Master Thesis

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Alpine treeline ecotone of Orava Beskyds-Beskid Żywiecki, Slovak-Polish borderland

- structure and ecological conditions

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Abstract

Alpine treelines are some of the most obvious and important vegetation boundaries in the mountains worldwide, separating the forest zone and the treeless alpine zone. They deserve interest both in context of climatic change and implications of the treeline advance for alpine areas, and in context of avalanche prevention actual for many European countries. The causes of their formation are, however, not fully understood yet. Heat deficiency has been suggested by many researchers as one of the plausible explanations of the phenomenon. A recent study has suggested that the soil temperatures at the treelines of the world are within a very narrow range. A datalogger campaign and case study were therefore devised to investigate the structure and ecological conditions in the alpine treeline ecotone in the Orava Beskyds on the border between Poland and Slovakia, as this mountain range is known for undisturbed natural conditions enabling the forests to attain their climatic limit. The ecotone was divided according to the structure into three relative altitudinal bands, where the air temperatures, soil temperatures, tree parameters such as height and circumference at breast height, and ecological conditions (using average Ellenberg indicator values and canopy shading as surrogates) were assessed. Hypotheses tested were that the relative altitudinal bands would possess unified temperature regimes overriding the effects of altitude, slope grade and aspect. The heat deficiency was quantified by the mean temperatures during the growing season, and by a day-degree sum above a certain threshold.

The results have shown that only the lowest part of the ecotone, the edge of the closed forest, possessed an unified thermal regime regarding both air and soil temperatures. The temperatures in the upper parts of the ecotone were much more dependent on the actual altitude, slope grade and aspect than on the position within a certain relative altitudinal band. The lowland-timberline air temperature lapse rate was found to differ substantially from the standard lapse rate used in earlier studies of the treeline. The relationship between air and soil temperatures was observed to incorporate a delay in the effect of air temperatures, and a moderating effect of air humidity was observed. Regarding the overall ecological conditions measured by average Ellenberg values and canopy shading, only soil humidity and light conditions were observed to change consistently with altitude. The tree height and diameter decreased with altitude at different rate, resulting in changes in the height to diameter ratio. This may be a hint of differences in performance between apical and cambial meristems. Insufficient performance of the apical meristems in the conditions of heat deficiency was suggested by the treeline researchers to be a possible explanation of the cessation of arborescent growth at the treeline. The actual mechanisms are, however, yet to be fully explored.

Sammendrag

Alpine tregrenser er noen av de mest iøynefallende og viktigste vegetasjonsgrensene i fjellområder over hele jordkloden. De er interresante både i forbindelse med klimaforandring og mulig tap av alpine områder og i forbindelse med beskyttelse mot snøskred, viktig for mange land i Europa. Hvilke faktorer som best definerer tregrensa er fortsatt ikke helt klarlagt. Mange forskere har foreslått mangel på varme som en sannsynlig forklaring. En nylig publiser artikkel antyder at jordtemperaturene i tregrenser over hele jordkloden ikke er veldig forskjellige. Denne undersøkelsen er fokusert til tregrenseøkoton av Orava Beskyder på grensa mellom Polen og Slovakia for å undersøke strukturen og de økologiske forholdene innenfor økotonen. Orava Beskyder ble valgt på grunn av uberørt natur som gir muligheter for skog å etablere en naturlig grense som trolig er klimatisk betinget. Økotonen ble delt i tre relative høydenivåer hvor lufttemperaturer, jordtemperaturer, egenskaper av trær som høyde og omkrets på brysthøyde, og økologiske forhold ble undersøkt. Gjennomsnitt av Ellenbergverdier og målinger av lysforhold ble brukt som forklaringsverdier for økologiske forhold. Hypoteser som ble testet var om temperatureforholdene innenfor de ulike relative høydenivåene var stabile på tross av forskjellige høyder over havet, helningsgrad og eksposisjon. Varme ble kvantifisert som gjennomsnittstemperatur i vekstsesongen, og som døgn-grad summer av temperaturer høyere enn 5 °C.

Resultatene viser at de temperaturforholdene bare er stabile i det laveste nivået, dvs. på kanten av sammensatt skog. Det gjelder både luft- og jordtemperaturene. Temperaturforhold i de øvre delene av økotonen er mer påvirket av høyde, helningsgrad og eksposisjon. Temperatur lapserate mellom lavlandet og tregrensa var forskjellig fra standard lapserate som har vært brukt tidligere i tregrenseforskninga. Forholdet mellom luft- og jordtemperaturene viste en forsinket respons og påvirkningen av denne responsen ble forklart ved forskjeller i luftfuktighet. Når det gjelder øvrige økologiske forhold kvantifisert gjennom Ellenbergverdier og lysmålinger, var det kun jordfuktighet og lysforhold som forandret seg konsekvent med høyde over havet. Trehøyde og diameter minsket med høyde over havet med forskjellige rater som resulterte i forandringer av trehøyde-diameter forholdet. Det kan være en antydning av forskjeller i responsen mellom apikalmeristemer og kambium knyttet til mangel på varme. Utilstrekkelig respons av apikalmeristemet kan være forklaringen på hvorfor trær ved tregrensa ikke klarer å oppnå vanlig oppreist form. Presise mekanismer bak dette blir imidlertid et spørsmål for framtidige undersøkelser.

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Foreword

This thesis is an outcome of two demanding field research seasons and many hours spent in front of the computer and reading the books and articles. It would most certainly not have been possible without many people's help and advice, and I would like to name some at least. My deepest thanks go to all who have helped me in any way with the work on this thesis.

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Ján Šulavík

1 Introduction

Alpine treelines are some of the most obvious vegetational boundaries (Holtmeier 2003) present in the mountains worldwide - with exception of the Antarctic - representing the boundary between the continuous upper montane forest and alpine tundra. Alpine treeline is a line, or, more precisely - as will be mentioned later in the text - a transition zone separating the upper montane vegetation belt dominated by trees as a lifeform from alpine vegetation dominated by shrubs, graminoides and herbs.

Due to the importance and apparent omnipresence of this phenomenon, it has been extensively studied in the past two centuries, yet for the most part in the temperate mountains of the northern hemisphere (Körner 2012). However, even when fairly abrupt, the transition from upper montane forest to the treeless alpine tundra is rarely in a form of sharp line - notable exception being genus *Nothofagus* of the southern hemisphere, whose status as a 'treeline-forming' taxon (i.e. *Nothofagus*-treeline representing a lifeform, not a species-specific, boundary) is disputed (Körner 2012). More commonly, a multitude of various transitions takes place in different mountain areas and with different taxa, may it be gradual diminishing of stature and/ or opening and increasing patchiness of the forest, formation of a distinct 'krummholz' belt with bush-like shrubs and crippled individuals of tree taxa etc., making the term 'treeline ecotone' more appropriate. Multitude of various variants of ecotone's composition is described in great detail by Holtmeier (2003).

Holtmeier also calls in an earlier article for separation of true 'Krummholz' - genetically shaped bush-like individuals of species as, for example, dwarf mountain pine (*Pinus mugo*) or green alder (*Alnus viridis*) from crippled tree individuals altered by mechanical disturbance (e.g. by wind, ice particle abrasion etc.) for which he uses term 'elfin wood' (Holtmeier 1981). This is a very important and well founded remark, as the true 'Krummholz' forms a distinct belt with occasional azonal occurrences of its typical species in sites non-favourable for tree growth (e.g. avalanche tracks), while the crippled tree individuals - or 'elfin wood' - represent merely an attempt of an otherwise dominant forest tree species to advance far beyond its biological and ecological optimum.

The general nature of the ecotone – being a gradual, rather than abrupt transition from forest to treeless tundra – and the great variety of its composition causes a problem in detecting the transition and extremities of the ecotone in the field. It causes also a great deal of confusion, especially in terms of nomenclature of various parts of the ever-changing ecotone. This holds true also regarding the practical, arbitrary norms, such as tree height, tree group density etc. Körner (2012, p. 18) gives an overview of the nomenclature with a proposal of its simplification:

'Timberline' *sensu* Körner is described as "*upper limit of the closed forest*" - even though the author himself argues that the 'closure' of the forest is rarely abrupt – something that makes 'timberline' rather difficult to identify. Nevertheless, it's an important boundary, since it can be regarded as the 'lower edge' (or beginning) of the ecotone.

'Treeline' proper, also called 'forest line' is described as "*a line connecting the highest patches of forest (composed of trees of at least 3 m height) within a given slope*". This line can be regarded as the 'centre', or 'core', of the ecotone, since this is the line that would be regarded as "the treeline" from a birds-eye - or opposite-slope - view.

'Outpost-treeline' is described as the line which results from connecting the positions of isolated full-stature trees found above the treeline proper. These tree individuals "*may reflect by chance recruitment in a particularly favourable topography*". This line can be regarded as the upper edge (or end) of the ecotone; even though a 'tree species limit' can also be identified as the uppermost occurrence of tree species individuals regardless of stature, its association with the aforementioned "*gets very loose...because of the substantial deviation of microclimate from macroclimate at high elevation*".

A significant and well-documented relationship has been found between the overall mean elevation (or altitude) of a mountain region, as well as its spatial extent, and the altitudinal position of the treeline ecotone (and other related vegetation zones with relatively parallel course). The so-called "mass-elevation effect" (German: Massenerhebungseffekt) results in a higher position of the treeline in the mountain areas with higher mean elevation, usually in central mountain regions (Holtmeier 2003). An opposite effect is observed in the isolated mountains in the form of the so-called "summit phenomenon" (German: Gipfelphänomen), which leads to comparatively lower position of the treeline and other associated vegetation zones in these isolated mountains when compared to spatially more extensive mountain regions of similar altitude (Holtmeier 2003).

Both are possibly based on the same physical and ecological principle and can be, so to say, "two sides of the same coin": elevated spatially extensive mountain regions possess a great surface for interception of incoming short wave radiation (combined with increased continentality and decreased cloudiness due to clouds being blocked by peripheral mountains) as well as sufficient mass for effective heat storage (Holtmeier 2003). On the contrary, the isolated mountains are freely exposed to atmospheric conditions while at the same time they lack the surface and mass for effective heat interception and storage. Heat deficiency is one of the most important factors considered to play a decisive role in the treeline formation, as will be discussed later.

1.1 General views on causes of the treeline formation

The question of the causes of the treeline formation is, as most questions in ecology, a rather complex and difficult one. There are several types of treeline obviously caused by various physical or mechanical impacts, being located in avalanche tracks etc., by absence of sufficient substrate – so called edaphic treeline, by substrate instability, or by the anthropogenic activities such as logging, cattle grazing and fires, among others (Plesník 1971). There are, however, areas where the cessation of tree growth is not caused by any apparent direct physical or mechanical impacts, but rather by other driver(s), most probably an effect of unfavourable climate and heat deficiency (Körner 2012). In the later years, the works of Holtmeier (2003), Wieser and Tausz (2007) and Körner (2012) gave a complex view on the treeline phenomenon citing results of various researches conducted to study its various aspects and probable causes.

Being present worldwide in the distribution limits of various species at various altitudes and latitudes with multitude of patterns and apparent complex relationships causing it, the treeline phenomenon has been subject to many researches conducted under varying standpoints. Both Holtmeier (2003) and Körner (2012) describe the history and present state of treeline research. There are roughly two major standpoints: first, described by Körner (2012) as “everything matters” standpoint arguing that the treeline formation is far too complex phenomenon always dependent on the local factors for to be able to identify a general global driver behind it; and second, proposed by, among others, Körner (2012), with major global drivers causing the existence of the phenomenon modulated by regional drivers of local variability.

A relevant argument for support of the latter is that globally observable phenomenon - however heterogeneous in the close-view appearance it might be - calls for a globally present driver/ drivers. Since the phenomenon is tied to the mountainous areas and associated higher altitudes (although decreasing with increasing latitude), major global drivers have to be connected to the peculiarity of the high mountain environment. Körner (2012) identified several variables specific for this environment and varying consistently with altitude. However, only low temperatures seem to be the only omnipresent variable relevant for tree growth. This is in accord with ideas of earlier researchers about heat deficiency as an underlying cause of treeline formation (Holtmeier 2003).

Slope aspect (orientation) and grade (gradient) have a considerable impact on the plant life and, not least, treeline ecotone as well, not just in terms of sheer physical influence and limitation (e.g. as in orographic treeline), but also in altering the radiation loading, wind exposure, moisture conditions etc., and may at times even override the effect of altitude on certain variables (Friedel 1967, cited in: Holtmeier 2003; Scherrer and Körner 2011, cited in: Körner 2012). Slope grade governs various variables such as avalanche and debris exposure and snow duration (Holtmeier 2003) and, in combination with latitude, also radiation loading and associated thermal conditions (Oke 1978).

The role of slope aspect can be considered a subject of debate for some researchers. Körner (2012, p. 27) argues that "*treeline elevation was not found to vary significantly with slope direction*" (or aspect); its importance for treeline position has been, however, acknowledged by numerous articles and books, both past and recent (Holtmeier 2003). Slope aspect obviously alters exposure both to radiation, precipitation and wind progressively with increasing latitude - an attribute hardly not having an impact on the vegetation and treeline.

It is important to note at this point that many (if not all) mountain treelines in the northern hemisphere are currently in the state of "rebound" after profound changes in the land use that took place in the 20th century after the decline of human activity in the mountains connected to, among other things, logging and pastoralism, which had caused noticeable downward shift of the treeline in the previous centuries (Körner 2012). This development was largely connected to modern nature protection and lifestyle changes. The fact that the treeline is in many areas basically just in the state of recovering from centuries-long anthropogenic pressure, connected with the notion that "*treeline position will always lag behind climatic change by at least 50, but possibly more than 100 years*" (Körner 2012, p. 179), makes separation of the impact of the climate from the effects of diminished anthropogenic pressure a rather challenging task. It is also important to mention that due to longevity of tree individuals combined with rather slow growth in the treeline ecotone – and associated deferred response to changing conditions, the current treeline position reflects (and always will) the past climate rather than the contemporary (Körner 2012).

In spite of all difficulties this poses for drawing conclusions, it is, after all, still meaningful and important to study environmental conditions in the treeline ecotone to illustrate its development in the context of both climate and management changes.

1.2 Heat deficiency

There is a broad agreement that given otherwise favourable soil conditions and topography, heat deficiency is the most plausible factor restricting the tree growth in the treeline ecotone (Wieser and Tausz 2007).

