Forest cover in watershed of mountain stream Javorinka in 2010

J. SOLÁR and P. STRAŽOVEC

Institute of High Mountain Biology, Žilina University, Tatranská Javorina 7, SK-059 56, Slovak Republic; e-mail: solar@uniza.sk

Abstract. Tatra forests in the watershed of the river Javorinka represent a complex of natural and man-made forest habitats. Utilizing geographic information systems, we were able to identify four classes of forest based on aerial photographs from 2010. These forests are spatially connected with abiotic properties as well as properties of individual stands, according to the forest stand map. Around 20 % of forest cover was in some way associated with the degradation of forest stands. The most degraded stands were alpine spruce forests (*Sorbeto-Piceetum*), especially in the higher age classes, on the southern to western slopes and in places where the water accumulation flow conditions were lower. We are of the opinion that the natural degradation of these forest communities occurs in the area, and this degradation may be exacerbated by the effects of a changing climate.

Key words: Watershed of mountain stream, Javorinka, forests, forest degradation, GIS, Tatra Mountains

Introduction

The fact that we are currently witnessing global climate change is becoming increasingly obvious and acceptable, and changes are observed the world over. In Europe, the Paris Agreement has the professional community searching for synergies between adaptation and mitigation and linking them to sustainable development goals (Harrison *et al.* 2019). This issue is also closely related to the benefits of biodiversity, nature protection (Prober *et al.* 2019) and sustainable forestry (Sesana *et al.* 2018). It is necessary to adapt ecosystem management and conservation practices to climate change goals, but widely accepted goals are geared toward the ecosystem's recovery to historical form, or to adaptation in changed conditions. These types of habitat-based measures are limited in efficiency (Wessely *et al.* 2017). Most tree species currently face a significant decrease in suitable habitat area (Dyderski *et al.* 2018). Assuming limited migration possibilities, ecological consequences would be serious for forestry, nature conservation and provided ecosystem services (Fleischer *et al.* 2017). Climate change varies regionally (Lindner *et al.* 2014). In a study by Sousa-Silva *et al.* (2018) authors pointed to general awareness among foresters (from Europe countries), with almost three quarters convinced that climate change will impact their forest, but only one-third reporting modified management practices. Though approaches vary throughout the European Union, in Slovakia more than half of foresters have already changed their management plans. The primary issue for this ecosystem is that current forests will have to cope with future climate conditions (Wagner *et al.* 2014).

In the Tatra Mountains, current forest composition exhibits a higher occurrence of spruce, reflecting postglacial development of vegetation and human activity from the 16th century. Lower elevations were completely clear-cut and replanted. Tatra forests were also periodically affected by windstorm disturbances (Koreň 2005; Koreň *et al.* 1997; Zielonka *et al.* 2009, 2010) and the consequences of bark beetle degradation (Fleischer *et al.* 2009). In the European context, some authors (Gregow *et al.* 2017; Brázdil *et al.* 2018) refer to increased occasion and impact of these events over last few decades. Bebi *et al.* (2017) observed changes in forest cover in the Alps due to disturbance, and noticed that forests established before 1880 were more damaged, perhaps due to their age increasing susceptibility to damage. Climate drivers, topography, human influence, and forest structure may also play a part. Some studies from the Research Station of TANAP (Fleisher and Koreň 1993, 1995) observed that forest stands were in poor condition, especially at higher elevations, prior to the most recent large windstorm (2004) in the Tatras. Naturalness and other parameters of these damaged forests have already been discussed (Koreň, 2005; Melicharová *et al.* 2007; Minár *et al.* 2009; Fleisher and Homolová 2011) with consequences to future management objectives and adaptation to climate change (Fleisher *et al.* 2009). Results from established reference plots (Fleisher 2008) after 15 years show that forest recovery was successful with higher tree diversity and a higher share of *Larix decidua* (Šebeň and Konôpka 2019). While the abundance of species increased at all sites, those with fallen trees were left with lower diversity and a higher prevalence of spruce individuals (Homolová *et al.* 2019), which lead to the formation of vegetation struc-

tures (spruce monoculture) prone to decay from wind or insects. This development of natural forest communities could contrast with the generally accepted need to apply adaptation and mitigation measures in the management of forest ecosystems, but will be driven by new natural conditions, where surviving individuals will support the emergence of a new generation. Ferenčík (2019) pointed to increased degradation from bark beetle, which has affected 50 % of adult forest stands in recent history. He described that this "catastrophic situation" exists primarily in old forest stands (130-180 years) in almost all valleys in the Tatras, with an even higher occurrence in forest stands at 300 m that have sustained damage from wind already, and remain unmanaged. Prevalence of dry and dead trees will increase as the spatial extent and location of vertical climatic belts have shifted over the last 50 years (Łupikasza and Szypuła 2019) in the region. In recent decades, the annual air temperature has increased (Zeleňáková *et al.* 2018a, b) along with a slight amount of precipitation (Repel *et al.* 2021), but the trend of water runoff has not changed significantly (Bičárová and Holko 2013; Zeleňáková *et al.* 2013). Generally, skeletal soil without vegetation cover can filter more water and remaining soil moisture could evaporate faster due to higher temperatures or consumption by young stands (Gebhardt *et al.* 2014). The situation is critical because indicators of ecological stability in dominant alpine spruce forests, such as low tree species diversity, and higher share of biomass, as well as other abiotic conditions defined by topography are unfavourable (Fleisher and Homolová 2011).

More attention to the issue of forest degradation could encourage additional studies utilizing remote sensing (Jakuš *et al.* 2003; Havašová *et al.* 2015;

Ochtyra 2020). In this study we focused on a basic spatial model determined by remote sensing, where we chose the coloured orthophoto mosaic of 2010, a year when consequences of forest degradation were fully evident in the Tatra Mountains. High resolution orthophoto mosaics with digital terrain models provide the ability to analyse spatial distribution data with regard to the damaged forest cover in relation to topography. The aim of this study is the analysis of forest cover in the watershed of Javorinka stream, with an emphasis on analysis of habitat conditions within the damaged forest. This is a pilot study, with the potential for more complex research on the entire mountain watershed area in the future.

Material and Methods

The Study area

The study area was comprised of the watershed of Javorinka stream, from mountain ridges to the crossing of road 66 in Podspády (Fig. 1). Javorinka stream originates in the Zadná Javorová valley of the High Tatras and flows to the Baltic Sea via Biela voda, Dunajec and Visla. The average annual flow is 1.8 $m^3.s^{-1}$ at the site where it crosses road 66 (SHMÚ 2007). The whole area is within Tatra National Park.

