). The related change in allocation of carbon into cell wall thickening might result in depressed radial growth in other part of stem or in depressed height growth (Coutand et al. 2008), which is in line with our findings.

Height growth below 2m was negatively influenced by tree age, i.e. contemporary individuals reach 2 m height faster than individuals few decades ago. There was weak collinearity of age and temperature trends (temperatures in all areas have been increasing since 1980s), however there are probably more important reasons for temporal trend in height growth below 2 m. First, stand densities at treelines have been increasing (Treml et al. 2016, Czajka et al. 2015), which enforces facilitative effect on growth of newly established individuals (Šenfeldr et al. 2014). Second, trends in pollution fallout including decreasing sulphur deposition since 1990s and continuing nitrogen deposition might be supportive for the recent height growth increase (Kolář et al. 2015).

At two treelines with relatively high treeline temperatures (Králický Sněžník, Hrubý Jeseník Mts.), the effect of high temperature was counterbalanced by biomass loss evidenced by irregular crowns (Králický Sněžník, Hrubý Jeseník Mts.) and high proportion or reaction wood (Králický Sněžník Mts. only). At the remaining treelines with high temperature (the Harz Mts., the Veľká Fatra Mts.), warm temperatures were not compensated by any symptom of biomass loss or other wind-induced growth anomalies. These two treelines are thus not driven by current temperature conditions but they are either the remnant of past disturbances or their lag behind the warming since the Little Ice Age is substantially greater than in the remaining treeline areas. Treml et al. (2015b) reported decades during the Little Ice Age that were about 3 °C cooler than reference period (1961-1990) in the Sudetes (Krkonoše, Králický Sněžník and Hrubý Jeseník Mts.), which could be reflected in depressed treeline position. Because the spatial temperature variability is relatively low over Central Europe, the same might be anticipated for the Harz and Veľká Fatra Mts. Subsequent human use of these treeline areas during the period of warming might prevent treeline advance.

Conclusions

At ten temperate European treelines, the variability in radial growth was primarily governed by temperature, while the effect of temperature on apical growth decreased with increasing tree height. Height increment of stem sections above 2 m was highly variable with minor effect of temperature suggesting importance of site-specific factors. Temperature-sensitive radial growth and limited effect of temperature on height growth above 2 m result in higher stem taper at warm compared to cold treelines. In addition, warm treelines were typically located close to mountain summits and trees had highly tapered stems due summit climatic conditions. Warm treelines with high radial growth rates were characterized by formation of reaction wood and frequent symptoms of biomass loss - the factors counterbalancing warmer conditions. However, we determined also warm treelines with high growth rates and limited presence of symptoms of biomass loss. We suggest that these treelines are remnants of past human-induced disturbances or, alternatively, their response to recent temperature increase is lagged due to past human land-use.