There are several ways of assessing the heat deficiency at the treeline. A traditional method has been correlating the treeline position with a certain temperature mean during a selected period (e.g. warmest month, three ('tritherm') or four ('tetratherm') warmest months etc.). Holtmeier (2003) gives an overview about various theories and research results. He criticizes the use of mean temperatures, however, since, as he argues, mean temperatures do not exist in nature, and therefore may be regarded merely as an indicator, but not as a causal factor (Holtmeier 2003). Mean temperatures do not exist in nature, indeed, yet they can be used as surrogates to assess the heat sum acquired by the treeline trees. Another source of criticism can be the fact that many temperatures used, especially in the older articles, were not measured directly *in situ*, but extrapolated from the data of adjacent meteorological stations (located almost exclusively in the lowland areas) using the standard lapse rate of 0,65 °C/ 100 m, which, as shown by research done by using actual measurements in the field, for example results of Perttu (1972), does not correlate sufficiently with the actual conditions in the mountain environment (with actual lapse rates measured being generally lower than the standard lapse rate). Inversion situations, typical for autumn and winter seasons in the temperate zone, are also virtually undetectable without *in situ* measurements.

Another way of assessing the heat is calculation of so called day-degrees of accumulated temperatures (Crawford 1989). Forbes and Kensworthy (1973) have, for example, found that limitations of *Betula pendula* and *Betula pubescens* ssp. *odorata* distributions were correlated with certain thresholds of accumulated temperature in the form of day-degrees. These day-degree sums were calculated as sums of daily temperatures exceeding a certain threshold (in their case, a temperature of 5,6 °C). Prevalence of *Betula pendula* as a more heat-demanding species gradually diminished along an altitudinal (and associated temperature) gradient while *Betula pubescens* ssp. *odorata* as a more cold-tolerant species adapted to mountain environments gradually became dominant. This is in full accord with a standard notion in ecology, namely ecological valence or ecological amplitude. Tree species, similarly to all other living organisms, have certain heat requirements for survival and well-being, and their particular thermal minimum, optimum and maximum can be identified. Overlap of species' ecological (in this case - more concretely - thermal) minima and maxima along a gradient (either altitudinal or latitudinal) combined with various interspecific, not to mention intraspecific, relationships generally lead to formation of ecotones. The treeline ecotone is certainly not an exception in this.

When trying to find a comparable way of measurement of heat acquired by the treeline trees, one factor becomes soon apparent, and that is the striking variability of temperature regimes the trees worldwide have to endure (Körner 2012). From diurnal cycles of mild daily temperatures and sub-zero nightly temperatures in tropical mountain ranges to long periods of winter dormancy in the mountains of the temperate zone, to obtain a method that would make research results and temperature measurements comparable across the globe is a rather difficult task.

Körner and Paulsen (2004) used a method based on datalogger measurements of soil temperatures in the root zone of the treeline trees. Mean temperatures of the growing season in their, territorially speaking, remarkable sample (46 treeline sites located between 68°N and 42°S) were calculated to lie in a rather narrow range - given the aforementioned great variability of the overall temperature regimes - of 6,7 ± 0,8 °C (mean ± SD) (Körner and Paulsen 2004). Despite some questionable decisions (e.g. method of calculating the length of growing season), their research showed an interesting evidence of a global driver connected to heat deficiency present in the formation and maintaining of global treeline phenomenon. Results of this research were later supported also by a test of the theory in an environment of a lowland permafrost site (Körner and Hoch 2006).

All these methods might be criticized at one point or another for obtaining mere approximations of the heat conditions in the treeline ecotone. However, in order to obtain absolutely precise and reliable data with temperatures replaced by (more appropriate) energy values, one would have to set up a radiation budget and water and energy balance research in accord with Oke (1978) on a massive scale and detect all possible energy sources and sinks, something that is probably beyond possibilities of most research facilities, and most certainly beyond possibilities of a master thesis research. Therefore, a datalogger campaign is a fairly reliable method, and certainly among the best methods available for heat deficiency assessment in the treeline ecotone.

The heat deficiency has several important impacts on the growth and performance of tree individuals in the treeline ecotone, for example, a certain length of vegetation period is required for cells to form, mature and harden properly in order to be able to withstand the adversities of sub-zero temperatures (Holtmeier 2003), which means that there is a certain amount of 'warmth' (or thermal energy) required both for survival and growth of the individual. A difference in performance of apical and cambial (lateral) meristems under unfavourable temperature conditions may also play its role in the trees' inability to attain full stature, resulting in shrub-like, 'elfin wood' forms, as has been hinted by Körner (2012).

1.3 Main aims

As a synthesis of what was previously stated, the questions in the global treeline research are manifold, the subject is vast, and it is not possible in scope of a master thesis to cover all possible environmental and ecological aspects playing a role in the phenomenon.

The heat deficiency in the treeline ecotone was chosen as one of the supposed principal drivers of formation and sustenance of the treeline. Therefore, a datalogger campaign in the form of a case study was devised to take place in the treeline ecotone of Babia hora and Pilsko mountain massifs as the highest mountains of the Orava Beskyds-Beskid Żywiecki mountain range on the border between Poland and Slovakia.

Hypothesis tested was based on paper by Körner and Paulsen (2004), that the soil temperatures in the analogous positions (or relative altitudinal bands) in the ecotone will not differ significantly with various slope orientations, grades, and especially altitudes - Pilsko is lower than Babia hora and the treeline there is located somewhat lower (in itself an example of 'summit phenomenon'); the same applies to some degree to the north-facing versus south-facing slopes of both massifs: the treeline is somewhat lower on the north-facing slopes.

Another main aim was to assess the climatic conditions in the ecotone and the impact of slope aspect, slope grade and altitude on the annual course of soil temperatures and temperatures in the growing season.

The environmental conditions in the ecotone and tree parameters were assessed in order to obtain an overview of its structure and ecology. Vegetation analyses were conducted in order to obtain Ellenberg indicator values usable as surrogates of additional ecological variables to study ecological variation in the ecotone. Direct measurements of light conditions were conducted as well with the same aim. Tree parameters such as diameter, height and stem character were quantified to assess the changes in tree stature and height to diameter ratio with increasing altitude, as this can aid in demonstration of differences in performance between apical and cambial meristems under adverse environmental conditions within the ecotone.

2 Research area

The research area is located in the Central Europe, in the north-western part of Slovak Republic and south-western part of Republic of Poland at 49° N latitude and 19° E longitude (see Fig. 1). Due to the position on the border between Poland and Slovakia, two names are used for the same mountain range: "Orava Beskyds" (Slovak: Oravské Beskydy) in Slovak and "Żywiec Beskid" (Polish: Beskid Żywiecki) in Polish. However, the Polish term encompasses a larger area due to different terminology (terming collectively several mountain ranges and sub-units regarded in Slovakia as separate) and also due to the presence of several sub-units of the mountain range located solely in Poland (Merganič et al. 2003). Thus, term 'Orava Beskyds' will be used in the further description for the sake of clarity and simplicity, as they are regarded a sub-unit of Beskid Żywiecki.

Figure 1. Geographical position of the research area (own work, composed from various free sources)

Orava Beskyds are a part of the Carpathians, and are the highest mountain range in the Outer Western Carpathians sub-province (Kocián 1990) especially due to the prominence of Babia hora (Polish: Babia Góra) and Pilsko massifs, with Babia hora reaching at its highest point (in Polish called also "Diablak") 1725 m asl and Pilsko reaching 1557 m asl.

Only these two massifs in the mountain range have sufficient altitude for occurrence of natural, non-anthropogenic treeline ecotone, and are two cores of the research area.

2.1 Geology and geomorphology

Geologically, the research area is a part of outer Western Carpathian flysch belt (Merganič et al. 2003). 'Flysch' is a quite specific term used in this context which denotes a sequence of various marine sedimentary rocks (sandstone, shale, claystone) deposited in multiple series (Kocián 1990). Different resistance of these rock types to weathering and erosion resulted according to Kocián (1990) in general forms of the land relief (with resistant rocks forming the concave and the less resistant forming the convex forms); while the orientation of the rock layers and tectonics influenced the morphology on a more intricate scale (Merganič et al. 2003).

Massifs of Babia hora and Pilsko are mainly composed of resistant sandstone rocks, also called “Magura sandstones”, however, the Polish side of Babia hora has somewhat more complicated geology (Merganič et al. 2003). For a detailed geological description of Orava Beskyds see Fig. 2.

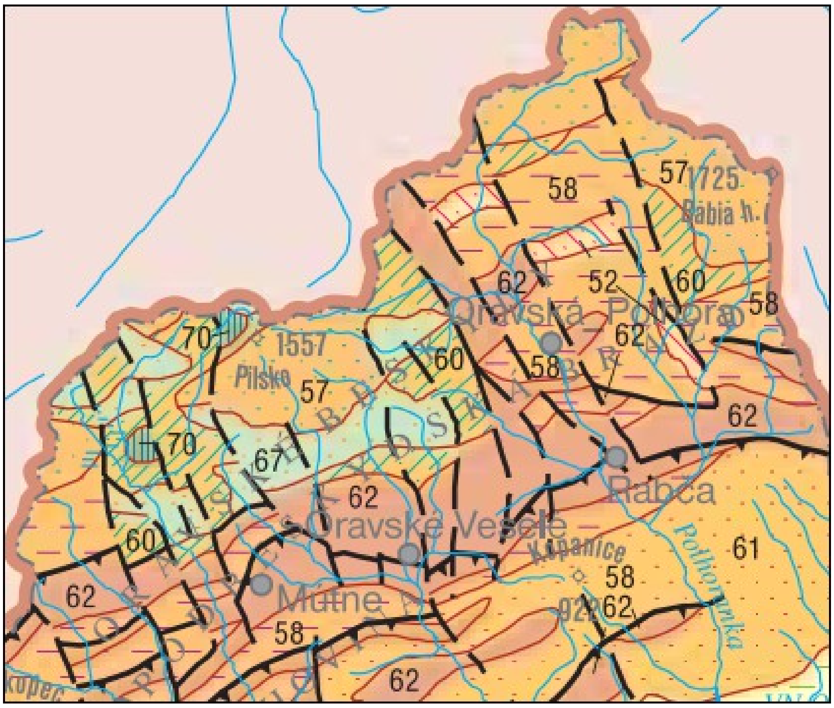

Figure 2. Geological map of Orava Beskyds (Biely et al. 2002). ***Lines*** *– thin: geological boundary; thick continuous/ thick discontinuous: fault line proven/ assumed; with triangles: overthrust line.* ***Codes*** *– 52: calcareous claystones, siltstones, sandstones, slumps; 57: graywacke/ arkosic sandstones, mudstones; 58: mudstones, glauconitic sandstones, marlstones; 60: greenish-gray/ red claystones, glauconitic sandstones, pelitic Fe-carbonates; 62: sandstones, shales, thin-bedded flysch, red claystones; 67: graywacke/ arkose muscovitic sandstones, microconglomerates; 70: dark gray and green shales, sandstones (description provided only for Orava Beskyds area)*

Babia hora and Pilsko massifs have generally rather gentle slopes and smooth land relief, however Babia hora is rather asymmetrical as the northern slopes are much steeper than the southern: 35° – 75° on the north side as compared to 15° - 25° on the south side (Merganič et al. 2003). Northern slopes of Pilsko massif are also comparably steeper than its southern slopes; western slopes are, however, even steeper than the northern.

Several interesting phenomenons occurring in the higher zones of Babia hora massif (and, to a lesser degree, also Pilsko massif) can be mentioned: blockfields in the uppermost part of the massif, talus cones, frost splitting and erosion, scree lakes (in the Polish part) and sinkholes (Merganič et al. 2003). At least the northern slopes have been under the last glacial maximum also presumably affected by glaciation.

In the western part of Babia hora massif in the area of so-called Lesser Babia hora (Slovak: Malá Babia hora; Polish: Mała Babia Góra/ Cyl), pseudokarst phenomenons can be observed in form of minor fissure and sinkhole caves.

The topography of the research area resulted in rather great spatial gradient lengths and distances within the treeline ecotone on the gentle slopes with smooth relief; these were somewhat shorter and the treeline ecotone more restrained on the steep slopes. Rocks of Babia hora are described as rather nutrient-rich (i.e. rich with Ca2+) in the literature (Merganič et al. 2003); the vegetation composition did not, however, reflect this very distinctly, as the attributes of the bedrock are presumably overridden by acidic organic matter deposited by coniferous trees and shrubs in the treeline ecotone.

2.2 Vegetation

Vegetation of Orava Beskyds is strongly influenced by the climate, altitudinal profile and latitude. Generally speaking, it is a part of Western Carpathian phytogeographical area, Western Beskids district (Kocián 1990).

Being the highest mountain of the Outer Western Carpathians and possessing an exceptional topographic prominence of approximately 1100 m, Babia hora can be regarded as a "*model mountain*" for studies of altitudinal zonation of vegetation (Merganič et al. 2003, p. 15). Five distinct zones have been identified: sub-montane (670 – 900 m asl.), lower montane (900 – 1200 m asl.), upper montane (1200 – 1440 m asl.), sub-alpine (1440 – 1700 m asl.) and alpine (1700 – 1725 m asl.); each possessing different plant associations (Merganič et al. 2003).

Of special importance for this particular research is the fact that compared to many areas in Slovakia with Norway spruce (*Picea abies*) forests, Babia hora and Pilsko are of the few areas in Slovakia where *Picea abies* is found naturally, i.e. not due to planting and forest management. Forests in the highest forest zone (above 1200 m asl.) are considered to be mostly in their natural state and only marginally influenced by human impacts (Merganič et al. 2003), and fulfill the criteria to be deemed primeval forests (Korpeľ 1989).

Apart from *Picea abies*, several other tree species are present in the area. They do not, however, normally reach treeline ecotone – notable exception being rowan (*Sorbus aucuparia*), whose individuals, sometimes also in 'full tree' stature, are present scattered in the ecotone (yet in numbers greatly falling behind of those of *Picea abies*).

In the upper zones adjacent to the treeline ecotone are fir (*Abies alba*)-*Picea abies* forests (800 – 1200 m asl.) and *Picea abies* forests (> 1200 m asl.) present; these forest types are floristically rather similar (Merganič et al. 2003). Understorey is dominated by *Vaccinium myrtillus*, *Homogyne alpina*, *Dryopteris dilatata* and *Avenella flexuosa* (Merganič et al. 2003). Other species present in the treeline ecotone and adjacent to it are *Vaccinium vitis-idaea*, *Deschampsia caespitosa*, as well as *Rubus idaeus*, *Gentiana asclepiadea*, *Calamagrostis villosa*, *Calamagrostis arundinacea*, an occasional dominance is achieved by *Athyrium distentifolium*; these species have variable impact on *Picea abies* propagational success ranging from creating favourable conditions to completely hindering propagation and growth (Vorčák and Jankovič 2009).