From a geomorphological perspective, the study area of the watershed belongs to three subdivisions within the Western Carpathians: High Tatras (south and west), Belianske Tatras (east) and Ždiar furrow (north). Its geological composition is varied. The southern part of the studied area was formed in the Paleozoic, older and younger Carboniferous, which is composed of tonalite granodiorites and
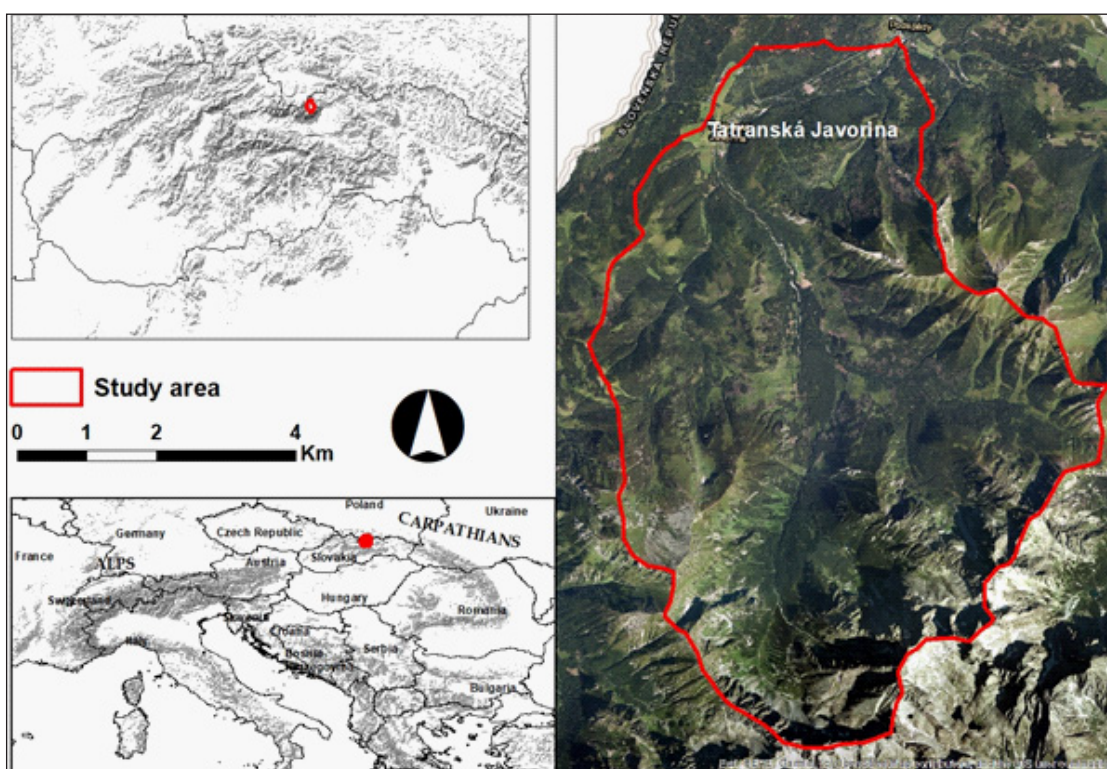

Fig. 1. Study area in watershed of mountain stream Javorinka (N49.22632°, E20.16171°).

granites. As we continue down the river, the surrounding hills are limestone and dolomites from the Middle Triassic period. The closer we get to the riverbed, the more the geological structure of the area changes to claystone, sandstone, shale and quartzite from the time of the younger Jurassic and older Cretaceous. The riverbed itself is formed of glacigenic sediments - gravel and boulders and deluvial-proluvial sediments - gravel and sand, which came to the surface in the Pleistocene (ŠGÚDŠ 2017). In the studied area we can observed altitude zonality of soil types, from rankers, rendzinas, pararendzina, cambisols, and podzols, to alluvial soils dominated by acid reaction, as well as neutral soils where silicates or carbonates elements are dominant (Bedrna and Račko 2000). The region is in a cold climatic area with continental weather patterns and typical features of the alpine climate. The annual average temperature in July is 16°C and total annual average precipitation 1512 mm. This region has significantly more precipitation compared to southern areas of the Tatra Mountains due to its windward position. This means that precipitation in Tatranská Javorina at 1030 m asl. is equal to precipitation on the south side of the Tatra Mountain at Skalnaté tarn, with an elevation of 1778 m asl. (see Bičárová and Holko 2013). Therefore, this area belongs to the cold and humid district.

Data collecting and processing

For the purpose of this study, we used aerial images (orthophoto mosaic) along with a reference system (s-jtsk) from year 2010. The orthophoto mosaic with high resolution (pixels with 0.5 x 0.5 m) was provided by the Geodetic and Cartographic Institute Bratislava (GCI). The layer of forest cover was manually digitalized (using edit tools) by ArcGis software (ESRI, USA) in a scale of approximately 1:1000. Four classes were used to identify forest cover in study area. Healthy forest (green, defined as a forest without visible degradation, young forest (light green), damaged forest (dark olivenite) and dry or dead forest (red). Damaged forests were identified as places where the forest was in a degradation stage, exhibiting fallen trees or clear-cut areas. These places were compared to aerial images from 2003. Forests that existed in 2003, but no longer exist the same capacity in 2010 were deemed damaged. Similarly, young forests were also identified through image comparison, in this case forest stands were observed in 2003 and in 2010. Forests identified for the first time in 2010 were considered new forests. Dry or dead forests were identified by the gray colour of the standing trees. After finishing manual digitalization, we obtained forest cover proportions of individual classes.