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Figures and tables

Figure 1: Central Europe with location of mountain ranges under study. Abbreviations: BG – Babia Góra Mts.; Hrz - Harz Mts.; Jes – Hrubý Jeseník Mts.; Kra – Králický Sněžník Mts.; Krk – Krkonoše Mts.; MF – Malá Fata Mts.; NT – Nízké Tatry Mts.; VF – Veľká Fatra Mts.; VT – Vysoké Tatry Mts.; ZT – Západné Tatry Mts.
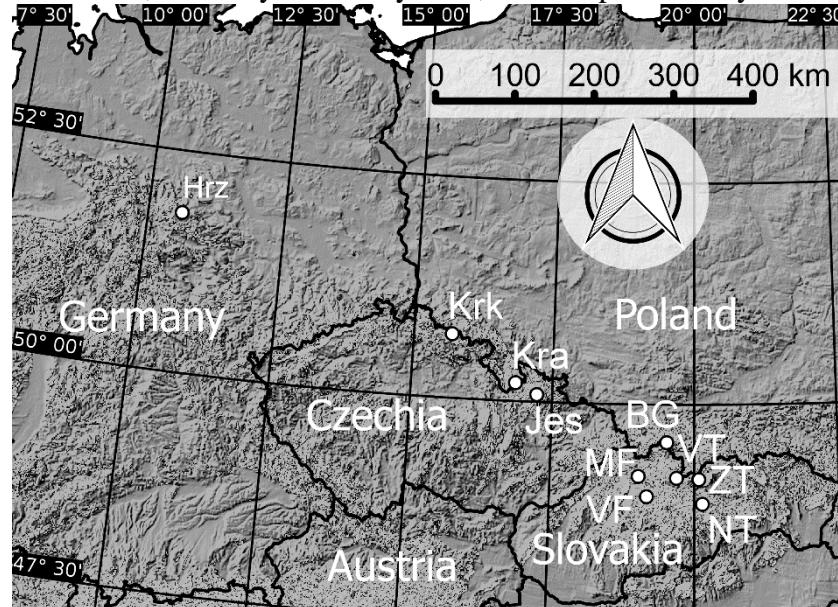
Figure 2: Tree growth and shape parameters stratified according to mountain ranges. For mountain range abbreviations see Figure 1.
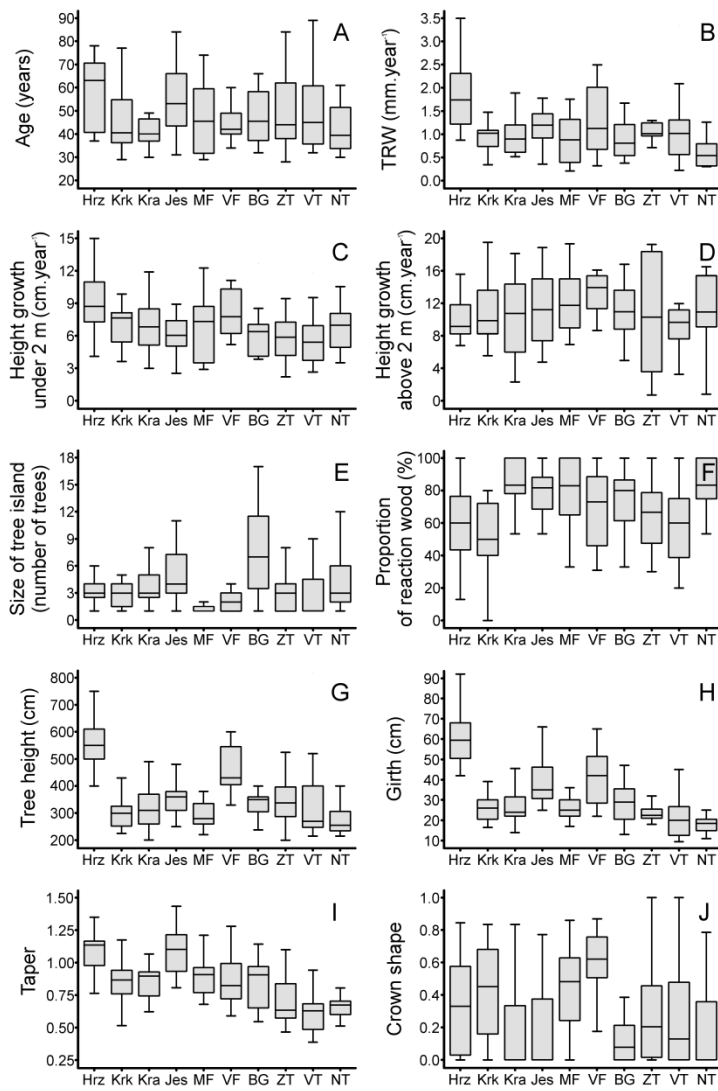
Figure 3: Correlations between main growth parameters and tree age. Full bars denote significant correlations (p<0.1). For mountain range abbreviations see Figure 1.