Above the ecotone, a distinct 'krummholz' belt is observable dominated by dwarf mountain pine (*Pinus mugo*) with shrubs of alpine juniper (*Juniperus communis* subsp. *alpina*) also present

(Merganič et al. 2003). *Pinus mugo* descends often deep into the ecotone along concave land forms with long-lasting snow cover, preventing both the sexual and asexual propagation of *Picea abies* in these particular areas (Vorčák and Jankovič 2009). However, *Pinus mugo* attains dominance only in the sites generally unsuitable or sub-optimal for *Picea abies*, as there are known examples from Tatra mountains where the 'full-stature' *Picea abies* individuals with favourable growth conditions gradually attain dominance in *Pinus mugo* stands, which usually leads to *Pinus mugo* being outcompeted for light and exterminated (Plesník 1971). Proof for this are dead relict *Pinus mugo* individuals in the emergent dense *Picea abies* stands.

Even though the vegetation in the research area is generally in rather natural state, a past anthropogenic impact of, among other things, pastoralism is visible by presence of secondary ruderal vegetation in few sites, most notably in area around former shepherd's cottage (Slovak: salaš) of Šťaviny (Merganič et al. 2003); ruderal communities there form a triangular gap descending deeply into the forest vegetation, artifically lowering the treeline. Dominant species is *Rumex alpinus*, other species present include *Urtica dioica*, *Stellaria nemorum*, *Milium effusum* and *Phleum alpinum* (Merganič et al. 2003).

Noteworthy, albeit of little importance *per se* to the treeline ecotone, is the presence of natural mires and wetlands in the region. This can, however, help illustrate the climate of the research area, as the mires are known to be associated with peculiar climatic conditions. Formation of these mires is caused by combination of geological and geomorphological conditions (poorly drained concave land forms on impermeable marine sediments) with the cold and humid climate of the northern Orava region (Kocián 1990). They are regarded as relict stands connected to the last glacial maximum and are mostly of the bog type (Kocián 1990). Several rare relic plants have used these bogs as refugia: among others, *Andromeda polifolia*, *Calla palustris*, *Drosera anglica*, *Drosera rotundifolia*, *Ledum palustre*, *Oxycoccus palustris*, *Rhynchospora alba* (Kliment 2003). It has to be noted that the aforementioned mires are located mostly in the lowland part of the northern Orava region and the foothills of the mountains of the research area. This makes the region comparable, at least in terms of climate, with areas lying rather further north.

2.3 Climate

Climate of the research area is affected by several factors: latitude, altitude and continentality play an important role in the general character of the climate.

Compared to Tatra mountains, Babia hora massif possesses a harsher climate at comparable altitudes which influences also the vegetation and its zonation (Merganič et al. 2003) – this is also true for Pilsko massif, as the two massifs share very similar temperature and precipitation regimes. During the winter season, temperature inversions are quite common due to the spatial heterogeneity causing cold air drainage and storage in the valleys and basins (Kocián 1990); therefore, the altitude-temperature relationship in the winter is usually not linear (unless the weather is controlled by overall low-pressure cyclonic situation). Mean temperature in January, which is the coldest month, is in the highest altitudinal zone of Babia hora (1450 - 1725 m asl.) on the average, given the width of the zone, around -7 °C (Merganič et al. 2003). During the summer, a more reliable altitude-temperature relationship is observed, and average temperature for three summer months - June, July and August - is 10 °C in the same altitudinal zone (Merganič et al. 2003); both average temperatures are from period 1901 – 1950. Average number of so-called “frost days”, i.e. days with minimal daily temperature under 0 °C is 160 – 180 in the research area, while the average number of so-called “summer days”, i.e. days with maximal daily temperature being 25 °C or more is around zero (Kocián 1990).

Orava Beskyds mountain range presents a significant barrier for humid northern and north-western winds coming from the sea (Baltic Sea and North Sea). This leads to substantial amount of precipitation in the main ridge with average values exceeding 1200 – 1400 mm per year (Kocián 1990), as well as increased cloudiness in the region. Major part of precipitation falls during the summer season from June to August, while the season from December to April has comparatively less precipitation (Merganič et al. 2003). Precipitation in the latter is mostly in form of snow, the length of the season with substantial snow cover is on average between 150 – 200 days (depending on altitude) and date of first snowfall is typically in the half of October, while the last snowfall is usually in the beginning of May (Merganič et al. 2003).

As mentioned earlier, Orava Beskyds are exposed primarily to northern and north-western winds bringing humidity and lowering the temperatures in the region; another dominant wind direction is from the east, which makes the wind conditions in the research area somewhat more complex (Merganič et al. 2003).

2.4 Brief history of land use, nature protection and research

Nature in the research area has been exploited by humans for centuries, however, the impact and extent of anthropogenic pressure have varied in different areas and altitudes, with forests in the highest forest zone remaining only marginally disturbed (Merganič et al. 2003).

The basins and valleys in the research area were colonised quite lately compared to other parts of Orava region – for example, villages of Oravská Polhora and Oravské Veselé situated closest to Babia hora and Pilsko were founded only in the end of 16th/ beginning of 17th century – and remained rather sparsely populated throughout most of the subsequent history (Stanovská 1990).

There was some historical anthropogenic pressure connected to logging and pastoralism in the research area as mentioned earlier, but the effects of this pressure are diminishing and remaining visible only in some confined areas (as for example the aforementioned area of Šťaviny). Most modern anthropogenic pressure is due to tourist trampling and disrespect for marked trails. Negative impact of air pollution is also quite important.

Forests in the highest forest zone (above 1200 m asl.) are generally deemed to be governed by natural regeneration processes (Merganič et al. 2003); an attribute rarely found in Central European mountain areas and certainly one of the decisive points in favor of the choice of this area for research of non-anthropogenic treeline ecotone.

This fact can also be attributed to quite early (in the European context) steps for nature protection in the research area in the modern sense of the word, carried out in a remarkable accord on both sides of the border. In 1926, a nature reserve on Babia hora was established in the Czechoslovak part of the massif under the name “Basin under Babia hora” (Slovak: Kotlina pod Babou horou), it was later extended to cover also the highest part of the massif (Kocián 1990); a “Babia Góra nature reserve” (Polish: Rezerwat na Babiej Górze) was established in the Polish part in 1933. The Polish nature reserve was extended in 1954 and reconstituted into “Babia Góra national park” (Polish: Babiogórski Park Narodowy). Polish Babia Góra national park was in 1977 admitted into the UNESCO Man and the Biosphere Programme's network of biosphere reserves (Merganič et al. 2003). In Pilsko area came such measures several decades later: nature reserve was established in 1967 in the Czechoslovak part (Kocián 1990) and in 1971 in the Polish part.

Czechoslovak nature reserves of Babia hora and Pilsko became part of a larger protected area “Upper Orava Protected Landscape Area” (Slovak: Chránená krajinná oblasť Horná Orava) in 1979

(Kocián 1990); Polish nature reserve in Pilsko became a part of similar “Żywiec Landscape Park” (Polish: Żywiecki Park Krajobrazowy) in 1986.

The protected areas in the research area have shifted borders and became extended several times. Most recently, in 2003, was Slovak Upper Orava Protected Landscape Area divided into zones with different management approach in accordance with the newly adopted law on nature protection. With this zonation have the nature reserves ceased to exist and have been replaced by a more complex zone approach. Highest parts of both Babia hora and Pilsko (roughly identical to the former reserves) became part of the A-zone with the strictest form of protection.

Research area has due to its peculiar and valuable natural environment been an object of numerous studies conducted by both Polish and (Czecho)-Slovak scientists. A pioneer study conducted by Polish botanist Walas (1933) was certainly among the first, if not the very first, to describe the vegetation of Babia hora in great detail. Several studies were conducted with focus on the forest ecology of the research area, for example: chapters on both Babia hora's and Pilsko's primeval forests in the book describing Slovakia's primeval forests by Korpeľ (1989), joint Polish-Slovak proceedings on status, development and use of Babia hora's and Pilsko's forests by Saniga and Jaloviar (eds.) (1998), and extensive montane forest research by Slovak researchers Merganič et al. (2003); among others. A Polish monograph on Babia Góra national park and its nature was published by Wołoszyn, Jaworski and Szwagrzyk (eds.) (2004). Polish researchers have also a long and succesful tradition of dendrochronological studies, and several were conducted on Babia hora as well, e.g. studies conducted by Bednarz et al. (1999) and by Wilczyński, Feliksik and Wertz (2004) focused specifically on upper montane forests of Babia hora. Autovegetative propagation of *Picea abies* in the treeline ecotone of Babia hora and Pilsko was studied by Slovak researchers Vorčák and Jankovič (2009).

3 Methods

In the following chapter will be described the methods of field research and environmental sampling used during the course of this research. Methods of statistical analyses will be discussed as well. The term 'krummholz' used throughout the thesis matches Holtmeier's true 'Krummholz'; ecotone nomenclature used in this master thesis generally follows Körner's division (with minor deviations and adjustments) for the sake of clarity and simplicity. For Körner's and Holtmeier's terms see Introduction.

3.1 Selection of the research area

Choice of the research area was based on a preliminary assessment of land use and history of the upper montane forests in the mountain ranges of Slovakia. With regard to the aims of the research – study of the environmental conditions and soil temperature profile during the course of a year in a “as-natural-as-possible”, non-anthropogenic treeline ecotone – two areas were chosen for possible future research, with second considered a “back-up” area.

Area of north-western part of Belianske Tatras (Slovak: Belianske Tatry), an eastern sub-unit of Tatra mountains was chosen due to the site history and was originally a preferred choice. The ownership issues ensured that the area has been under various pretexts - both personal interests (in this case, hunting) and state nature protection - under continuous protection from logging and pastoralism since at least 1879. South-eastern parts of Belianske Tatras and Javorova valley (Slovak: Javorová dolina) lying adjacent to the area had been, however, heavily grazed until the prohibition of pastoralism in newly established Tatra national park in 1952. To obtain comparable measurements from all slope aspects, area of Ticha and Koprova Valleys (Slovak: Tichá a Kôprová dolina) in High Tatras (Slovak: Vysoké Tatry) were also briefly considered due to their NE-SW direction. Small spatial extent of the undisturbed area in Belianske Tatras and difficulties with obtaining permission for research in the Tatra national park, combined with somewhat complicated accessibility of the area itself led to dismissal of this area for the purpose of research.

Area of Orava Beskyds, at first of Babia hora only, was chosen due to the undisturbed natural environment outlined in chapter on area description, and also due to peculiar shape of the mountain massif covering all slope aspects. The rather simple accessibility of the area – with several marked tourist trails, forester's hut on the Slovak side and a mountain hostel on the Polish side – was also very important factor for the choice. To obtain comparative data, Pilsko massif was later also added, also accessible by marked tourist trails and possessing a mountain hostel on the Polish side, usable as a base for research in the whole massif.

3.2 Field research

The first stage of the field research was conducted in the second half of August 2013, the second stage in September 2014. First, a map of the area was inspected to find slopes with suitable aspects and treeline present. Areas with significant disturbance and/or evident lasting impact of past anthropogenic activity (logging, pastoralism) were discarded, and the areas with highest occurring treeline within the given aspect (according to the map) were given priority.

In all, eight slope aspects were inspected (N, NE, E, SE, S, SW, W and NW). This was somewhat more difficult for Pilsko massif than for Babia hora, as the northern aspect was present on a steep and inaccessible slope and south-western aspect was present in an area surrounded by impenetrable *Pinus mugo* 'krummholz' vegetation. These two aspects were therefore omitted in Pilsko, and replaced by dual north-western aspect monitoring (one slope with more north-north-western aspect, another with more north-west-western aspect) and measurement on more gentle, yet still south-western inclined slope located adjacent to the marked trail. When slopes with suitable aspects and treeline were identified, a hypothetical line was drawn upslope to mark a transect route. This was, however, not strictly followed, as the vegetation composition limited accessibility greatly, especially in the upper parts of the ecotone where the *Picea abies* groups and individuals became increasingly mixed with dense *Pinus mugo* 'krummholz' thickets. The locations of the datalogger placement, vegetation analyses and measurements were therefore selected on an opportunistic basis based on their accessibility, which in itself by its stochastic character ensured a certain reasonable degree of randomization.

3.2.1 Study plot selection

Three relative altitudinal bands (or levels) within the ecotone were chosen for placement of dataloggers and environmental sampling on Babia hora, and two of those were covered on Pilsko:

1) 'timberline' *sensu* Körner (2012) - **L1** - as an edge of the closed forest of full-stature trees comparable in their stature and density with the forests under the treeline ecotone itself. As discussed in the Introduction, identification of this “line” in the field conditions is rather difficult, yet the very same can be said about any specific relative “line” in the treeline ecotone.

2) 'treeline proper' or, more precisely, 'tree group/ biogroup line' - **L2** - as a relative altitudinal band or “line” of the highest occurrence of full-stature trees forming distinctive groups of five and more individuals. A 'full-stature' tree in this case was chosen to be approximately 5 m and more. Any definition of 'full-stature' is in itself arbitrary and requires explanation. This value is based on two premises: 5 m were used as a minimum criterion by Jeník and Lokvenc (1962; cited in: Holtmeier 2003) in their research of the treeline in the Giant Mountains (Czech: Krkonoše, Polish: Karkonosze), Czech-Polish borderland - an area similar to Orava Beskyds in terms of latitude, altitude and vegetation composition. Approximate height of the trees was at first estimated by visual comparison with an object of known height (in this case, a research companion) in the first round of field research, later measured by tree height measuring equipment in the second round. Minimum height used by Körner (2012), namely 3 m, was not applicable in this case because *Pinus mugo* is often up to 2 m tall in the area, and therefore would remove one of the premises for 'full-stature', i.e. that “*a tree* (in this case, a *Picea abies* individual growing in a *Pinus mugo* 'krummholz' thicket) w*ould have its crown closely coupled to prevailing atmospheric conditions*” (Körner 2012, p. 18) – something hardly applicable to a 3 m tall tree growing in 2 m tall 'krummholz' thicket.