We analysed abiotic conditions according to a digital model of relief (DMR 3.5 from GCI 2018) using spatial analyst in ArcGis. Initially, we created a basic raster of elevation (m asl.), slope (degree), aspect (slope orientation), solar radiation (watt hours per square meter - WH/m^2) and water flow accumulation (potential surface precipitation build-up). The forest cover vector map was transformed to raster in same parameters as of DMR. One pixel represented 10 meters squared, and forest cover information was stored in pixels given
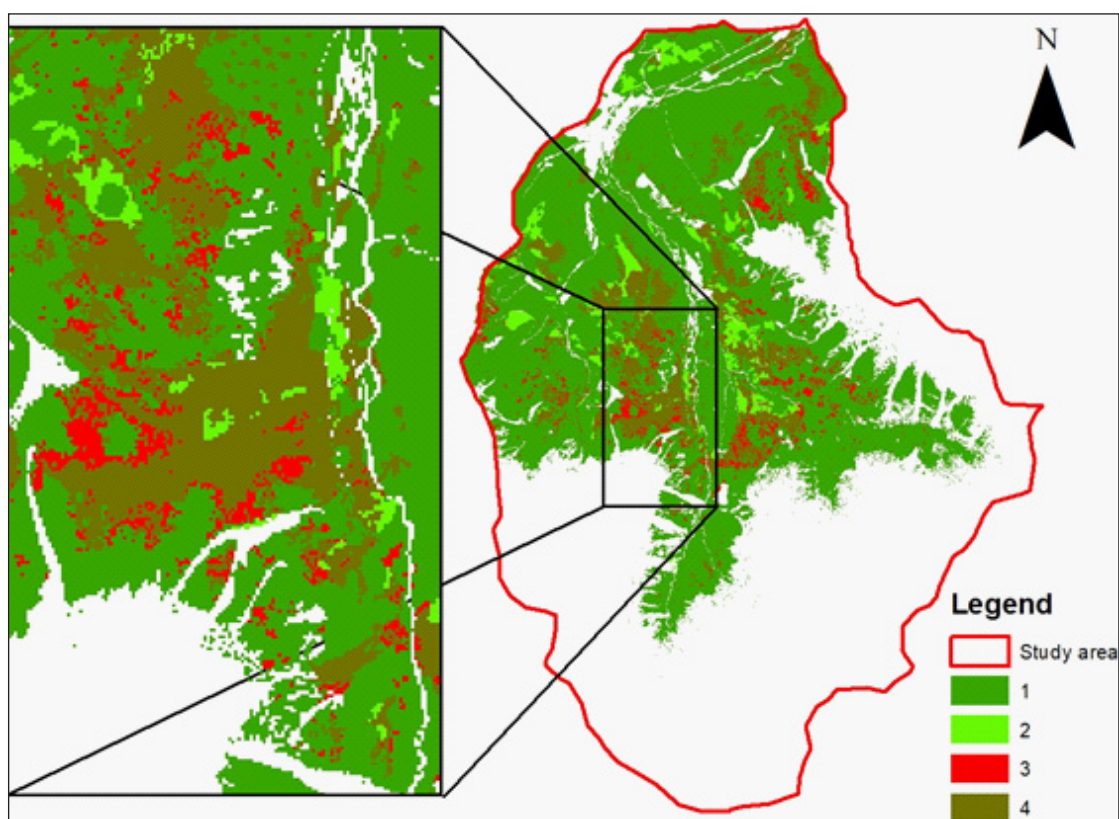

Fig. 2. Forest cover map in watershed of mountain stream Javorinka (1 - health forest; 2 - young forest; 3 - dry or dead forest; 4 - damaged forest).

from centroid position. This raster was then converted to points (centroids) and abiotic characteristics were extracted from the mentioned abiotic raster (derived from DMR). Finally, the point layer was spatially joined with layer of forest stands from National Forest Centre (NFC 2007). From these procedures we were able export table as a matrix for statistical evaluation.

Statistical analysis

The data matrix of forest cover for this region was evaluated by STATISTICA 8.0 (StatSoft Inc., USA). We used basic descriptive statistics, methods and analysis of variance One-Way ANOVA to identify potential differences between forest cover classes and selected abiotic variables extracted from DMR.

Results

The results of forest cover mapping according to the orthophoto mosaic from 2010 is shown in Fig. 2. White spots are places without forest cover, they include subalpine (dwarf pine stands), alpine (treeless) or subnival (bare rocks, debris) areas at higher elevations. At lower elevations we can distinguish meadows and urbanized parts of this mountain landscape. In total, forests covered 2 372 hectares (Table 1) out of the total watershed area of Javorinka stream (4733 ha), or approximately 50 %. In terms of forest class, 78.5 % forests identified as healthy forest (class 1), without visible damage to the forest structure. Damaged forests (class 4), defined as areas without trees or fallen trees, covered 329.44 ha. Dry or dead forest (class 3), defined as dry and dead standing trees, covered 78.14 ha. Young forests, which are often replanted areas that suffered from previous damage, covered 102.51 ha. All together,

more than 21 % of forests in this area were impacted by various disturbances over the last few decades. Visually, sites with dry or dead forest are located around the existing damaged forest. This suggests that active forest management present in area is insufficient to counter disintegration of forest communities already underway.

Almost no differences were observed between forest classes and mean radiation values based on the studied abiotic factors (Table 1). The highest elevation forest occurrence was at an altitude or 1776 m, but forests were affected by disturbances were at maximum altitude level of 1597 m. In 2010, forests in this belt (179 m) were unaffected by ongoing forest degradation and forestry management. Although the mean elevation value is slightly higher (58 m) for the class of dry or dead forests, using One-Way ANOVA, we were able identify that mapped dry or dead forests occurred at higher elevations than damaged forests and sites that were replanted (Fig. 3a). This may be associated with increasing degradation of forests at higher elevations close to damaged forest areas. Dry and dead forests were also found on steeper slopes (Fig. 3b), indicating that this was a factor in their degradation. The biggest differences were observed in values of water flow accumulation, especially in the case of dry or dead forests, where we can see the possible effect of a water deficit (Fig. 3c). This means that forest stands identified as dry or dead, or young replanted stands were at sites where values of water flow accumulation were significantly lower. Based on an analysis of road distance, it is clear that young damaged forests tend to appear closer to roads (Fig. 3d), likely because new roads were built in places where logging was underway or other forestry management practices were utilized.

Differences in solar radiation between observed forest classes yielded average values (Table

Class	Area			Elevation	Slope	Radiation	Flow	Roads
1	1 862.08	ha	Mean	1 264	24	5 504	1 036	105
	78.50	%	Minimum	913	0	1 166	0	0
			Maximum	1 776	81	6 720	473 440	855
2	102.51	ha	Mean	1 212	22	5 679	349	64
	4.32	%	Minimum	936	0	3 239	0	0
			Maximum	1 470	48	6 547	249653	347
3	78.14	ha	Mean	1 322	26	5 477	103	103
	3.29	%	Minimum	929	1	1 815	0	0
			Maximum	1 589	77	6 617	130 969	638
4	329.44	ha	Mean	1 265	24	5 598	906	86
	13.89	%	Minimum	913	0	3 521	0	0
			Maximum	1 597	60	6 640	473 062	414
Total	2 372.17	ha	Mean	1 264	24	5 523	957	101
	100	%	Minimum	913	0	1 166	0	0
			Maximum	1 776	81	6 720	473 440	855