Figure 4: Relation between basic growth parameters (tree ring width, height growth below 2 m, height growth above 2 m) and treeline temperature metrics. Points represent individual trees. Linear fit is buffered by standard error. Regression line is not drawn when linear fit is not statistically significant (p<0.05).
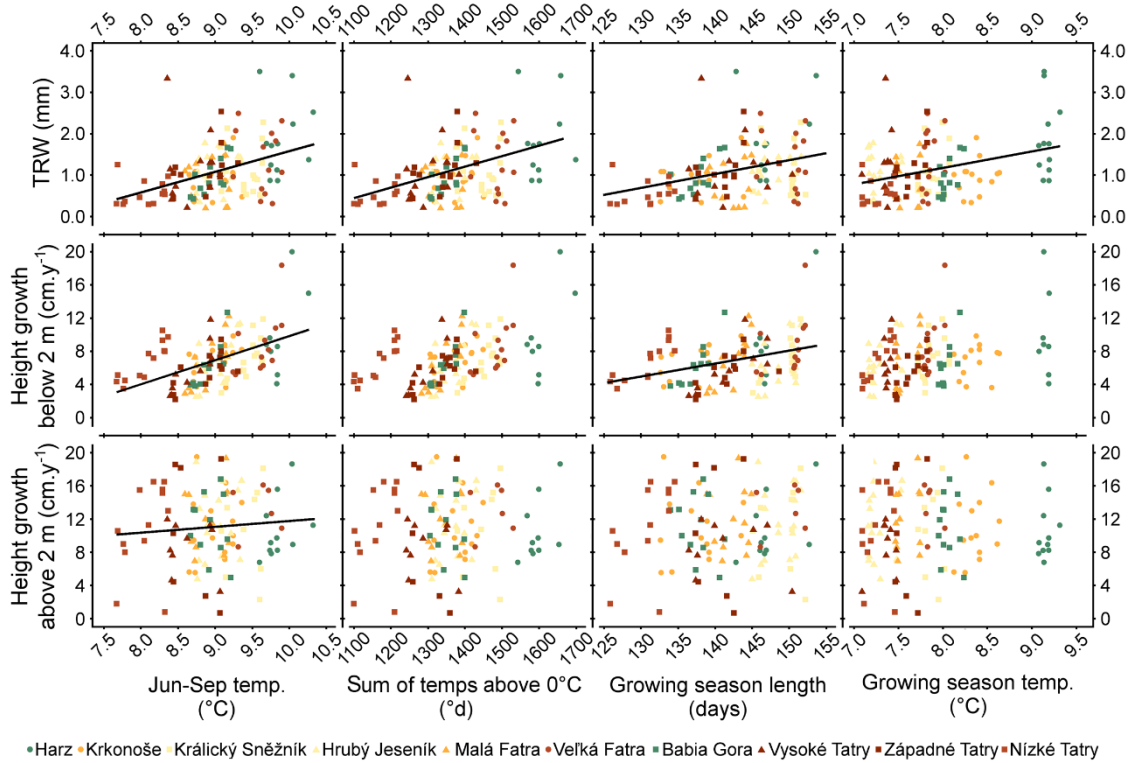
Figure 5: Estimates of fixed effects (points) with confidence intervals (whiskers).
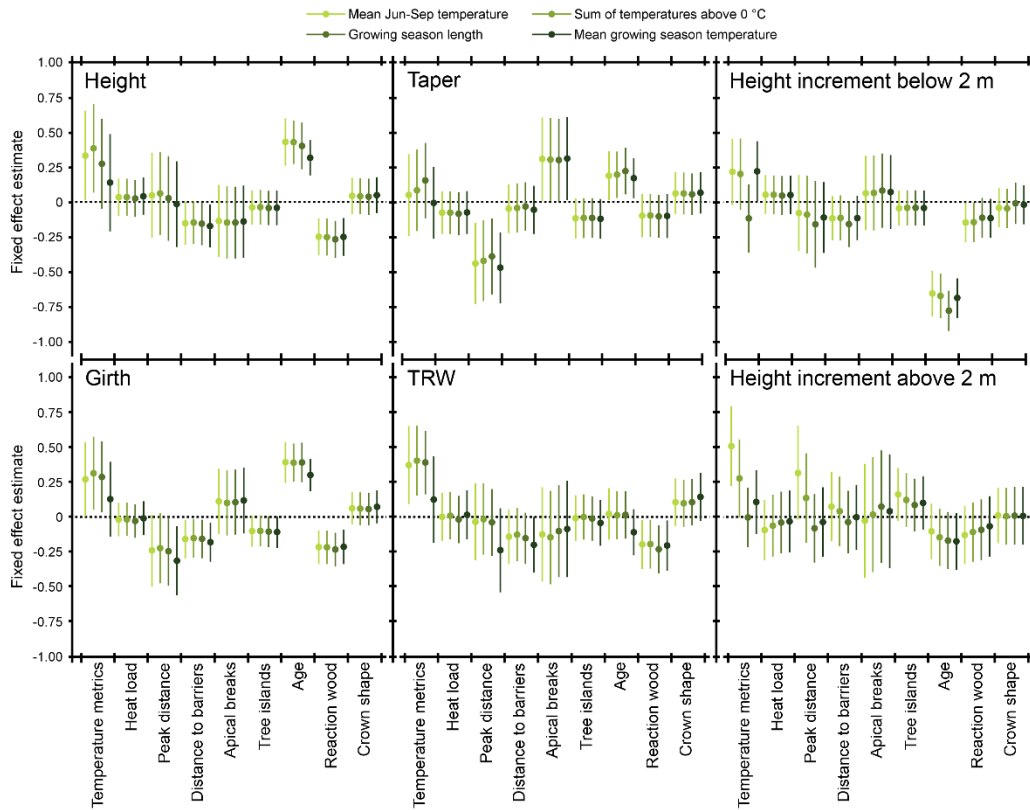
Table 1: Descriptive characteristics of treelines in the study area. Climate variables refer to study Kašpar and Treml (2016).