3) 'outpost-treeline' *sensu* Körner (2012) or, with other words, 'single-tree line' - **L3** - as a relative altitudinal band of the highest occurrence of 'full-stature' (see previous paragraph) trees, mostly scattered in the continuous *Pinus mugo* 'krummholz' vegetation. This particular band was omitted in the case of Pilsko massif because of several reasons: peculiar composition of the ecotone – a gentle slope in the Slovak part causes the ecotone to vastly stretch both spatially and lengthwise with 'outpost-treeline' virtually unidentifiable; difficult weather conditions with permanent fog and difficult orientation in the upper part of the ecotone combined with impenetrable *Pinus mugo* thickets; and, maybe most importantly, due to lack of available dataloggers.

3.2.2 Environmental sampling

Data sampling included several environmental measurements and simple vegetation analysis. Following variables were measured: altitude, slope aspect, slope grade, light index. Simple vegetation analysis was composed of the analysis itself, measurement of tree circumference at breast height (approximately 1,5 m) and tree height measurement. Measured circumference was later used to calculate tree diameter. All analysed trees were also classified either as unicormic, or as polycormic, depending on number of stems the measured tree had.

Altitude was measured by the in-built altimeter function of the GPS-device used for orientation and marking of datalogger positions. Altimeter was several times re-calibrated to obtain as precise measurements as possible. GPS-device used was Garmin™ GPSMAP® 62s (Garmin International Inc., Olathe, Kansas, USA). Slope aspect was identified by map study, GPS-device and lensatic compass.

Slope grade was measured approximately by a simple method combining protractor, roll-up tape measure and bull's eye spirit level of the compass for the horizontal plane. After the field work, GIS slope grade measurement was conducted to control and rectify the *in situ* slope grade measurements. GIS measurements were preferably used in the further analyses, with sole exception of one point (P2) where the GIS measurement was not available. The original field measurement was used in this case, as the field measurements were found to generally correspond sufficiently to the GIS measurements.

Light index was calculated as a ratio of illumination under the tree canopy (measured on the point where the datalogger was buried) and the illumination on adjacent free, unshaded place. For illumination measurement, Hagner EC1 Digital Luxmeter (B.Hagner AB, Solna, Sweden) was used.

Simple vegetation analysis was done on a 4 m^2 (2 x 2 m) plot. Plot was located under the tree canopy (if this place was accessible) and adjacent to the point where the datalogger was buried (with this place being preferably a part of the plot itself if possible) on as homogeneous understorey vegetation as possible. Vascular plant species were identified and their relative coverage (in percent) was estimated for each species as well as total coverage for each stratum of the vegetation: for tree canopy, shrubs and graminoids and herbs (combined into one class). Due to the different strata present were the sums of coverage percentages often higher than 100%. Relative coverage for mosses was also estimated, but the species were not identified. As a result of rather sparse vegetation under the dense tree canopy, relative coverage of bare ground and/or rocks was estimated as well if present. There were 40 vegetation analyses total, one for each study plot, i.e. soil datalogger location (24 from Babia hora and 16 from Pilsko). Data from the vegetation analysis were used for calculation of weighted average Ellenberg indicator values (German: Zeigerwerte) of study plots. Weighted average values of a plot were calculated by averaging of indicator values of plants present in the plot according to relative dominance within the plot expressed by coverage percentage. Variables assessed were: light conditions (L), temperature (T), continentality (K), humidity (F), soil reaction (R) and nitrogen content (N); and were calculated according to Ellenberg and Leuschner (2010).

Tree circumference was measured at the breast height of approximately 1,5 m by a roll-tape measure. It was also noted whether the tree was polycormic or monocormic; in case of polycormic individuals was measured the circumference of the highest and thickest trunk.

During the second round of the field research, tree height measurements were conducted using clinometer. Laser rangefinder was used to measure distance from the tree, which had to be fixed (clinometer used allows for either 15 or 20 m) for proper height measurement with clinometer. In case of too dense branches hindering direct line of sight to the tree trunk, the target pole with fixed length of 1 m was used for partial distance measurements (i.e. from the tree trunk outwards through the branches to a place with unobstructed line of sight). The 15 m scale of the clinometer was used exclusively. In case of impenetrable vegetation surrounding the measured tree and obscuring the view totally, making the 15 m long direct line of sight impossible, a cross-multiplication technique was used. It was based on quasi-measuring an object of known height – in this case again the target pole – with the clinometer, and then adding the tree measurement to the equation. This technique was used especially in *Pinus mugo* thickets for measurements in 'outpost-treeline'. The clinometer used during the field research was Suunto PM-5/1520 P (Suunto Oy, Vantaa, Finland). Laser rangefinder used was Bosch DLE 40 Professional (Robert Bosch GmbH, Stuttgart, Germany).

3.2.3 Dataloggers and temperature measurements

In total, 40 dataloggers were buried in the depth between 5-10 cm (depending on the substrate depth, presence of roots, rocks etc.; depth of 10 cm was used where possible) in the root zone of the inspected trees. Depth chosen was based on the research of Körner and Paulsen (2004) and measured by a roll-up tape measure. Dataloggers used for soil temperature measurements were LogTag® TRIX-8 (LogTag Recorders Ltd., Auckland, New Zealand) and were set up to monitor temperatures twice a day at 00:00 and 12:00. Rated temperature reading accuracy stated by manufacturer is ± 0,5 °C in the temperature interval -20 - +40 °C. Dataloggers were packed in a protective coating of plastic bag and adhesive tape to protect the dataloggers from soil moisture. A cord fixed on an iron nail buried with the datalogger was used to mark its position together with several photos and GPS coordinates. There were 24 dataloggers buried on Babia hora (8 aspects x 3 relative altitudinal bands) and 16 on Pilsko (8 aspects x 2 relative altitudinal bands).

Additional 10 dataloggers were hung on the branches of the inspected trees in the 'timberline' relative altitudinal band in a height of approximately 2 m above ground. Dataloggers used for atmospheric measurements were LogTag® HAXO-8 (LogTag Recorders Ltd., Auckland, New Zealand) and were set up to monitor atmospheric temperatures and humidity in the same way as soil loggers, i.e. twice a day at 00:00 and 12:00. Average accuracy stated by manufacturer is ± 0,5 °C for temperature measurements and ± 3 % for humidity. Dataloggers were hung through a protective plastic cylinder to prevent damage from adverse atmospheric conditions; the diameter of the cylinder of 110 mm allowed the dataloggers with diameter of 54,5 mm to hang freely and monitor the temperatures and humidity without significant bias, yet it sat tightly enough to protect from wind, mechanical damage from branches etc.. Protective cylinders were also painted in dark green to help reduce unwanted attention from tourists. There were 8 dataloggers placed on Babia hora (one for each aspect) and 2 dataloggers placed on Pilsko (one for north-western aspect as the least favourable due to the prevailing winds and one for south-eastern aspect as the opposite slope of the massif - see 'Research area' chapter, paragraph on climate).

3.3 Data analysis

3.3.1 Environmental and vegetational data

Sampled data were analysed in several ways. In order to avoid well-known problems with using untransformed aspect data in form of degrees, two approaches were used: firstly, a division of aspects was conducted similarly to Odland et al. (1990) and Aarrestad (2002) and they were assigned a rank from 1 to 8 according to their generally known favourability (with NE ranking as least and SW as most favourable aspect). Secondly, a trigonometric transformation of aspect according to Zar (1999) was conducted, effectively splitting the aspect into two quasi-variables: “northness” (cosine of the aspect) and “eastness” (sine of the aspect). This approach is purely mathematical and is completely assumption- (and therefore also bias-) free. Both the relative aspect favourability index and aspect expressed as “northness” and “eastness” were used instead of aspect value in degrees. Plot altitudinal data were analysed for correlation with topographic variables (i.e. altitude, slope and aspect).

Chi-squared test of association was used to assess the association of unicormic/ polycormic trees to different relative altitudinal bands.

Tree diameter was calculated from tree circumference, and was subsequently used in calculating height to diameter ratio. Height and diameter data were in the same units (i.e. metres) in the ratio. Tree height to diameter (H/D) ratio was analysed both in relation with altitude, aspect and slope, and with relative altitudinal band. Relation with topographic variables was assessed using regression. Kruskal-Wallis non-parametric analysis of variance was used to assess differences in H/D ratio in different relative altitudinal bands due to asymmetric dataset, i.e. unequal number of trees.

Species compositional data were used for calculation of weighted average Ellenberg indicator values for all study plots. These indicator values were used to detect any obvious trends or changes within the ecotone using a correlation matrix with topographical variables and light index. Due to the data structure (i.e. often unequal number of observations etc.) and several variables not being normally distributed, Spearman's rank correlation was used. Principal component analysis (PCA) was also conducted to explore the Ellenberg indicator values in different plots with topographical variables added as supplementary (i.e. passive, not used in calculation of PCA axes).

3.3.2 Temperature data

The measurements obtained from dataloggers were first trimmed to contain only the measurements after placement and before extraction of dataloggers because the dataloggers were set up to log temperatures from a certain date and time and were neither started nor stopped manually in the field. The raw data records contained therefore many measurements which had to be discarded (e.g. from during the transfer to different locations etc.).

First step of the analysis was selection of a full year (i.e. 365 days) of temperature measurements. Start of this period was chosen as the first reliable measurement in order to maximize usefulness of data records and varied somewhat between different study plots. This didn't, however, alter the results in any way since it was always whole period which was considered, but only portions of it were used (e.g. calculated growing seasons), and subsequent analyses used always either periods of time common for all study plots (in case of growing seasons) or with equal number of data entries (in case of full year periods).

Full year period was used as a base for all subsequent analyses. Daily means were used in certain analyses, in others were the measurements used directly. To obtain a comparable description of thermal conditions in the different parts of the treeline ecotone, growing season (GS) period was selected for all plots. Odland (2011) describes several different methods of calculating the GS and evaluates their reliability.

For the purpose of this thesis, two methods of GS calculation were chosen: first, according to Körner and Paulsen (2004), which uses threshold value of 3,2 °C for daily means of 7 consecutive days calculated as the running average – over the threshold in the spring (start of the GS) and under the threshold in the autumn (end of GS). Rationale behind use of this method is to obtain data comparable with Körner's and others studies using his method (e.g. Gehrig-Fasel et al. 2008). This threshold was used for soil temperature measurements only. Since there was no explicit threshold mentioned for air temperatures, threshold of 0 °C was chosen for aerial measurements. Rationale behind this choice is a reference by Körner and Paulsen (2004) stating that 3,2 °C weekly mean of the soil temperatures "*corresponds to*" (p. 716) 0 °C mean in the air/tree canopy temperatures.

Second method, based on Odland (2011), uses threshold value of 5 °C for daily means of 5 consecutive days calculated by visual inspection of daily mean temperatures. Rationale behind this method is that the threshold of 3,2 °C may be reached by chance as a result of, for example, early snowmelt in some plots, but may be soon followed by a new snow deposition and prolonged drop in ambient temperatures, therefore making the GS unjustifiably long. Of course, the biological activity of a tree is a continuous process ongoing at different intensity levels rather than a process with a sharp and precisely defined start and end, and therefore, any but a strictly physiological description of start and end of growing season is in itself arbitrary. Temperatures around 5 °C were generally observed to be the threshold value for biological activity of both above-ground and underground plant tissues (Holtmeier 2003; Körner 2012). Therefore, the GS start/ end threshold of 5 °C in 5 consecutive days ensures that only the period with significant biological activity will be accounted for in terms of GS. This method was used both for soil and air temperature data.

Strict adherence to the selection rules of start and end point under preliminary calculations led in some case to unjustifiable differences in GS length within the same relative altitudinal band and at similar altitudes (in some cases more than several weeks, and in the most extreme cases more than two months). This was caused, among other things, also by the phenomenon described above – an early warm spell caused that the threshold values were exceeded in some plots, but not in others. A subsequent cold period caused the temperatures to drop under the threshold again. When this occurred, a date of second threshold exceeding was chosen in some plots in order to obtain comparably long GS in as many plots as possible within one relative altitudinal band. Besides, the difference of several days in GS length between the study plots didn't alter the results since the non-parametric tests were used.

The GS and also the annual temperatures were subsequently used for calculation of several derived values (or temperature indices), such as mean temperature, day-degrees etc. (see Results). Day-degree sums were calculated in two ways: either as adjusted, i.e. summing only the fraction of daily mean temperature above the given threshold – in our case 5 °C (cf. Körner and Paulsen 2004, Gehrig-Fasel et al. 2008); or as unadjusted, i.e. summing the daily mean temperatures exceeding the threshold in form of positive difference from 0 °C (cf. Odland 2011). Rationale behind this decision is to obtain comparable data with articles using both methods. Visual inspection of the mean daily temperatures was used for selection of final snowmelt date – this was the date when the mean soil temperatures began rapid increase without subsequent sinking under 1 °C again, indicating snow-free terrain. Daily means from weather stations of Slovak Hydrometeorological Institute (SHMI) were compared with daily means from nearest *in situ* aerial datalogger measurements to calculate temperature lapse rate per 100 m.

Temperature data and their derivatives (temperature indices) were used in multiple regressions with several explanatory variables such as altitude, slope grade and aspect. Entire data series from calculated GS's were compared using Kruskal-Wallis analyses of variance. Aerial data series from full year periods were also analysed in this way for comparative purposes. Temperature indices were analysed using PCA with supplementary topographical variables.

Data were generally not transformed in analyses apart from aforementioned aspect transformation and data centring and standardising as a preliminary step of PCA (automated procedure).

The standard significance (α) level used in the statistical tests in this thesis is 0,05 unless explicitly stated otherwise.

For data preparation and analyses, Apache OpenOffice 4.1.1 Calc (Apache Software Foundation), Minitab 16 and 17 - trial version - (Minitab Inc.) and CANOCO 5 (Biometris; Plant Research International, The Netherlands and Petr Šmilauer, Czech republic) were used.

4 Results

'Results' chapter is divided into two main parts: ecotone structure and environmental conditions.

In the part about the ecotone structure, general characteristics of the ecotone and the trees will be assessed in order to illustrate the changes associated with increasing altitude, changing aspect and slope grade etc. and differences between relative altitudinal bands.

In the part about ecological conditions, Ellenberg indicator values, air and soil temperatures will be assessed in the same fashion.

Unpublished data from weather/ climatological stations 11869 Rabča and 11890 Oravské Veselé were obtained by courtesy of Slovak Hydrometeorological Institute (SHMI).