Table 1. The basic characteristics for individual classes of forest cover in watershed of mountain stream Javorinka (1 - health forest; 2 - young forest; 3 - dry or dead forest; 4 - damaged forest; Elevation (m asl.), Slope (degree), Radiation (WH/m^2), Flow accumulation (potential surface precipitation build-up), Roads (distance from roads in meters)).
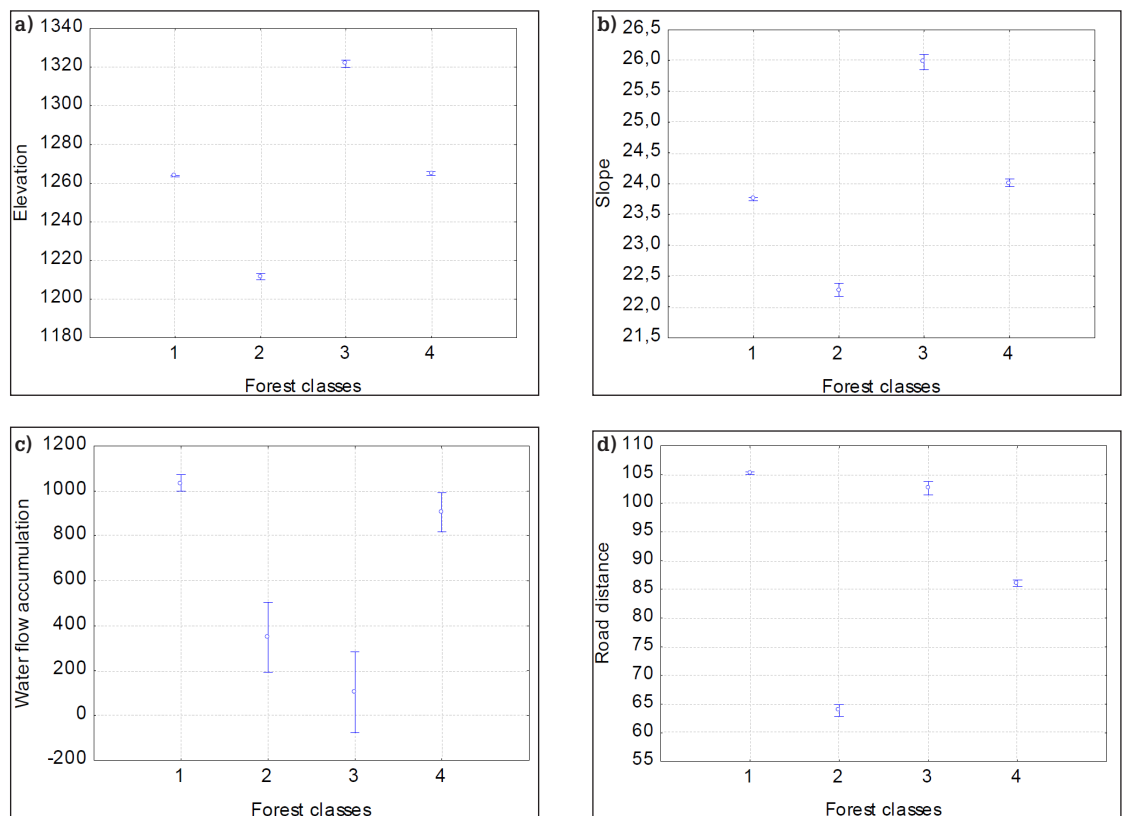
Fig. 3. Distribution of forest classes in relation to selected abiotic conditions. One-Way ANOVA (Means of least squares, vertical bars denote +/- standard errors); **a)** altitude (m asl.) $F_{(3, 237\ 213)} = 628.00$, $p = 0.001$; **b)** slope (degree) $F_{(3, 237\ 213)} = 168.74$, $p = 0.001$; **c)** water flow accumulation $F_{(3, 237\ 213)} = 14.257$, $p = 0.001$; **d)** road distance (m) $F_{(3, 237\ 213)} = 807.87$, $p = 0.001$; 1 - health forest; 2 - young forest; 3 - dry or dead forest; 4 - damaged forest.

1), although using the analysis of variation we achieved significant differences ($F_{(3, 237213)} = 484.60$, $p = 0.001$) between classes, particularly between young and damaged forests and either healthy forests or and dry or dead forests. We looked into individual classes in relation to orientation of slope (aspect). Generally, forests cover slopes from north to east and from west to north (Fig. 4a) in the study area. Forest classes connected to forest degradation (classes 2, 3, 4) are mostly oriented on slopes from east to west with a higher presence on south facing slopes. While young forests are predominantly located on southeast or west slopes (likely as a result of forest regeneration), the dry or dead forest stands are at south and southwest slopes (Fig. 4b). South slopes are often warmer, but with increasing air temperature and evaporation during the day, the slopes from southwest to west may be more greatly impacted by water deficits.
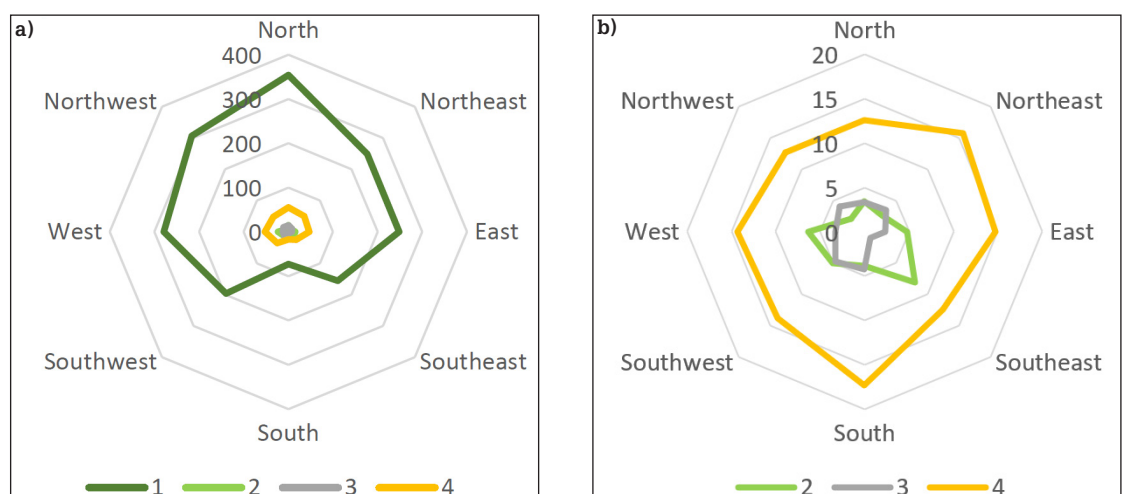

Fig. 4. Distribution of forest classes in relation to orientation of slopes (aspect). **a)** distribution according to total area of individual forest classes in hectares; **b)** distribution of individual forest classes as percentage from total area of individual forest classes) 1 - health forest; 2 - young forest; 3 - dry or dead forest; 4 - damaged forest.