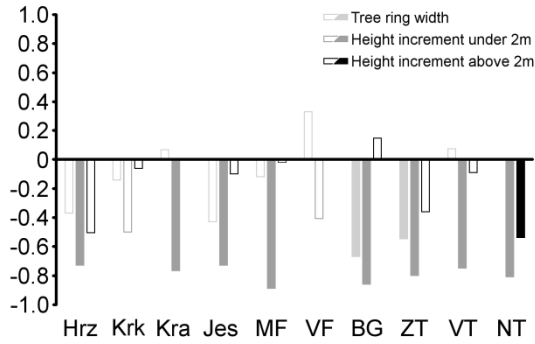| Mountain range	Mountain range elevation (m ASL)	Treeline elevation [m ASL]	Growing season length	Growing season temperature	Jun-Sep temperature	Sum of temperatures above 0 °C
Harz	1141	1110.6 ±4.8	139	7.4	9.4	1495
Krkonoše	1603	1490 ±10.7	127	6.4	7.7	1136
Králický Sněžník	1424	1405.8 ±2.1	142	7.4	8.8	1336
Hrubý Jeseník	1491	1466.2 ±2.5	144	7.1	8.3	1252
Malá Fatra	1709	1632.6 ±11	137	6.4	8.2	1245
Velká Fatra	1552	1513.6 ±10.4	141	7.0	8.7	1338
Babia Góra	1725	1615.7 ±18.7	130	6.6	8.5	1293
Západné Tatry	2248	1716.1 ±34.7	132	6.4	7.6	1317
Vysoké Tatry	2655	1717.2 ±42.2	133	6.8	8.5	1302
Nízké Tatry	2152	1773.1 ±19.5	121	6.1	7.2	1038

Appendix 1: Explanation of response variables (tree height, girth, taper, TRW, height increment below and above 2 m of tree height) using explanatory variables in linear mixed effect models. Mountain range was designed as a random variable. For each variable with fixed effect, a variable importance is indicated. Plus or minus signs in brackets denote direction of a fixed effect coefficient. Marginal R^2 refers to the full model.