As a remark about the specific statistical programmes used: all data preparations and air temperature lapse rate calculations were done in Apache OpenOffice 4.1.1 Calc; all descriptive statistics, regressions (simple linear, multiple and stepwise), analyses of variance and quasi-post-hoc Mann-Whitney U tests were done in Minitab 16 and 17 – trial version; all Spearman's rank correlations were done in Minitab 17 – trial version; and both principal component analyses were done in CANOCO 5.

4.1 Ecotone structure

4.1.1 General description of ecotone structure

The treeline ecotone in the Orava Beskyds can be characterised by a rather great vertical and horizontal width which varies with different aspects. Plot altitude (as a surrogate for relative altitudinal band's altitudinal position) was found to be significantly positively correlated with numeric expression of aspect favourability (r_s = 0,511; n = 40; P = 0,001) and significantly negatively correlated with aspect “northness” (r_s = -0,514; n = 40; P = 0,001) and slope grade (r_s = -0,370; n = 40; P = 0,019). Aspect “eastness” was not found to be significantly correlated with plot altitude (r_s = -0,130; n = 40; P = 0,424). Since the different relative altitudinal bands were chosen arbitrarily, the altitudinal differences between them cannot be used as an absolute measure of ecotone's width; they can, however, illustrate it quite well (see Tab. 1). There was no significant correlation between plot altitudinal difference and topographic variables at Babia hora (all P > 0,05). At Pilsko, aspect “eastness” was found to be significantly positively correlated (r_s = 0,886; n

= 8; P = 0,003) and mean slope grade to be significantly negatively correlated (r_s = -0,857; n = 8; P = 0,007) with plot altitudinal difference. All correlations are Spearman's rank correlations.

Table 1. Baseline altitude of 'timberline' plots (L1) in metres asl. in different aspects and altitudinal difference between study plots at L1 and at 'outpost-treeline' (L3) at Babia hora massif (BH) and L1 and at 'tree group/biogroup line' (L2) at Pilsko massif (PI) in metres.

BH	L1	L1-L3	PI'	L1	L1-L2 (PI)
S	1453	131	**S**	1430	76
SW	1394	137	**SW**	1436	71
W	1437	102	**W**	1403	56
NW	1419	51	**NW**	1378	64
NE'	1367	100	**NE'**	1355	90
N	1356	86	**NW(N)**	1392	46
E	1398	58	**E**	1366	87
SE	1411	74	**SE**	1409	103

Trees in the ecotone became increasingly smaller in size and the tree density diminished greatly with altitude, while *Pinus mugo* 'krummholz' becomes gradually dominant vegetation type.

Average tree height (± standard deviation) at the 'timberline' (L1) plots was 14,07 ± 2,56 m; n = 15. Measurement was not done in one plot due to tree breakage.

At the 'tree group/biogroup line' (L2) plots, the mean height was 7,82 ± 2,48 m; n = 16.

Average tree height at 'outpost-treeline' (L3) plots was 6,42 ± 1,16 m; n = 8.

There was a significant negative correlation between breast height diameter and altitude (r_s = -0,501; n = 40; P = 0,001). Amount of polycormic trees was during the course of the fieldwork observed to generally increase with altitude. However, chi-squared test of association has not found significant association between ratio of unicormic/polycormic trees and relative altitudinal band (X^2 = 3,19; df = 2; P = 0,2).

4.1.2 Tree height to diameter ratio

Tree height to diameter (H/D) ratio decreased slightly with increasing altitude. Mean H/D ratio at L1 was 36,96 ± 6,29, at L2 was 32,39 ± 7,42 and at L3 was 30,51 ± 10,04. There was a significant negative correlation between H/D ratio and altitude (r_s = -0,329; n = 39; P = 0,041). Using a linear regression, decrease of H/D ratio with altitude was, however, not found to be significant at significance (α) level of 0,05 (H/D = 97,9 – 0,0445 alt.; $F_{1,37}$ = 3,70; P = 0,062) and the regression model explained a very low percentage of variation in H/D ratio (R^2 (adj.) = 6,6 %). Addition of aspect and slope as predictors to the model neither yielded a significant result nor increased the explanatory power of the model (see Tab. 2).

Table 2. Results of multiple regression of H/D ratio on altitude, aspect and slope. Two ways of aspect expression considered: 1. Asp.num. - numeric expression of aspect favourability; 2. Asp.NN.EE. - aspect expressed as unitless "northness" and "eastness".

Asp.num.	H/D = 110 – 0,0534 alt. + 0,310 asp.(num.) - 0,036 slope	$F_{3,35}$ = 1,26	P = 0,304	R^2 (adj.) = 2,0%
Asp.NN.EE.	H/D = 111 – 0,0530 alt. + 0,05 asp.NN - 1,71 asp.EE - 0,073 slope	$F_{4,34}$ = 1,12	P = 0,365	R^2 (adj.) = 1,2%

Similarly to regression results, the differences in H/D ratio between different relative altitudinal bands (L1, L2 and L3) were not found to be statistically significant (H = 4,5; df = 2; P = 0,105). Since the post-hoc tests were not available for Kruskal-Wallis non-parametric analysis of variance in the statistical program used, multiple Mann-Whitney U were conducted as quasi-post-hoc tests. Bonferroni or Šidák correction was not applied due to low number of levels assessed resulting in only three separate tests and the results of corrections would be too conservative with so few separate tests. Besides, none of the three tests had a significant result even at original α (see Tab. 3).

Table 3. Results of Mann-Whitney U tests of H/D ratio in different relative altitudinal bands (levels). In the first row: number of trees in level; in the first column: level median.

	L1 (n=15)	L2 (n=16)	L3 (n=8)
L1 (med.=36,960)		P = 0,0604	P = 0,1138
L2 (med.=33,614)	P = 0,0604		P = 0,7363
L3 (med.=30,29)	P = 0,1138	P = 0,7363	

4.2 Ecological conditions

4.2.1 Ellenberg indicator values and light index

Correlation matrix of plot average Ellenberg indicator values, light index and topographic variables has shown significant correlations between certain variables. Apart from several significant correlations between the Ellenberg indicators themselves, two indicators were significantly positively correlated with altitude: light indicator (r_s = 0,449; n = 40; P = 0,004) and humidity indicator (r_s = 0,649; n = 30; P < 0,001). Temperature indicator has shown significant positive correlation with numerical expression of aspect's favourability (r_s = 0,346; n = 40 ; P = 0,029) and significant negative correlation with slope grade (r_s = -0,325; n = 40; P = 0,041). Light index was significantly negatively correlated with altitude (r_s = -0,428; n = 40; P = 0,006); the correlation between light index and Ellenberg light indicator was not significant at significance level of 0,05 (r_s = -0,286; n = 40; P = 0,073). Complete correlation matrix in Tab. 4 on page 29.

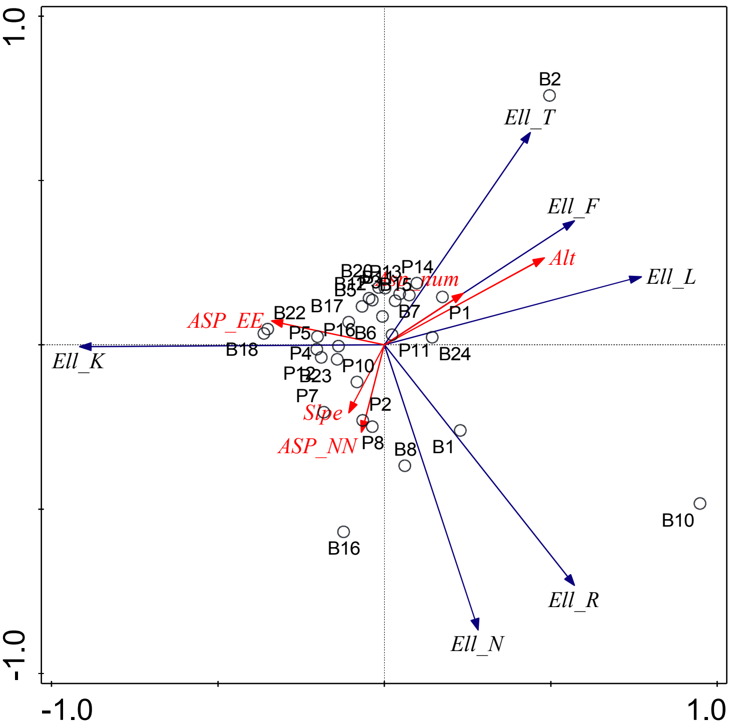

Figure 3. Study plot-variable biplot of Axis 1 and 2 of PCA of Ellenberg indicators and topographic variables. Ellenberg indicators are: L – light, T – temperature, K – continentality, F – humidity, R – reaction, N – nitrogen. Topographic variables are: Alt – altitude, Asp_num - aspect (numeric expression of favourability), ASP_NN - "northness", ASP_EE - "eastness", Slpe - slope grade. Supplementary variables are in red.

Principal component analysis of Ellenberg indicators with supplementary topographic variables was performed on 30 out of 40 plots due to missing values in some variables. There were 11 variables total, including 5 supplementary. PCA was centred and standardized on variables.

Total variation was 180. First four axes (or components) had eigenvalues 0,39; 0,32; 0,13 and 0,09. Cumulative explained variation of the first four axes was 93,5. For study plot-variable biplot of first two axes see Fig. 3.

Table 4. Correlation matrix of Ellenberg indicator values, light index and topographic variables. Correlation coefficients are Spearman's rho. Ellenberg indicators are: L – light, T – temperature, K – continentality, F – humidity, R – reaction, N – nitrogen. Topographic variables are: altitude, aspect (numeric expression of favourability), aspect ("northness" and "eastness") and slope grade.

	Ell_L	Ell_T	Ell_K	Ell_F	Ell_R	Ell_N	Alt	Asp_n	Asp_NN	Asp_EE	Slope
Ell_T	0,393										
P	0,012										
Ell_K	-0,546	-0,568									
P	0,000	0,000									
Ell_F	0,479	0,540	-0,432								
P	0,007	0,002	0,017								
Ell_R	-0,123	0,276	-0,430	-0,289							
P	0,449	0,085	0,006	0,121							
Ell_N	-0,399	-0,190	-0,035	-0,185	0,594						
P	0,011	0,240	0,831	0,328	0,000						
Alt	0,449	0,237	-0,130	0,649	-0,308	-0,286					
P	0,004	0,140	0,425	0,000	0,053	0,074					
Asp_n	0,103	0,346	-0,307	0,287	-0,044	-0,046	0,511				
P	0,526	0,029	0,054	0,125	0,788	0,779	0,001				
Asp_NN	-0,138	-0,290	0,253	-0,226	0,110	0,070	-0,514	-0,901			
P	0,397	0,070	0,115	0,229	0,499	0,667	0,001	0,000			
Asp_EE	0,001	-0,281	0,263	-0,137	-0,254	-0,064	-0,130	-0,376	-0,025		
P	0,994	0,079	0,102	0,472	0,114	0,696	0,424	0,017	0,879		
Slope	-0,134	-0,325	0,128	-0,285	0,063	0,164	-0,370	-0,181	0,262	-0,123	
P	0,409	0,041	0,433	0,126	0,701	0,311	0,019	0,264	0,103	0,451	
Light_sh	-0,286	-0,194	-0,033	-0,299	0,132	0,261	-0,428	-0,015	0,045	0,012	0,226
P	0,073	0,230	0,839	0,108	0,418	0,104	0,006	0,926	0,783	0,941	0,161

4.2.2 Air temperatures

Growing season and annual average temperatures:

For growing season calculated with start/end threshold of weekly means (i.e. 7 days running average) over/under 0 °C - **GS2**: overall mean temperature from growing season (GS) means from all aerial dataloggers was 7,71 ± 0,25 °C; n = 10. Mean GS length was 207,1 ± 4,8 days.

For growing season calculated with start/end threshold of daily means over/under 5 °C for five consecutive days - **GS_5CD**: overall mean temperature for growing season (GS) means from all aerial dataloggers was 9,63 ± 0,29 °C; n = 10. Mean GS length was 150,0 ± 0,5 days.

All aerial dataloggers were located at 'timberline' – in the lowest relative altitudinal band (L1).

There was a significant decrease of GS mean temperature with altitude in both GS with 0 °C threshold (GS2 mean = 17,6 - 0,00707 alt.; $F_{1,8}$ = 21,95; P = 0,002) and 5 °C threshold (GS_5CD mean = 19,8 - 0,00724 alt.; $F_{1,8}$ = 11,15; P = 0,010). Regression model explained high percentage of GS mean temperature variation: R^2 (adj.) = 69,9 % in GS2; and R^2 (adj.) = 53 % in GS_5CD.

Addition of aspect (in both forms mentioned in previous paragraphs) and slope to regression model didn't yield increased significance or higher percentage of explained variation (see Tab. 5).

Table 5. Multiple regression of GS mean air temperatures on altitude, aspect and slope. Rows 1 and 2: GS2. Rows 3 and 4: GS_5CD. Different expressions of aspect described in Table 2 (page 27).

Asp.num.	GS2 = 17,8 - 0,00731 alt. + 0,0084 asp.num + 0,0071 slope	$F_{3,6}$ = 6,13	P = 0,029	R^2 (adj.) = 63,1%
Asp.NN.EE.	GS2 = 16,7 - 0,00652 alt. + 0,035 asp.NN - 0,0529 asp.EE + 0,0102 slope	$F_{4,5}$ = 4,69	P = 0,061	R^2 (adj.) = 61,9%
Asp.num.	GS_5CD = 18,0 - 0,00607 alt. - 0,0182 asp.num + 0,0115 slope	$F_{3,6}$ = 3,48	P = 0,090	R^2 (adj.) = 45,3%
Asp.NN.EE.	GS_5CD = 17,4 - 0,00571 alt. + 0,073 asp.NN + 0,006 asp.EE + 0,0135 slope	$F_{4,5}$ = 2,26	P = 0,198	R^2 (adj.) = 35,9%

There was no significant difference between air temperatures in different aspects and altitudes neither in an annual perspective (H = 16,88; df = 9; P = 0,051), nor in GS2 (H = 9,44; df = 9; P = 0,397), nor in GS_5CD (H = 12,41; df = 9; P = 0,191).

***In situ* air temperature measurements and data from weather stations:**

Daily means from two weather/climatological stations of Slovak Hydrometeorological Institute (SHMI) in the adjacent villages (Rabča and Oravské Veselé) were compared with daily means from aerial datalogger measurements located closest in terms of direct distance. Direct distance between weather station 11869 Rabča and aerial datalogger AB1 on Babia hora was approximately 10,28 km and altitudinal difference was 808 m. Direct distance between weather station 11890 Oravské Veselé and aerial datalogger AP2 on Pilsko was approximately 7,16 km and altitudinal difference was 649 m.