According to data from the National Forest Centre (Maps of forest stand) from 2007, older forest stands dominate in the studied watershed (Fig. 5). Approximately 71 % of forests are older than 100 years and 40 % are older than 150 years. Twenty eight percent of forest stands are around 70 years old. The most abundant species within forest stands in this region is alpine spruce (*Sorbeto-Piceetum*), comprising 55 % of the cover. Next, fir beech spruce stands (*Fageto-Abietum*) constitute a 19 % share of the total (Fig. 6). If we take these proportions into consideration, in conjunction with forest classes 3 and 4, then the alpine spruce forest stands were most affected by disturbances (Table 2).

If we look closely at stands of alpine spruce (*Sorbeto-Piceetum*), we can see that these stands are often older (Fig. 7). Approximately 45 % of total forest cover is represented by stands of alpine spruce in age classes older than 130 years, constituting more than 1066 ha. Healthy forests covered 753.41 ha, young forests 42.25 ha, damaged forests covered 205.53 ha and dry of dead forest covered 64.66 ha. This may possibly mean that more than 30 % of alpine spruce stands were affected by age-related degradation. The situation facing these stands is unfavourable in terms of climate change if take a close look at abiotic conditions (Fig. 8a-d). These stands predominantly exist on warm, sunny, waterless and steeper slopes, but at higher eleva-tions, where due to lower temperatures and higher precipitation (clouds, misty, rain, snow) these stands have optimal conditions for life.

Types of forest stands	1	2	3	4
Abieto-Piceetum	3.12	**14.49**	0.69	0.23
Alnetum-incanae	1.22	0.00	0.03	2.31
Cembreto-Mughetum	0.50	0.16	2.42	0.44
Fageto-Abietum	**22.22**	**14.21**	3.22	7.63
Fageto-Piceetum	2.77	1.09	1.59	1.79
Fagetum abietino-piceosum	1.83	3.18	0.06	4.42
Fagetum humile	0.93	5.81	0.12	0.12
Mughetum acidofilum	13.46	0.61	3.66	1.13
Piceetum abietinum	1.41	0.70	0.01	0.95
Ribeto-Mughetum	2.59	1.28	3.21	0.53
Sorbeto - Piceetum	**49.08**	**58.46**	**84.94**	**80.44**

Table 2. Percentage of individual types of forest stands in relation to monitored forest classes in watershed of mountain stream Javorinka (1 - health forest; 2 - young forest; 3 - dry or dead forest; 4 - damaged forest).
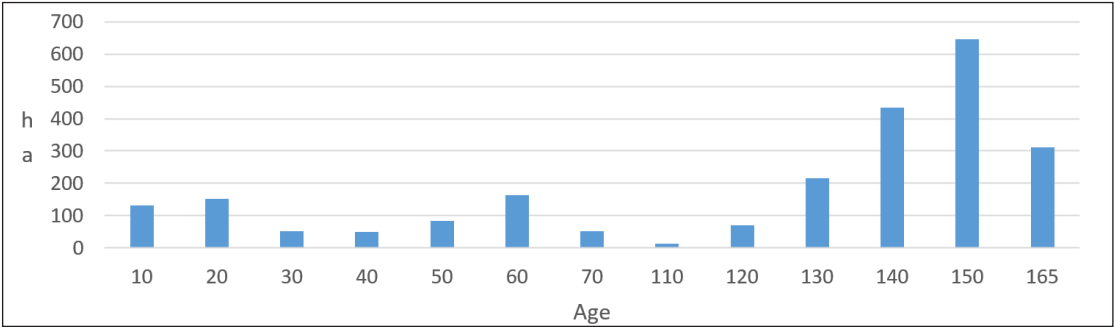

Fig. 5. Age classes of forest stands in watershed of mountain stream Javorinka.
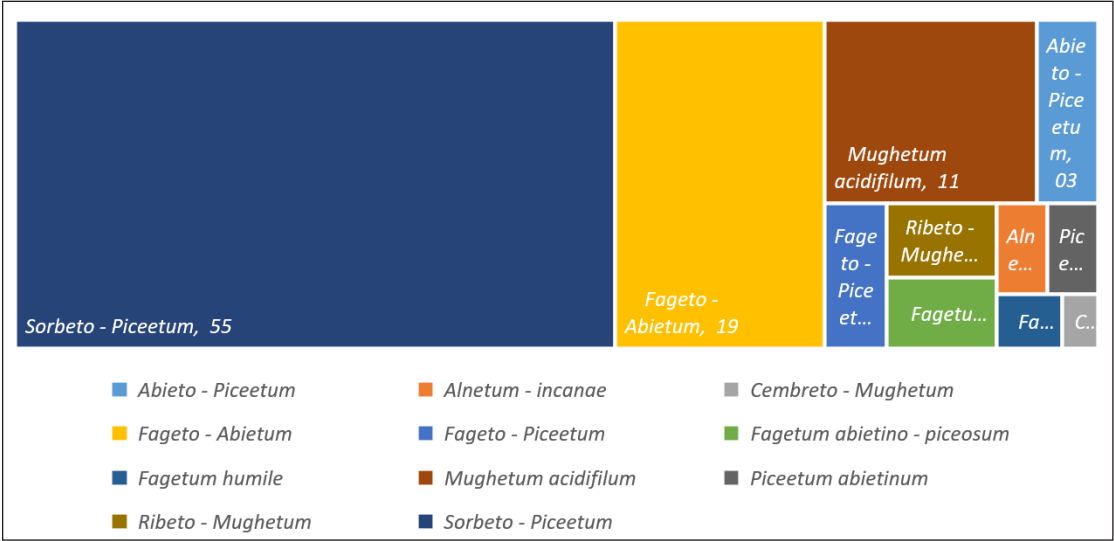