Response	Temperature metrics included	R^2m	Random variable significance (p)	Temperature metrics	Crown shape	Reaction wood	Age	Tree islands	Apical breaks	Distance to barriers	Peak distance	Heat load
											Variable importance	
Height	Degree days	0.39	0.00	0.59	0.06	0.99	1.00	0.05	0.18	0.38	0.11	0.05
	Jun-Sep temp.	0.36	0.00	0.45	0.06	0.99	1.00	0.05	0.17	0.41	0.12	0.05
	Growing season length	0.31	0.00	0.38	0.06	0.99	1.00	0.05	0.18	0.43	0.11	0.05
	Growing season temp.	0.26	0.00	0.16	0.06	0.99	1.00	0.05	0.18	0.46	0.11	0.05
Girth	Degree days	0.52	0.00	0.92	0.07	0.98	1.00	0.12	0.12	0.19	0.18	0.06
	Jun-Sep temp.	0.49	0.00	0.80	0.07	0.98	1.00	0.13	0.13	0.23	0.22	0.06
	Growing season length	0.48	0.00	0.84	0.07	1.00	1.00	0.14	0.12	0.24	0.21	0.07
	Growing season temp.	0.42	0.00	0.22	0.08	0.98	1.00	0.14	0.14	0.38	0.32	0.06
Taper	Degree days	0.37	0.01	0.17	0.08	0.25	0.54	0.17	0.71	0.09	0.89	0.13
	Jun-Sep temp.	0.36	0.01	0.15	0.08	0.25	0.52	0.18	0.72	0.09	0.91	0.13
	Growing season length	0.37	0.01	0.17	0.08	0.25	0.54	0.18	0.72	0.09	0.90	0.14
	Growing season temp.	0.35	0.01	0.11	0.08	0.25	0.50	0.18	0.73	0.09	0.92	0.13
TRW	Degree days	0.24	0.60	0.99	0.13	0.68	0.07	0.06	0.16	0.20	0.11	0.06
	Jun-Sep temp.	0.23	0.40	0.97	0.14	0.70	0.08	0.06	0.15	0.23	0.11	0.07
	Growing season length	0.24	0.60	0.99	0.13	0.91	0.06	0.06	0.13	0.25	0.08	0.07
	Growing season temp.	0.19	0.01	0.47	0.37	0.51	0.17	0.07	0.14	0.30	0.23	0.08
Height increment below 2m	Degree days	0.49	0.01	0.25	0.06	0.27	1.00	0.06	0.12	0.22	0.11	0.06
	Jun-Sep temp.	0.49	0.00	0.31	0.06	0.29	1.00	0.06	0.12	0.22	0.11	0.06
	Growing season length	0.45	0.00	0.13	0.06	0.25	1.00	0.06	0.12	0.26	0.12	0.06
	Growing season temp.	0.51	0.00	0.57	0.06	0.22	1.00	0.06	0.12	0.19	0.10	0.06
Height increment above 2m	Degree days	0.08	0.70	0.26	0.09	0.11	0.20	0.11	0.14	0.08	0.11	0.11
	Jun-Sep temp.	0.16	0.40	0.74	0.08	0.11	0.18	0.15	0.14	0.08	0.15	0.10
	Growing season length	0.05	1.00	0.08	0.09	0.11	0.20	0.10	0.14	0.08	0.11	0.12
	Growing season temp.	0.05	1.00	0.14	0.09	0.10	0.21	0.10	0.14	0.08	0.11	0.12

VI.   Conclusions

6 Conclusions

Treeline position is generally predetermined by temperature conditions. However, at regional or local scales, treeline position is modified by various other factors, from which the influence of wind is of high importance. Depression of treeline below its potential limit near summits with high wind speeds is called a summit syndrome. At natural treelines, tree growth rates should be similar because of their identical temperature limit. If the negative influence of temperature on tree growth is less limiting, then the tree growth at treeline should be governed by other factors, particularly by biomass loss or wind-induced growth decrease. If neither of above-mentioned assumptions is met, trees are not growth-limited anymore and the influence of past disturbances, anthropogenic interventions or recruitment limits should be taken into account.

Treeline elevation in Central Europe generally increases towards the east along the gradients of increasing continentality and mass-elevation effect. The mean treeline elevation ascent along the 50th parallel is about 94 m per 100 km. Treeline positions in Central Europe reflect an increase in temperature isotherms, which is attributed to increasing continentality as well as increasing mass elevation effect from west to east. Calculated climate metrics of uppermost tree stands from the Krkonoše Mts., the Babia Góra Mts., the Malá Fatra Mts., the Západné Tatry Mts., the Vysoké Tatry Mts., the Belianské Tatry Mts. and the Nízké Tatry Mts. were very similar (mean Jun-Sep temperature = 8.1 ±0.2 °C, mean sum of degree days above 0 °C = 122 ±47 °d, mean growing season length = 130 ±2 days, mean growing season temperature = 6.5 ±0.1 °C) indicating that the uppermost trees are located at their temperature limits. Furthermore, temperature metrics were similar to the temperature metrics of the uppermost tree stands in the Alps such as areas of Mt. Pascherkofel, Andermat or Säntis. However, based on temperature metrics we also determined that the uppermost tree stands in Harz Mts., Králický Sněžník Mts., Hrubý Jeseník Mts and Veľká Fatra Mts. are likely situated below the temperature limit (mean Jun-Sep temperature 7.5 ±0.2 °C, mean sum of degree days above 0 °C 1097 ±49 °d, mean growing season length 130 ±9 days, mean growing season temperature 6.8 ±0. °C).