Air temperature lapse rate (mean ± SD) in the period of one year (i.e. 365 days) per 100 m of altitude was 0,40 ± 0,36 °C/ 100 m for Rabča-Babia hora (R-BH) gradient and 0,49 ± 0,33 °C/ 100 m for Oravské Veselé-Pilsko (OV-P) gradient. Mean daily temperature difference between weather station and datalogger in the same period was 3,24 ± 2,87 °C in R-BH gradient and 3,21 ± 2,13 °C in OV-P gradient.

Air temperature lapse rate in July 2014 was 0,49 ± 0,24 °C/ 100 m in R-BH gradient and 0,53 ± 0,22 °C/ 100 m in OV-P gradient. Mean daily temperature difference between weather station and datalogger in the same period was 3,91 ± 1,88 °C in R-BH gradient and 3,48 ± 1,45 °C in OV-P gradient.

4.2.3 Soil temperatures

Growing season temperatures:

For growing season calculated with start/end threshold of weekly means (i.e. 7 days running average) over/ under 3,2 °C - **GS_K**: overall mean temperature from growing season (GS) means from dataloggers at 'timberline' (L1) was 7,91 ± 0,16 °C; n = 11. Mean GS length was 160,3 ± 1,6 days.

For growing season calculated with start/end threshold of daily means over/ under 5 °C for five consecutive days - **GS_5CD**: overall mean temperature for growing season (GS) means from dataloggers at L1 was 8,76 ± 0,19 °C; n = 11. Mean GS length was 130,4 ± 0,7 days.

Out of total 16 loggers at L1, datalogger P16 was stolen, measurements from P4 and P5 were not used in calculation of GS mean because of premature extraction (i.e. loggers were found lying on the surface). P11 had sensor malfunction and measurements from B13 were not used in calculation of GS mean temperature due to an exceptionally strong outlier position of its measurements, indicating either a non-climatic treeline character in the northern slope of Babia hora, partial sensor malfunction or incorrect placement of study plot (non-climatic treeline character being the most plausible explanation).

For means of 'tree group/ biogroup line' (L2) and 'outpost-treeline' (L3) see Tab. 6. At L2, datalogger P1 was stolen and measurements from P3 were not used in GS mean calculation due to premature extraction. No negative occurrence regarding dataloggers has happened at L3.

Table 6. Growing season temperature and length means ± SD in relative altitudinal bands L2 and L3. GS_K – mean of GS_K temperature, GS_5CD – mean of GS_5CD temperature, GSL – mean growing season length, n – number of dataloggers.

	GS_K	GSL GS_K	GS_5CD	GSL GS_5CD	n
L2	7,81 ± 0,61	154,9 ± 7,7	8,66 ± 0,55	126,5 ± 11,8	14
L3	7,52 ± 0,56	151,4 ± 11,3	8,29 ± 0,56	124,1 ± 4,5	8

There was a significant decrease of GS mean temperature with increasing altitude both in GS_K (GS_K mean = 16,7 - 0,00614 alt.; $F_{1,32} = 19,77$; $P < 0,001$) and GS_5CD (GS_5CD mean = 18,1 - 0,00653 alt.; $F_{1,32} = 22,56$; $P < 0,001$). Percentage of explained variation of mean temperatures by altitude (R^2 (adj.)) was 36,3 % in GS_K and 39,5 % in GS_5CD. Addition of other topographic variables has increased the percentage of explained variation, the significance remained virtually unaltered (see Tab. 7). Especially addition of slope has increased the adjusted R^2.

Table 7. Multiple regression of GS mean soil temperatures on altitude, aspect and slope. Rows 1 and 2: GS_K. Rows 3 and 4: GS_5CD. Different expressions of aspect described in Table 2 (page 27).

Asp.num.	GS_K = 13,0 - 0,00401 alt. + 0,0066 asp.num + 0,0325 slope	$F_{3,30}$ = 10,25	P < 0,001	R^2 (adj.) = 45,7%
Asp.NN.EE.	GS_K = 13,8 - 0,00460 alt. - 0,142 asp.NN + 0,100 asp.EE + 0,0350 slope	$F_{4,29}$ = 9,05	P < 0,001	R^2 (adj.) = 49,4%
Asp.num.	GS_5CD = 16,2 - 0,00549 alt. + 0,0087 asp.num + 0,0176 slope	$F_{3,30}$ = 8,13	P < 0,001	R^2 (adj.) = 39,3%
Asp.NN.EE.	GS_5CD = 16,8 - 0,00586 alt. - 0,106 asp.NN + 0,072 asp.EE + 0,0193 slope	$F_{4,29}$ = 6,50	P = 0,001	R^2 (adj.) = 40,0%

After exclusion of B13 as an outlier from analysis of variance (for rationale behind this decision see explanation on page 31) there was no significant difference between soil temperatures at L1 neither when considering GS_K (H = 9,53; df = 10; P = 0,483) nor GS_5CD (H = 13,09; df = 10; P = 0,219).

There were significant differences between soil temperatures in different aspects at L2 and L3, both when GS_K and GS_5CD was considered (see Tab. 8). Exclusion of northern aspect didn't yield a non-significant result, therefore remained the data from dataloggers from northern aspect part of the analysis.

Table 8. Results of Kruskal-Wallis non-parametric analysis of variance of soil temperatures in different aspects in relative altitudinal bands L2 and L3. H-values adjusted for ties.

	GS_K			GS_5CD		
	H	df.	P	H	df.	P
L2	136,63	13	< 0,001	124,38	13	< 0,001
L3	68,80	7	< 0,001	80,51	7	< 0,001

Comparing mean GS temperatures of relative altitudinal bands as a whole, no significant difference was found between overall mean soil temperatures in different relative altitudinal bands neither for GS_K (H = 4,69; df = 2; P = 0,096) nor for GS_5CD (H = 4,25; df = 2; P = 0,119). Exclusion of B13 didn't alter the significance of the result, therefore it remained a part of the analysis.

Day-degrees:

Day-degree sums were calculated as a sum of all daily mean temperatures within a selected period over the given threshold.

For GS_K, overall mean sum of day-degrees over 5 °C from measurements at L1 was 511,4 ± 23,7 °C; n = 11.

For GS_5CD, overall mean sum of day-degrees over 5 °C from measurements at L1 was 501,4 ± 21,1 °C; n = 11. Unadjusted day-degree sum (i.e. sum of temperatures over 5 °C expressed as positive difference from 0 °C, not from 5 °C) at L1 was 1104,1 ± 27,8 °C; n = 11.

Outlier measurements from datalogger B13 were excluded from calculation of day-degree means. For means of L2 and L3 see Tab. 9.

Table 9. Growing season day-degree (over 5 °C) sum means ± SD in relative altitudinal bands L2 and L3. GS_K – means of GS_K, GS_5CD – means of GS_5CD, U – unadjusted day-degree sums (see Methods for explanation); n – number of dataloggers.

	GS_K	GS_5CD	GS_5CD (U)	n
L2	487,0 ± 90,0	477,5 ± 90,2	1057,1 ± 128,7	14
L3	430,5 ± 75,5	421,7 ± 71,6	984,2 ± 84,2	8

There was a significant decrease of day-degree sum with increasing altitude both in GS_K (DD>5 GS_K = 1913 - 0,986 alt.; $F_{1,31} = 24,70$; P < 0,001) and GS_5CD (DD>5 GS_5CD = 1888 - 0,975 alt.; $F_{1,31} = 25,07$; P < 0,001). Percentage of explained variation of day-degree sums (R^2 (adj.)) was 42,55 % in GS_K and 42,93 % in GS_5CD. Addition of other topographic variables has increased the percentage of explained variation, the significance remained unaltered (see Tab. 10). Especially addition of aspect "northness" and slope has increased the adjusted R^2, while the addition of numerical expression of aspect favourability and aspect "eastness" has had rather low impact.

Table 10. Multiple regression of day-degree sum means on altitude, aspect and slope. Rows 1 and 2: GS_K. Rows 3 and 4: GS_5CD. Different expressions of aspect described in Table 2 (page 27).

Asp.num.	DD>5 GS_K = 1669 - 0,857 alt. + 2,25 asp.num + 2,55 slope	$F_{3,29} = 9,02$	P < 0,001	R^2 (adj.) = 42,9%
Asp.NN.EE.	DD>5 GS_K = 1817 - 0,958 alt. - 29,1 asp.NN + 16,7 asp.EE + 3,00 slope	$F_{4,28} = 9,11$	P < 0,001	R^2 (adj.) = 50,3%
Asp.num.	DD>5 GS_5CD = 1634 - 0,841 alt. + 2,22 asp.num + 2,63 slope	$F_{3,29} = 9,28$	P < 0,001	R^2 (adj.) = 43,7%
Asp.NN.EE.	DD>5 GS_5CD = 1784 - 0,942 alt. - 29,0 asp.NN + 16,4 asp.EE + 3,07 slope	$F_{4,28} = 9,41$	P < 0,001	R^2 (adj.) = 51,3%

Since the day-degrees are fundamentally a derived variable and no daily measurements were available, no intra-band analysis of variance could be conducted in different relative altitudinal bands. In a inter-band analysis, the difference between day-degree sums in different relative altitudinal bands was found to be non-significant both in GS_K (H = 5,33; df = 2; P = 0,070) and in GS_5CD (H = 5,77; df = 2; P = 0,056). As the non-significance was rather marginal, multiple Mann-Whitney U tests were conducted as quasi-post-hoc tests; this time, Šidák's correction was used to adjust α level because the total number of independent tests exceeded 5 (three for each GS). Using the adjusted α level of 0,0169 (adjusted for three independent tests), significant difference was found between L1 and L3 when GS_5CD was considered (P = 0,0149). When considering GS_K, result was marginally non-significant at the adjusted α level (P = 0,0186). For all pairwise comparisons within a given GS considered see Tab. 11.

Table 11. Results of Mann-Whitney U tests of day-degree sums in different relative altitudinal bands (levels). In the first row: number of plots in level; in the first column: level median. Two time periods considered: GS_K and GS_5CD.

	L1 GS_K(n=11)	L1 GS_5CD(n=11)	L2 GS_K(n=14)	L2 GS_5CD(n=14)	L3 GS_K(n=8)	L3 GS_5CD(n=8)
L1 GS_K(med.=516,1)			P = 0,3961		P = 0,0186	
L1 GS_5CD(med.=504,6)				P = 0,2857		P = 0,0149
L2 GS_K(med.=479,3)	P = 0,3961				P = 0,1618	
L2 GS_5CD(med.=468,9)		P = 0,2857				P = 0,1832
L3 GS_K(med.=418,6)	P = 0,0186		P = 0,1618			
L3 GS_5CD(med.=411,1)		P = 0,0149		P = 0,1832		

Temperature indices:

Following indices has been derived from the soil temperature data: growing season (GS) length and mean temperature, day-degree sum over 5 °C in the GS, mean annual temperature, number of days with mean temperature over 5° and under 0° in a year, day of snowmelt (in form of day-of-year), annual frost sum (i.e. sum of temperatures under 0 °C), mean and maximum July temperature.

Principal component analysis (PCA) of temperature indices with supplementary topographic variables was performed on 37 plots including four supplementary plots. Four plots were made supplementary either because of previously mentioned premature extraction (three cases) or because of strong outlier position (one case). For three plots, no temperature data were available either because of datalogger theft (two cases) or because of sensor malfunction (one case).

There were total 18 variables including 5 supplementary. PCA was centred and standardized on variables.

Total variation was 429. First four axes (or components) had eigenvalues 0,60; 0,20; 0,10 and 0,04. Cumulative explained variation of the first four axes was 94,8. For study plot-variable biplot of first two axes see Fig. 4.

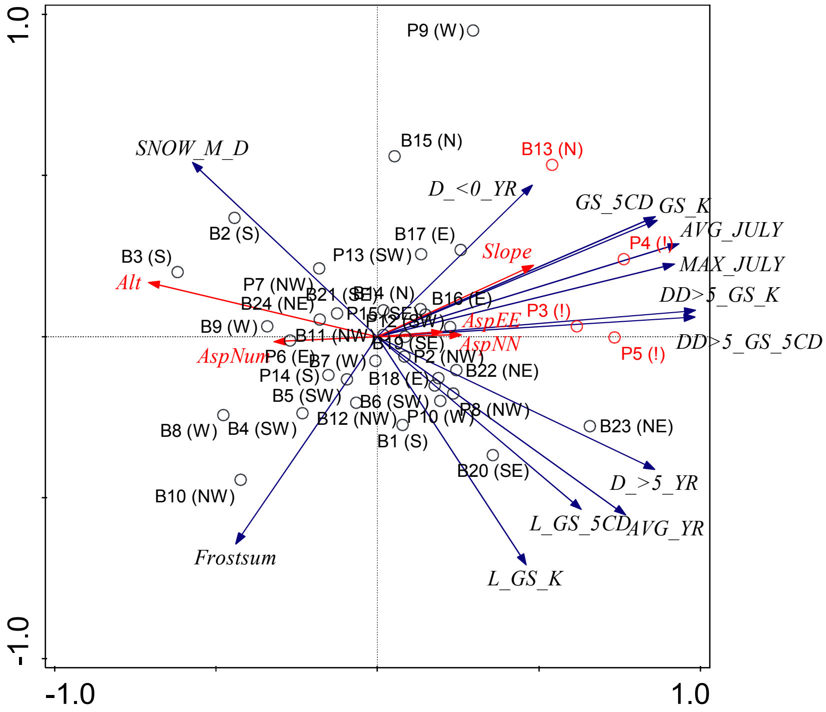

Figure 4. Study plot-variable biplot of Axis 1 and 2 of PCA of temperature indices and topographic variables. Temperature indices are: GS_K and GS_5CD – mean temperature of GS, L_GS_K and L_GS_5CD – length of GS, DD>5_GS_K and DD>5_GS_5CD day-degree sums over 5 °C in GS, D_>5_YR and D_<0_YR – number of days over 5 °C/under 0 °C in a year; Frostsum, SNOW_M_D, AVG_YR, AVG_ and MAX_JULY – self-explanatory (see page 34 for overview of indices). Topographic variables as in Fig. 3. Supplementary variables and plots in red. Plots with exclamation marks – premature extraction.