Fig. 6. Types of forest stands in watershed of mountain stream Javorinka.
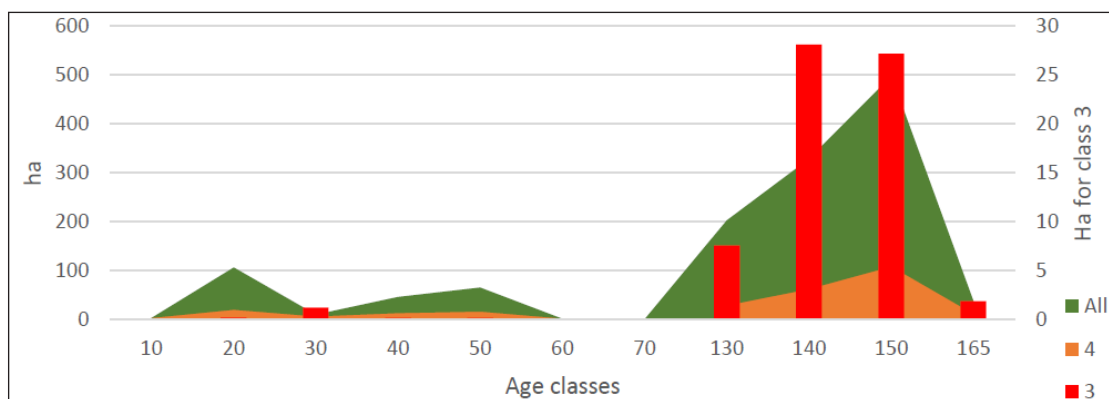
Fig. 7. Age structure (classes) of alpine spruce (*Sorbeto-Piceetum*) forest stands in watershed of mountain stream Javorinka. All - all identified forest classes; 3 - dry or dead forests; 4 - damaged forests.
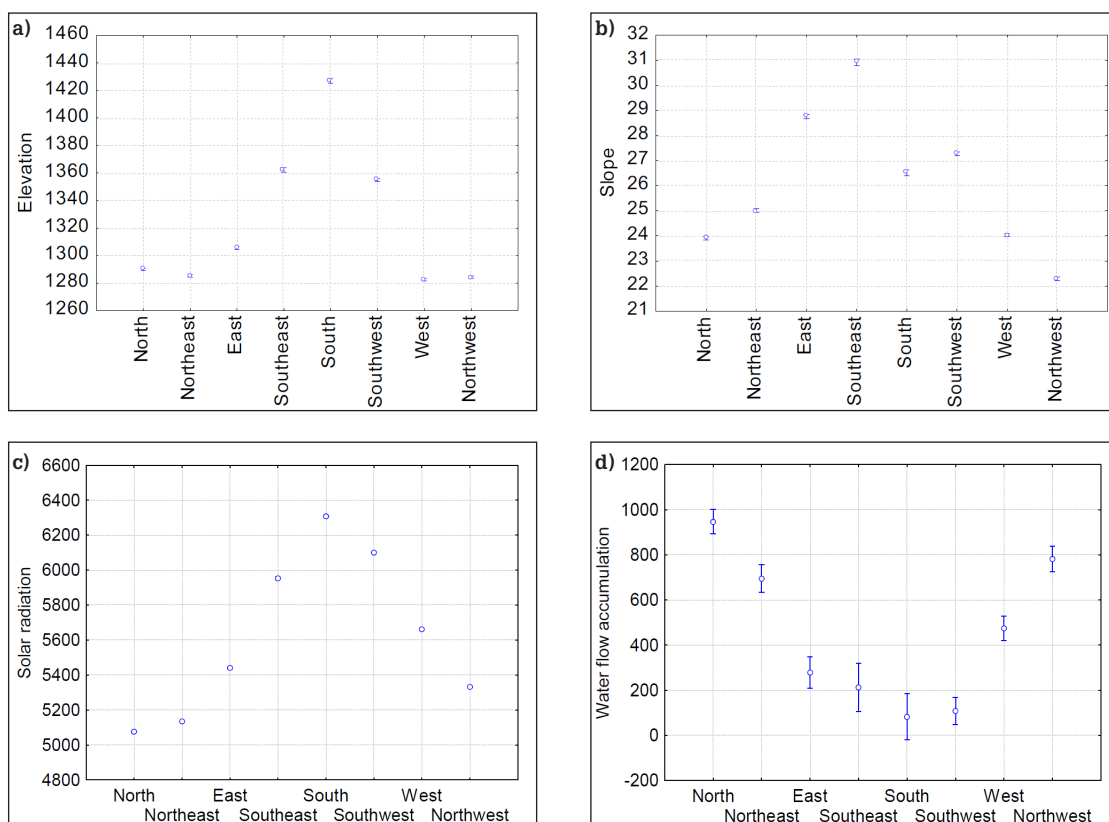

Fig. 8. Distribution of alpine spruce (*Sorbeto-Piceetum*) forest stands in relation to selected abiotic conditions. One-Way ANOVA (Means of least squares, vertical bars denote +/- standard errors); **a)** – altitude (m asl.) F (7, 130 520) = 1 626.9, p = 0.001; **b)** – slope (degree) F (7, 130 520) = 983.94, p = 0.001; **c)** – solar radiation (Wh/m²) F (7, 130 520) = 12 162, p = 0.001; **d)** – water flow accumulation F (7, 130 520) = 25.236, p = 0.001.

Discussion

It is not surprising that forests in this area are in a state of degradation. Naturally, spruce forests expanded to the narrow valleys of the Tatra Mountain during the dry boreal era (6800-5500 BC) (Jankovská 1988). However, current composition of stands reflect postglacial development of vegetation as well as natural development associated with climate change over time in specific topography conditions, as a result of human interference in forest communities starting in the 16th century. Formation of settlements in the Tatras during the 18th and 19th centuries was a crucial period for forests (Fleischer

et al. 2009). Lower parts of Tatra valleys as well as our study area were deforested. There is no doubt about that deforested areas were replanted, but the replanted forests lost structural diversity (Koreň *et al.* 1997), and potentially in situ autochthonous species, which have evolved over the ages and could thus be more resilient in these extreme conditions. In the study area, larger windfalls occurred in 1936, 1950, 1959 and throughout 1966-1971, paired with the effects of bark beetle overgrowth (Koreň *et al.* 1997). Starting in the 1970s foresters systematically worked at divided stands and tried to improve the health status of individual forest stands. However, these efforts have failed, and to-

day we are witnessing the disintegration of forest communities, predominantly at sites which have experienced long-term impacts by man. There are many reasons that the condition of forests in the region requires additional discussion and consideration. On the other hand, we must consider that periodical windstorms combined with bark beetle overgrowth are not a new phenomenon in the Tatra region (Koreň 2005; Zielonka *et al.* 2009, 2010). These are the kind of natural disturbances necessary to maintain the dynamic of the entire forest ecosystem (Whittaker 1975). This is especially true in the Western Carpathians, where huge forest fires are limited. In this sense, it is more appropriate to think about the catastrophic climax by Odum (1977) as it relates to our study area.