To further test above-mentioned hypotheses, we compiled growth and morphometric measurements from the uppermost tree stands. We found that radial growth, height growth below 2 m and height growth above 2 m showed high, weak, or almost no

correlation with temperature, respectively. Certain warm treelines with high radial growth rates were characterized by high proportions of reaction wood, frequent symptoms of biomass loss and high stem taper (apply to Králický Sněžník and Hrubý Jeseník). However, other treelines provided limited evidence of biomass loss or presence of reaction wood, indicating that they are either a remnant of past disturbances, or their response to the recent temperature increase is delayed because of anthropogenic land use (apply to Harz and Veľká Fatra).

These results were further elaborated in extensive study focused on the effect of wind on tree growth in treeline ecotone in the Krkonoše Mts. Across a set of sites distributed along the gradient of wind speed, we exemplified that high wind speeds are reflected in the presence of clonal tree islands and irregular tree crowns. Despite evident wind-induced biomass loss, radial growth was not significantly affected, and the effect of wind on height increment was limited only to parts of the stem from 2 m above ground. This limitation attains approximately 0.65 cm.year^{-1} per 1 m.s^{-1} increment of wind speed. Considering that the height growth was substantially reduced by wind in about half of the treeline area, and wind was able to limit only growth of trees taller than 2 m, the overall wind-induced depression of highest treeline positions is probably low, even in windy mountain regions. Wind could be thus significant agent at local scale, where it can maintain local treelines below summits, however at global scale its influence might be probably neglected.

While wind influences height growth of the trees high enough to be exposed to wind action, the radial growth is governed by soil and stem temperature. Across alpine treeline ecotone in the Krkonoše Mts. the difference in mean growing season air and soil temperature between upper and lower part of treeline ecotone was unexpectedly high. This was most likely caused by higher exposure to wind at treeline than at timberline, which increased environmental lapse rate. Based on three seasons of wood formation monitoring in treeline ecotone (2010 – 2012), the differences in onset of individual phases of wood formation of *Picea abies* between treeline and timberline were significant only in cases of several-weeks delay in soil warming at the treeline versus the timberline site. Otherwise, the treeline/timberline differences in onsets of individual wood formation phases were smaller than our weekly sampling resolution. The first pronounced increase in cambial activity was associated with the first warming of the soil from near-zero temperatures to 4 – 5 °C in the spring. This might indicate that in *Picea abies*, full resumption of cambial activity at the basal part of the stem requires all parts of the tree to be sufficiently warm. Irrespective of simultaneous or shifted onset of cambial activity at our study sites,

significantly more cambial and enlarging cells were observed at the warmer, timberline location than at the colder, treeline site during the early part of the growing season. Whereas differences in the number of cells at the beginning of the growing season were likely due to temperature, timberline trees also displayed greater duration of the cell-enlargement and wall-thickening phases, associated with more prolonged enlargement of the larger tracheids there. Therefore, we conclude that for *Picea abies*, both temperature and size effects govern differences in wood phenology across the treeline ecotone.

In conclusion, this dissertation thesis brings evidence that the uppermost tree stands of the major mountain ranges of Central Europe (Vysoké, Západné, Nízké Tatry, Malá Fatra, Babia Góra, Krkonoše) are located near their temperature limit. However, as exemplified on the example of the Krkonoše Mts., apical growth of trees reaching tree height (2 – 3 m) might be limited by wind at wind-exposed stands. Remaining treelines located close to summits can be divided into two groups. In the first group (Králický Sněžník, Hrubý Jeseník), less limiting temperature conditions are outweighed by a substantial wind influence on biomass loss and depressed height growth. In the second group (Harz, Veľká Fatra), tree growth at treeline is limited neither by temperature nor by biomass loss from wind action. Summit syndrome affects treeline trees through wind-limited height growth and through increase in environmental lapse rate.

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VII.   Appendix

Subject: Specification of the authorial share

As the leading author, I hereby declare that Jakub Kašpar contributet to reserch article „Mountains, Czech Republic" published in Trees as follows:

- data collection in growing seasons 2011 and 2012,
- sample preparation of samples from the half of vegetation season 2010 and from vegetation seasons 2011 a 2012;
- statistical evaluation of data obtained in growing seasons 2011 and 2012;
- preparation of data for inclusion into international database.

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