4.2.4 Relationship between air and soil temperatures

A detailed air-to-soil temperature transfer model will not be a part of this master thesis. A preliminary stepwise regression was, however, conducted in order to assess the importance of air temperature and humidity of present and previous days for soil root zone temperatures. The variables were ranked according to their addition into the regression model by stepwise regression and their importance in it (see Tab.12). Total of 9 plots (air-soil datalogger pairs) were assessed in the stepwise regression. Measurements were used directly (i.e. not daily means). Both GS_K and GS_5CD were considered.

Table 12. Ranked addition order and importance of air temperatures and humidity as predictors in stepwise regression model of soil temperatures. Values are median ranks from 1 (earliest introduction and highest importance in the model) to 6 (latest introduction and lowest importance). D+0: same day measurements; D – 1: previous day measurements; D – 2: measurements from two days ago. T: temperature measurements; H: humidity measurements. GS_5CD and GS_K – periods considered.

GS_5CD	**D+0_T**	**D+0_H**	**D-1_T**	**D-1_H**	**D-2_T**	**D-2_H**
MEDIAN_R	1	2	3	4	5,5	5
GS_K						
MEDIAN_R	2	4	1	2	5	6

5 Discussion

This study has examined the structure and ecological conditions in the alpine treeline ecotone of Orava Beskyds and quantified the biological and ecological variation.

Discussion follows generally the same order as Results. The results have shown several important observations. Most notably - in relation with main hypothesis, the temperature regime in the growing season at the 'timberline' relative altitudinal band (L1) appears to be very stable both regarding the air and soil temperatures, effectively overriding the effects of altitude, aspect and slope which were generally shown to have a significant impact on both air and soil temperatures.

In the upper parts of the ecotone ('tree group/biogroup line' and 'outpost treeline'), the opposite was true – soil temperatures differed significantly with altitude, aspect and slope.

5.1 Ecotone structure

Altitudinal variation and zonation of the ecotone

Altitude of the treeline ecotone's relative altitudinal bands correlated significantly with aspect and slope in such a way, that the ecotone's baseline was located highest at southern facing slopes and slopes with rather gentle grade while the lowest positions were associated with northern facing slopes and slopes with steep grade. This is in accord with earlier findings summarized in e.g. Holtmeier (2003) and observed by, among others, Autio (2006). This significant correlation is in contrast with Körner's assertion about non-significant relationship between treeline altitude and aspect (Körner 2012). It can be, of course, argued that the lower position of treeline ecotone in the northern exposed slopes of Babia hora is at least partially caused by avalanches and/or debris flows and they should be excluded from comparisons with other slopes where the treeline's position is climatically controlled. It would be, however, a rather circular reasoning as these occurrences (i.e. avalanches, increased weathering etc.) themselves are indeed at least partially caused by the climatic peculiarities of northern slopes. Altitudinal differences between uppermost and baseline relative altitudinal bands (or, in other words, the “ecotone width”) varied in different aspects. It was not possible to associate the variation unambiguously with certain aspect(s) or range of slope grade. At Pilsko, greater ecotone width was associated with eastern exposure and lower slope grades, yet no such association could be proven at Babia hora. The ecotone is generally narrower in sharper gradients (Körner 2012), but the steepest slopes were avoided during the fieldwork because of accessibility issues, but also in order to study the highest tree occurrences (see Methods).

Tree characteristics

Tree height diminished with altitude in the ecotone, and the most conspicuous reduction happened between the 'timberline' and 'tree group/ biogroup line' (almost 50 % reduction in the mean tree height). Height decline then continued evenly. This is in accord with findings of Ohsawa (1995, cited in: Camarero and Gutiérrez 2001) for temperate treelines in general.

Tree diameter at breast height diminished as well with increasing altitude, yet its decline was much more gradual than the decline of tree height. This leads to changes in tree height-diameter ratio, which will be discussed later.

The ratio of polycormic (i.e. multi-stemmed) vs. unicormic (single-stemmed) trees didn't change significantly with altitude, even though there were hints of increasing percentage of polycormic trees. Too little sample size might have been an issue in this case, as only the trees associated with dataloggers and vegetation analyses were assessed. There are many possible drivers for polycormic growth generally – chemical, climatic and disturbance-based (Bellingham and Sparrow 2009). However, *Picea abies* has a very pronounced apical dominance (Przybylski 2007) and therefore it becomes polycormic practically solely by disturbance. Verwijst (1988) has in his studies of mountain birch (*Betula pubescens* ssp. *tortuosa*) found that the soil pH in B and C horizons described best the degree of polycormism, followed by snow depth. Bellingham and Sparrow (2009) have found that percentage of polycormic trees increased with increasing altitude in temperate montane forests of New Zealand, making the temperature more important for polycormic growth than other factors (e.g. soil nutrients) in the temperate forests. Tree species assessed in both these studies were broad-leaved/ deciduous. In a study of a conifer with apical dominance fairly similar to *Picea abies*, white pine (*Pinus strobilus*), Chamberlin and Aarssen (1996) have found that polycormic *Pinus strobilus* had in comparison with unicormic trees lower heights, but greater diameters and stem volumes. They stated that "*there is a potential fitness cost of apical dominance (in terms of biomass production)*" (Chamberlin and Aarssen 1996, p. 268); a very important remark also in relation with questions of treeline formation.

Tree height to diameter ratio

Tree height to diameter (H/D) ratio decreased with increasing altitude. The results were, however, somewhat ambiguous, as there was a significant result of (non-parametric) correlation, but marginally non-significant results of regression analysis and analysis of variance. As in case of polycormic/ unicormic ratio, an increased sample size might have given a clearer answer. Tree H/D ratio was observed to decrease significantly with altitude in articles by Merganič et al. (2003), Homeier et al. (2010) and Bošeľa et al. (2014) based on studies with extensive sample sizes and long altitudinal gradients – first and third named study were actually conducted in the research area of this thesis (first wholly and third partially). Used in forestry theory predominantly as a measure of forest stand stability and resistance against wind and snow damage (Wonn and O'Hara 2001), H/D ratio may thus also be useful as an indicator in ecological research of the treeline ecotone and its causation, as proposed by Körner (2012). Also Holtmeier's (2003) remark about the carbon allocation, rather than gain or balance, being more likely the "*critical factor*" (p. 60) in the formation of the treelines seems to be in full accord with this finding. What exactly is the driver behind uneven decrease in tree height and diameter, and to discriminate between impact of ecotone structure (i.e. increased scattering and patchiness of tree groups) and impact of climatic peculiarities of high altitude on these variables is a task for future research.

5.2 Ecological conditions

Ellenberg indicators and light index

Ecological conditions expressed by average Ellenberg indicator values didn't vary greatly in the ecotone. Certain indicators, such as light or humidity, were positively correlated with altitude, which is in accord with earlier studies (e.g. Odland 2009), while the temperature indicator correlated with aspect favourability (positively) and slope grade (negatively). The fact that the altitude wasn't one of the primary drivers in variability of Ellenberg indicator values can also be illustrated by the fact that it wasn't clearly correlated with neither the first, nor the second PCA axis. Besides, the overall variability expressed by the PCA total variation was rather low. This was due to the relatively short altitudinal gradient assessed, but also due to rather low vascular plant species richness which was a basis for indicator values' calculation. A question can be therefore raised whether or not Ellenberg indicators are reliable enough to identify changes in environmental variables in shorter gradients which are inherently associated with the treeline ecotone research.

An interesting finding is the non-significant correlation between Ellenberg light indicator and light index calculated by actual measurements, even though both were separately significantly correlated with altitude. Light index (plot light measurement/ light measurement in the open space) decreased with increasing altitude while the Ellenberg light indicator (i.e. measure of plants' light demands) increased with altitude. This at the first sight absurd result requiring an explanation. As such can serve the fact that the crowns of *Picea abies* become longer (i.e. higher percentage of the trunk being covered by branches) when the spaces between the trees become bigger and with increasing altitude (Bošeľa et al. 2014). Thus the area under the tree canopy and adjacent to the trunk becomes increasingly darker (with associated decrease in light index meaning less light comes through the canopy) with altitude. The species present in the vegetation analysis which is done in a larger area (2 x 2 m) and include the dominant tree species can at the same time be more light-demanding as the area for which the average indicator values apply is much larger than the point measurement used in calculating light index. Anyway, this tremendous difference shows that direct measurements of light conditions should be preferred in treeline ecotone research.

Air temperatures

Air temperature conditions in the 'timberline' relative altitudinal band were remarkably stable in different aspects and altitudes. Unfortunately, there were not enough dataloggers available to obtain results from the other two relative relative altitudinal bands for the sake of comparison.

Mean temperatures in the growing season (GS) differed from results of a study by Gehrig-Fasel et al. (2008) from a comparable Central European mountain range (i.e. Alps). Gehrig-Fasel et al. (2008) used namely also two different methods for calculating GS length (in their work called "*thermal indicator period*"), with their mean of longer period being higher than our (their 8,8 ± 0,8 °C vs. our 7,71 ± 0,25 °C), while their mean of shorter period was much lower (their 8,0 ± 0,6 °C vs. our 9,63 ± 0,29 °C). Difference can be explained by several facts: different methods for selecting GS/ indicator period; different climatic regimes in Alps and Orava Beskyds and different measuring equipment. The difference in climatic regimes is even more pronounced in the soil temperatures, as will be discussed later. The first method for GS selection (called GS2 in the thesis) was used to check the claim by Körner and Paulsen (2004) that 7-days running average of soil temperatures of 3,2 °C „*corresponds to*" (p. 716) 7-days running average of air temperatures of 0 °C – therefore a GS with threshold of air temperatures of 0 °C should be essentially the same as (or at least not significantly different from) GS with threshold of soil temperatures of 3,2 °C. Our results disagree with this statement as the GS based on the air temperature threshold was at the average 40 days longer than the GS based on the soil temperature threshold. On the other hand, the mean air temperature in the GS based on 0 °C threshold (7,71 ± 0,25 °C) is very similar to mean soil temperature in the GS based on 3,2 °C threshold (7,91 ± 0,16 °C), in accord with results of Körner and Paulsen (2004). Very important in the context of air temperatures generally are also unusually warm years 2013/ 2014 resulting in mean monthly temperatures being several degrees above normal: at the average 2,23 °C in the period August 2013-August 2014 and 1,2 °C in months associated with the period of growing season as used in this thesis (i.e. August-October 2013 and April-August 2014). For details about temperature anomalies see Tab.13 (data from Oravská Lesná climatological station, approximately 20 km from Pilsko and 34 km from Babia hora).

Mean temperatures obtained in this thesis cannot be therefore regarded as representative for the 'normal' conditions in the ecotone. The temperature stability expressed in non-significant differences between 'timberline' temperatures in different aspects, slope grades and altitudes in growing seasons obtained by both methods is, however, a very important feature. Of course, the altitude is generally without doubt a single most significant predictor for the air temperatures (cf. Barry 1992), and the same was also result of our regression analyses. Yet the 'timberline' trees have shown to create a distinctive microclimate within their closed canopy, effectively overriding effects of aspect, slope, and to a certain degree also altitude on air temperature. The microclimate effect of the tree canopy are well known also in earlier literature (e.g. Bonan 1992, Modrzynski 2007, Boggs and McNulty 2010), its overriding of effects of topography on temperatures are less so, though (e.g. Holtmeier 2003, Körner and Paulsen 2004).

Table 13. Monthly temperature anomalies/ deviations from the monthly normal temperature of the period 1961-1990. Weather/ climatological station of the SHMI (Slovak Hydrometeorological Institute): 11868 Oravská Lesná. Data: SHMI bulletins [http://www.shmu.sk/sk/?page=1613].

11868	Oravská Lesná	
month	anomaly (°C)	anomaly (°C)
August '13	2,1	2,1
September '13	-1,2	-1,2
October '13	1,7	1,7
November '13	1,7	-
December'13	2,5	-
January '14	5	-
February '14	5,7	-
March '14	4,5	-
April '14	2,5	2,5
May '14	0,7	0,7
June '14	0,7	0,7
July '14	2,4	2,4
August '14	0,7	0,7
Average	2,23	1,2

Air temperature lapse rates between the lowland (valleys) and the study area were observed to be on the average consistently lower than the standard lapse rate of 0,65 °C/ 100 m. The fact that the air temperature data at the 'timberline' were measured under the tree canopy while the weather stations are generally without tree canopy cover might have influenced the results as well, though (with variation in the weather station data being presumably higher than it would have been with tree cover). Lapse rates generally lower than the standard lapse rate are in accord with findings of Perttu (1972). However, a rather great variation in the results (in terms of high mean/SD ratio) shows that using just about any average - higher or lower than “standard” lapse rate - to extrapolate the treeline air temperature data from the lowland measurements bears a very high risk of over- or underestimation. Besides, Autio (2006) has found that within the treeline ecotone, the lapse rates of air temperature at 2 m are usually greater than the standard lapse rate and with great seasonal variability; making the total lowland-mountain summit course of air temperatures anything but linear. A similar result (i.e. high air temperature lapse rate) was reported from the treeline zone in the southern Patagonia (Hertel, Therburg and Villalba 2008). It was unfortunately not possible in the scope of this thesis to examine the air temperatures in the whole ecotone in a similar way.

The lapse rates in the mountains are generally known to be higher in the summer and in the middle of the day and consequently lower in the winter and during the night (Barry 1992). July lapse rate in the study area is apparently consistent with this rule. However, as the temperatures (and thus also lapse rates) are greatly influenced by seasonality and time of the day (Barry 1992), vegetation cover (Oke 1978) and other factors, using a temperature extrapolation from the lowland weather stations will most likely lead to greatly different results than those genuinely present in the treeline ecotone. Direct *in situ* temperature measurements are therefore strongly recommended for any studies focused to examine the temperature and ecological conditions in the treeline ecotone, especially when the stated strong effect of tree canopy microclimate is taken into account.

Soil temperatures

Soil temperatures were quite stable with little variation with altitude, aspect and slope grade in the growing season (GS) in the 'timberline' relative altitudinal band (L1), while there was much more variation in the 'tree group/ biogroup line' and 'outpost-treeline' (L2 and L3). Mean temperature in the GS decreased in upper parts of the ecotone and the difference between L2 and L3 (save the variation) was higher than between L1 and L2.