Systematic forestry activities and the indirect influence of human activities from the industrial sphere (pollution) also play a role in our perception of how these stands may persist in the future within this region (Koreň *et al.* 1997). If we take a close look at natural development of alpine spruce forests (*Sorbeto-Piceetum*) in relation to stand structure and biomass, according to Korpeľ (1986), the optimum age stage of these stands is somewhere from 140 to 180 years. Recently, Ferenčík (2019) pointed to a "catastrophic situation" in old forest stands (130-180 years) in almost all Tatra valleys, because of lack management after wind disturbances with bark beetle consequences. We observed significant forest degradation in old forest classes. Koreň *et al.* (1997) have discussed the issue of old forest stands paired with the absence of middle age classes in this area, and their fears came to pass. On the other hand, we must consider that the optimum age curve could be reduced due to less favourable conditions and pollution. A study by Šoltes *et al.* (1992) shows that the Javorinka watershed is the most heavily polluted area in the Tatra Mountains, where stands affected by bark beetle degradation were positively correlated with heavy metals. Defoliation analysis indicates that approximately 30 % of forest stands were affected, with an increasing trend (Koreň *et al.* 1997), especially in lower elevation sites of our study area. Generally, defoliation as a result of contamination increases with elevation. The structure of forest stands may also reduce their optimum age curve, because habitats with poor structure diversity are less resistant to disturbances (Jactel *et al.* 2017). Our analysis confirms that alpine spruce forests dominantly occurred at sites with unfavourable abiotic characteristics in terms of climate change, and where water stress plays a significant role. If we look at the data from the Slovak Hydrometeorological Institute, there is a significantly positive annual trend in air temperature (1962-2014) measured at all climatic stations, especially at sites with higher elevation (Lomnický peak - 2635 m asl., Skalnaté tarn 1778 m asl.) between April and August (Zeleňáková *et al.* 2018a,b). A significant decrease in the number of days without precipitation occurred in Tatranská Javorina between 1970 and 2019). A significant decrease in the number of days without precipitation, a significant increase in annual precipitation as well as maximum daily precipitation (Repel *et al.* 2021) were measured. Precipitation increased mostly at spring. This means

that temperature increased along with the amount of precipitation, but the trend of water runoff (1961-2010) has not changed significantly in recent decades (Zeleňáková *et al.* 2013, Bičárová and Holko 2013). This indicates that something is happening within the water cycle. Here we can consider additional features of monitored forest habitats. Areas with decaying biomass (dead fallen or standing trees) retain more water than clear-cut areas or areas where fallen and dead trees were extracted. Old forests with higher biomass retain more water; younger forest stands may consume more water for their growth; or more water tends to evaporate. Trees felled by wind or affected by bark beetle were predominantly extracted from stands by active forest management connected to bark beetle risk prevention. The proportion of old forest stands decreased due to disturbances. Young stands only covered 4.23 % of the area. This indicates that higher evapotranspiration is occurring, likely because the synergic effect of higher temperature and evapotranspiration might lead to higher landscape drying effect in the region, especially at the end of vegetation period. This trend of increased evapotranspiration was observed across Europe (Teuling *et al.* 2019), but water flow rate only increased where was enough precipitation. Another logical explanation for a lack of increase to runoff is the rocky soil, that without forest cover may be more absorbent. Therefore, we suggest carefull consideration of forest management practices with regard to a water balance assessment in this context of rising temperatures and natural dynamics of forest communities.

Current degradation of forest communities in this region are affected by a combination of various factors. In these complex conditions foresters must decide whether to direct change, or remain spectators, allowing changes to occur based on natural selection, and biodiversity.

Conclusion

This study analysed forest cover in the mountainous watershed area of the Javorinka river. Using the Geographic information system with high resolution data, we were able to identify four quality classes of forest, which were spatially compared with abiotic characteristics derived from a digital relief model and data from maps of forest stands. Results pointed to a general tendency of forest stand degradation. In total more than 20 % of forests in this area have been impacted by various disturbances in the last few decades. These stands covered mostly slopes oriented from east to west with a higher occurrence on south faced slopes. The dry or dead forest stands were most often located around the existing damaged forest areas, as well as on higher and stepper slopes where water flow accumulation was significantly low. The most degraded stands were alpine spruce forests (*Sorbeto-Piceetum*). These stands were commonly situated on warmer, sunnier, drier and steeper slopes. At higher elevations, with corresponding lower temperatures and higher precipitation (clouds, misty, rain, snow), these stands have

the optimal conditions for life. On the other hand, outlook is unfavourable for these stands, based on aspects of stand structure, climate change and abiotic characteristics. We maintain that the natural degradation of these forest communities has been accelerated by the effects of a changing climate and active forestry management in the region. It is questionable whether this degradation can be mitigated, as current forests will still need to cope with future unpredictable climate conditions.

Acknowledgements

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Growth responses of Norway spruce to climate (change) in the Javorová valley of the High Tatra Mountains, Slovakia

K. BRAUN

University of Passau, Innstraße 41, 94032 Passau, Germany;
e-mail: kira.braun@uni-passau.de

Abstract. Air temperature has increased more rapidly in the High Tatra National Park than the global average, which ranges between 0.85˚C [0.65˚C - 1.06˚C], over the last half a century (Hartmann *et al.* 2013). Between 1951 and 2018 the minimum air temperatures in the High Tatra National Park increased by 1.83˚C, and maximum temperatures have increased by 1.37˚C over 50 years. The change in temperature is evident in the dendroclimatological study of an alpine Norway spruce (*Picea abies* (L.) Karst) stand (1450 m asl.) in the Javorová valley. The growth response of the past decades deviates from the common pattern: previously the spruces responded positively to summer temperatures, which is a common response of mountainous conifers (Büntgen *et al.* 2007; Kaczka *et al.* 2016). However, during the last 33 years the Norway spruce of the Javorová valley have responded less positively. Additionally, the commonly observed negative response to winter and early spring temperatures (Büntgen *et al.* 2007) shifted to a more neutral or even positive response. On the one hand, these findings suggest that Norway spruce from the tree line can profit from an increase in temperature. On the other hand, the warming could harm the mountain forest ecosystem. A change in the response to precipitation is also evident.

Keywords: tree rings, *Picea abies*, dendrochronology, dendroclimatology, climate signal

Introduction

Background and Aim

A lively discussion on the existence and effects of climate change in the past several decades has moved from the scientific and political into the public realm. This has been triggered in recent years by a major increase in activism, mainly by young people, and has caught the attention of both the public and of politicians and policymakers. Causes and consequences of climate change, such as burning rain forests in Brazil, bushfires in Australia, melting glaciers worldwide, and the extinction of species, are just a few examples of headline stories in newspapers from 2019 and 2020, fueling the public outcry for political and social climate action.