Mean temperature in the 'tree group/ biogroup line' (L2) in the GS calculated by the method used by Körner and Paulsen (2004) is somewhat higher than their result from analogical 'treeline proper' from Alps (their 7,0 ± 0,4 °C vs. our 7,81 ± 0,61 °C). Our mean temperature is, however, within the range stated for temperate and Mediterranean treelines (7 – 8 °C) and, interestingly, very similar to Körner and Paulsen's results from cool temperate Asian (7,8 ± 0,3 °C) and temperate Australian (7,8 ± 0,1 °C) mountains. Our length of the GS is longer than the length in the Alps (their 135 ± 10 days vs. our 154,9 ± 7,7 days) or cool temperate Asian mountains (128 ± 3 days), yet again remarkably similar to length observed in Australian Snowy Mountains (153 ± 0 days). Since no information was given in Körner and Paulsen's study with regard to inspected years' deviations from normal temperature, the reason for the differences between results from Alps and Orava Beskyds might lie in the temperature anomalies during the period inspected in this thesis (see Tab. 13 on page 41). There are also other possible reasons, such as that although being geographically relatively adjacent, Orava Beskyds as a generally lower and significantly smaller (in terms of area) mountain range with certain oceanic influences are likely to have somewhat different climate from the Alps. When the oceanic influences are taken into account, comparison with Australian Snowy Mountains becomes much less bizarre, yet no hasty conclusions can or should be drawn from the similarity of the results. Length of the GS followed a similar course as soil temperatures (i.e. season became shorter and varied more in length in the upper parts of the ecotone).

The most important fact is that the 'tree group/ biogroup line' relative altitudinal band in the Orava Beskyds cannot be deemed to have a unified soil temperature regime in the same way 'timberline' has, as the temperatures were found to differ significantly with altitude, aspect and slope grade. Fact that measurements or data are “similar” to each other doesn't automatically mean they are a part of the same statistical population, and this was not confirmed neither for the 'tree group/ biogroup line' nor for 'outpost-treeline' soil temperatures. On the other hand, the soil temperatures at the 'timberline' were found to be rather similar in all expositions and altitudes. This, as an extension of the air temperature results, again shows the effect the forest canopy has on the microclimate, effectively levelling even the soil temperatures. Green, Harding and Oliver (1984) have found that vegetation height has a significant influence on soil temperatures while the canopy density plays only a minor role. Interesting in this context seems the fact that the mean temperatures within a given GS were not found to differ significantly between different relative altitudinal bands. However, it shows also that reducing the whole complex temperature regime into a single variable (i.e. temperature mean) removes very much of the information about the data, especially about the variation (which was much higher in the upper parts of the ecotone than at the 'timberline'). Körner and Paulsen (2004) and Gehrig-Fasel et al. (2008) have found that certain GS mean temperatures are associated with the treeline position, acting as indicators. Our results basically confirm the same, yet it should be stressed that they should really only serve as “indicators” while the real causal effects behind the treeline phenomenon need to be found in the biological responses of the trees to the ecological conditions in the ecotone (cf. Holtmeier 2003).

Day-degree sums as another way of indirectly assessing the heat in the environment generally followed the same course as GS mean temperatures: diminished with altitude and exhibited greater variability in the upper parts of the ecotone compared with the 'timberline'. Comparing the adjusted day-degree sums with results of Körner and Paulsen (2004), our observed sums are considerably higher than results from the Alps (their 301 ± 56 °C vs. our 487 ± 90 °C). Day-degree sums from Australian Snowy Mountains were more similar to our results, although with significantly less variation in the data (449 ± 5 °C). Results of Gehrig-Fasel et al. (2008) from the Alps can be described as “intermediate” between Körner and Paulsen's results from the Alps and ours (377,8 ± 96,9 °C). Odland (2011) used unadjusted day-degree sums, and his results from three treeline sites in southern Norway were somewhat lower than the results from Orava Beskyds (976, 960 and 802 °C vs. 1057,1 ± 128,7 °C). Körner and Paulsen (2004) have not found association between day-degree sums and treeline position based on the variation observed in their worldwide survey, and argue that the sums with threshold 0 °C are more useful in the global scope. Day-degree sums over a threshold of 5 °C in our study were, however, more robust to arbitrarily chosen GS lengths than mean temperatures, as can be illustrated by proportionally higher differences between mean temperatures than between mean day-degree sums in GS's obtained by two different methods. Besides, as temperatures below 5 °C are connected with none or low biological activity (Holtmeier 2003), threshold of 5 °C is biologically justified. In addition, unlike the mean temperatures, the day-degree sums were found to differ considerably (result for GS_5CD being significant and result for GS_K being marginally non-significant at adjusted α level) between the highest and the lowest altitudinal bands and were thus more adequate to describe structural changes in the ecotone than the mean temperatures in our case.

The stronger association between day-degree sums and altitude than between soil temperature GS means and the latter can be seen both in the results of linear regressions and the results of PCA. The July average and maximum temperatures' correlation with altitude is somewhat intermediate compared with the previous two variables, i.e. more correlated than GS mean temperatures, less than day-degree sums. July (or, generally, warmest month) temperature, traditionally used as one of the indicators of the treeline position (cf. Tuhkanen 1993) thus might be useful for this purpose in Central European mountain conditions. GS temperature means were associated with slope grade (results of both multiple regression and PCA), contrary to results of Körner and Paulsen (2004); they have, however, used mostly “*nearly horizontal ground*” (p. 716) for datalogger placement, a rather peculiar condition in the context of treeline research. The PCA as a multivariate statistical procedure has shown that the highest variation in the soil temperature indices expressed in the first principal axis (or component) is correlated with altitudinal gradient and aspect, a conventional result in the ecological research in the mountainous areas (Odland 2014, pers. comm.). Consequently, the day-degree sums were also correlated with the first principal component, major difference being that the day-degree sums were an active part in the ordination, while the altitude was a supplementary, i.e. passive variable. Later snowmelt date was associated with shorter growing season length. However, the snow-free period and growing season are far from identical, and Odland (2011) also warns against using the snow-free period as a substitute of growing season, as the biologically based growing season differs considerably from the snow-free period. Interestingly, neither the annual number of days with temperature under 0 °C nor the sum of sub-zero temperatures seems to correlate strongly with the altitude. Soil freezing is dependent on (non-)presence and thickness of snow cover (Sutinen et al. 2009), and this result can demonstrate the patchiness of snow distribution in the treeline ecotone which is independent of actual altitude (cf. Holtmeier 2003). Annual number of days with daily mean over 5 °C decreased with altitude, which is important with regard to the aforementioned importance of 5 °C as a threshold for biological activity. It is also interesting in comparison with relationship between altitude and annual number of days with temperature under 0 °C, showing that the relationships between temperatures and topographic variables including altitude are not completely linear.

Relationship between air and soil temperatures

As mentioned in the Results section, a detailed air-to-soil temperature transfer model is beyond the scope of this master thesis. However, predictive power of air temperatures on soil temperatures has been found to differ in relation with period considered, in such a way that when longer period (GS_K) was considered, air temperatures of the previous day had stronger predictive power on the soil temperature than the present day air temperatures, with present day temperatures being more important in a shorter period (GS_5CD). Importance of "*time-lag*" (p. 346) is crucial in air-to-soil transfer model by Gehrig-Fasel et al. (2008), and their model exhibits a very high degree of accuracy in modelling the soil temperatures. However, as our results have shown, the air humidity might have also an important role in the soil temperature modelling apart from air temperatures alone, in accord with results of Zheng, Hunt and Running (1993) who included precipitation as a part of their model. Similarly to results of Gehrig-Fasel et al. (2008), the temperatures from two days ago were also found to partially influence the present day soil temperatures, although in a rather minor way.

6 Conclusion

Altitudinal positions of the relative altitudinal bands of the treeline ecotone in Orava Beskyds were found to correlate with aspect and slope – highest positions associated with southern slopes with gentle grades and lowest positions associated with northern slopes and steep grades. Relative altitudinal bands' altitudinal difference (or “ecotone width”) was not clearly associated with certain aspect(s) or slope grades at Babia hora, at Pilsko had the eastern slopes and/ or slopes with gentle grades greatest “ecotone width”.

Percentage of polycormic trees wasn't confirmed to increase with altitude. Both tree height and diameter decreased with altitude, with height dropping significantly between 'timberline' and 'tree group/ biogroup line' relative altitudinal bands, while the diameter decreased more gradually. Tree H/D ratio in the ecotone decreased with altitude. The linear regression of H/D ratio on altitude was, however, marginally non-significant, most probably due to rather high variation of H/D ratio measured in the upper parts of the ecotone. The H/D ratio and associated changes in the performance of apical and cambial meristems should be investigated more in the context of the treeline research, as it may help to explain the fundamental principles of the treeline phenomenon.

Ellenberg indicator values weren't observed to vary greatly with altitude in the ecotone. Light and humidity indicators increased with altitude indicating increased presence and percentage of light demanding species and increasing humidity, the temperature indicator increased with aspect favourability and decreased with slope grade. Light index decreased with altitude indicating the increase in crown length and shading.

Air temperatures at the 'timberline' were observed to constitute a unified thermal regime effectively overriding the effect of aspect and slope, and to certain degree also altitude. Air temperature lapse rate calculated from *in situ* datalogger daily means and daily means from SHMI weather stations was at the average lower than the standard lapse rate, yet the great variation in the results speaks in favour of direct measurements instead of extrapolation from lowland measurements.

Soil temperatures at the 'timberline' similarly constitute unified thermal conditions, as they are dependent on air temperatures, modified by the physical properties of the soil and the vegetation cover. Temperature conditions in the upper parts of the ecotone ('tree group/ biogroup line' and 'outpost treeline' relative altitudinal bands) were observed to be much more variable with aspect, slope grade and altitude. No unified thermal regime was detected at these relative altitudinal bands. Mean temperatures in the growing season has generally decreased with increasing altitude, no significant difference was, however, found between the mean temperatures in different relative altitudinal bands. Day-degree sums over 5 °C, as a different form of measurement of heat, were found to generally follow the same course, yet contrary to mean temperatures they differ significantly between the 'timberline' and 'outpost-treeline' relative altitudinal bands.

The soil temperature indices in form of day-degree sums, mean season temperatures, length of growing season etc. (see Results and Discussion for details) were generally found to correlate with topographical variables (i.e. altitude, slope grade and aspect), with altitude exerting the strongest influence. There were, however, certain exceptions, most notably number of days with temperatures under 0 °C and associated sum of sub-zero temperatures.

Regarding the relationship between air and soil temperatures, the delayed response of soil temperatures to air temperatures was confirmed when assessing longer periods, while in the shorter term a more immediate response was found. Air humidity may play an important role in mediating the influence of air temperatures on soil temperatures.

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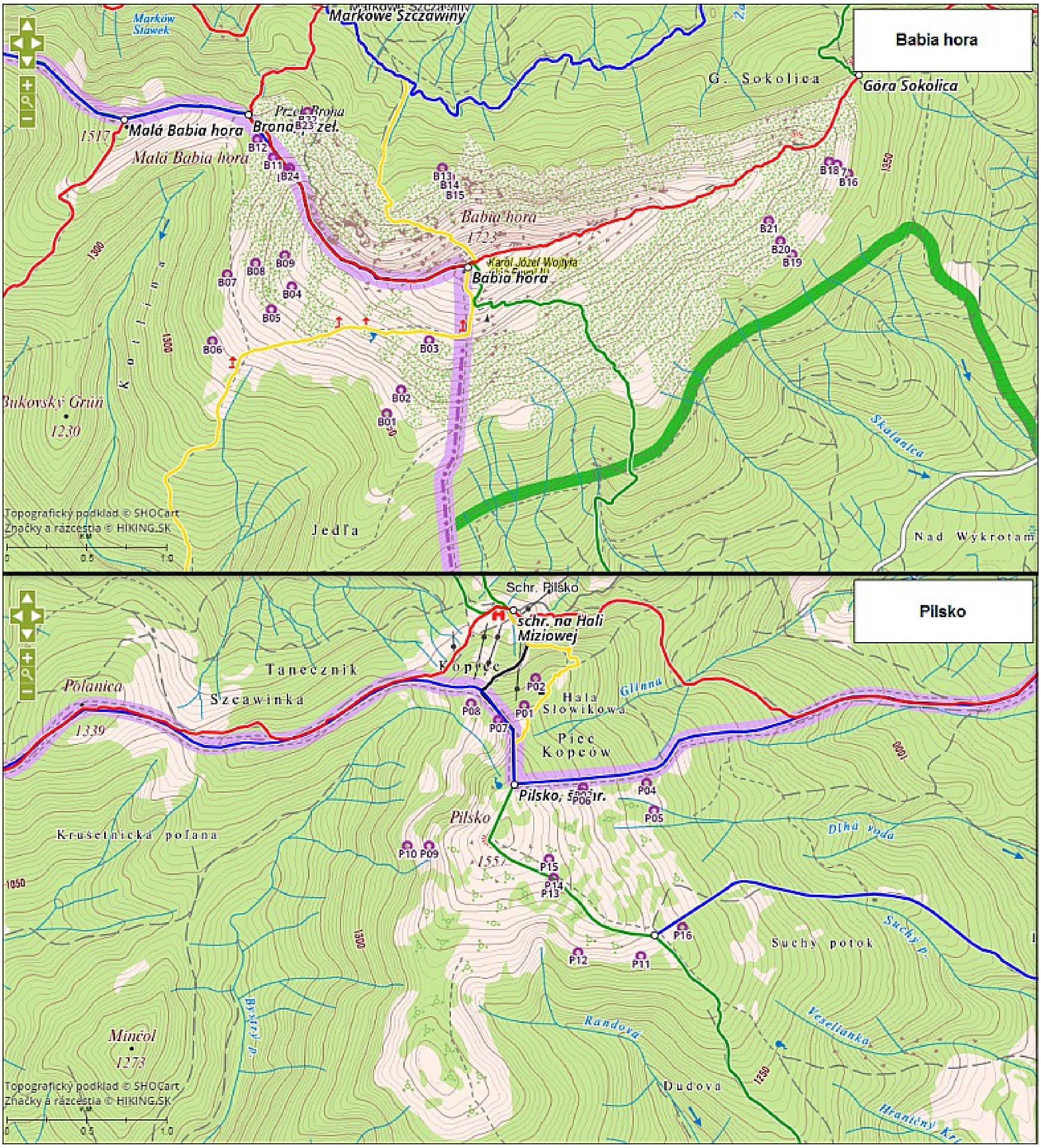
Overview of tables and figures

Appendix

Appendix 1. Map of the research area, study plots marked as blue rings (own work, map source: mapy.hiking.sk; © SHOCart and HIKING.SK)



Appendix 2. Alpine treeline ecotone (above L3) at Babia hora (own photo)

Appendix 3. Alpine treeline ecotone at Pilsko (within L2), Babia hora in the background (own photo)