While variations in temperature and precipitation on a daily, monthly, interannual and decadal scale are part of the climate system, changes that persist for an extended period of time are referred to as "climate change" by the Intergovernmental Panel on Climate Change (IPCC) (Hartmann *et al.* 2013). Between 1880 and 2012 the global mean surface temperature increased by 0.85˚C [0.65˚C to 1.06˚C], and over the past three decades has continuously been warmer than the previous decade since instrumental recording began (Hartmann *et al.* 2013). While climate change as a process is inevitable and its effects, such as melting glaciers and the extinction of plant and animal species are clearly visible, the extent of the global impact is as of yet, unforeseeable.

Dealing with climate change involves mitigation, where the world's forests play a substantial role in binding CO_2, a greenhouse gas that contributes to the warming of the atmosphere. Vegetation and especially forests serve as a natural carbon sink (Nabuurs *et al.* 2007). The ability of a tree to bind carbon depends on various factors such as the species, age, and stand ecology, amongst others. Further, forests have a positive ecological and social impact on the local, regional, and ultimately global scale, as they preserve water resources, while also protecting the biodiversity of plant and animal species. The importance of forests in slowing down climate change and contributing to an intact ecosystem is manifested in national and international policies which seek to organize forest management on a global scale. At the same time, forests are an important resource and income basis for many people. The effectiveness of policies is dependent on the regulatory capacity of governments, financial competitiveness of forestry, and on land use and cultural influences. Industrialized countries tend to have strong institutional and regulatory capacities, whereas countries mainly in the global south struggle with the implication of policies. Programmes aiming to slow down the deforestation of tropical rainforest, for example, have had minimal impact in the past (Nabuurs *et al.* 2007). Programmes of afforestation and the protection of forest in industrialized countries tend to be implemented more successfully, as regulatory institutions are already in place (Nabuurs *et al.* 2007).

In Europe, 215 million square hectares are covered by forests, which corresponds to 33 % of the total land area in Europe, and of those 215 million, 30 million hectares are protected (Forest Europe 2015).

Despite the ability of forests to mitigate, they are also at risk due to climate change. Diebacks, large fires, destructive storms, and the disruption of forest functions are hazards that have the tendency to increase with rising temperatures. To preserve and protect European forest stands, the European Commission published guidelines for forest management protection and preparation for climate change in 2010 (EC 2010). The European Commission has recognized the social, economic, and environmental functions of forests and has included forest protection in its strategy cope with climate change.

In addition to mitigating the effects of climate change in the present and the future, trees are also a witness to past climatic conditions. Vegetation cover is an expression of the competition and co-existence of species in a certain space dependent on environmental factors (Drescher-Schneider 1998). Plant growth becomes limited or accelerated, based on both its physical features, and on its dynamic processes, such as shifts in temperature or changes in the amount of precipitation. Because of their long life span, trees are considered to be an expression of these processes. The science of researching the impact of climate on tree growth is called *dendroclimatology*, which will be introduced shortly. In particular, those trees that grow on the margin of their elevational level are the most susceptible to temperature change, and as a result, supply the most reliable information on temperature (Fritts 2001).

Trees growing in a protected location, such a national park, are particularly well suited for study, because the impact of humans on the composition of the ecosystem remains minimal. Mountain forests in Europe today are often protected to some extent, but have been subject to major anthropogenic influence over the past centuries and decades. The timber industry would customarily replant forests with fast-growing trees in order to maximize profits. However, forest stands in national parks are often chosen for dendrochronological and dendroclimatological studies, as human influence is less than in unprotected forests.

Many studies have been conducted over the past decades, aiming to understand, first, how trees react to climate signals (Frank and Esper 2005; Büntgen *et al.* 2007) and, more specifically, their growth response to climate change (Savva *et al.* 2006; Hartl-Meier *et al.* 2014). A large number of these studies investigate stands in the Alps (Oberhuber 2004; Hartl-Meier *et al.* 2014), but Central European mountain forests, like the Carpathian range (Büntgen *et al.* 2007, 2015; Kaczka *et al.* 2016) are also the focus of study.

This study aims to serve as a further contribution to the investigation of growth response to climate of high elevation tree stands in the High Tatra Mountains, more specifically in the Javorová valley. On an excursion to the National Park in June 2019, samples of Norway spruce (*Picea abies* (L.) Karst) were collected and analyzed by students of the University of Passau. Following the excursion, dendrochronological analyses were applied to the samples taken. The following questions are being posed:

- How do trees at the margin of the elevational tree line in the Javorová valley respond to climate variables of air temperature and precipitation?
- How have these climatic variables changed over the past 70 years? Is a change in growth response due to shifts in climate visible at this site?

First, a short introduction to the science of dendrochronology and dendroclimatology will be given. After a site and species description, the materials and methods which were used to analyze the extracted samples are introduced. An overview of the tree data is then presented. Next, the climatic changes documented at the climate station Zakopane-Harenda by the National Research Institue of Poland, the Institute of Meterology and Water Management, which is the closest climate station to the investigation site, will be analyzed. Following this, the main research question on the trees' growth response to the climate signals minimum and maximum temperature and precipitation, as well as the change in these climate variables, will be considered. And thereafter, possible future responses and possible threats to the tree stands of the Javorová valley will be approached.

Dendrochronology and dendroclimatology

Dendrochronology is a "dating method based on variations in annual growth rings of trees" (Jacoby 2013). The prefix dendro- derives from the Greek word for tree *dendron*, -*chron*- refers to the assignment of the rings to dates (Fritts 2001), and the suffix -*ology* signifies that it is considered a scientific field. It is based on the strong tendency of trees in boreal and temperate environments to grow one increment of xylem cells per year (Jacoby 2013). For most trees in temperate latitudes one tree ring represents one year, since it starts to form during spring or early summer when the growing season begins, and ends when temperatures cool down at the end of summer or early autumn. In general, cambial growth remains active later in the season than does shoot growth. The growing season for trees at high elevations is, however, significantly shorter, and lasts between four and eight weeks, depending on the specific site. Younger trees tend to have longer periods of cambial activity than older trees (Fritts 2001). Rings can be easily discerned, because the wood cells produced at the beginning of the growing season referred to as early wood (EW), tend to be large, thin-walled and less dense in comparison to late wood (LW), when cells tend to be formed in a smaller, thick-walled and denser manner. The change in size and density between the latest and earliest formed cells marks the boundary between years (Fritts 2001) and is recognizable by the human eye, as shown in Fig. 1. Thus, the outermost ring closest to the bark was formed during the past year, or with dead trees, during the final year before felling. The first ring, which ultimately becomes the core, signifies the first year of growth when the tree was a seedling.

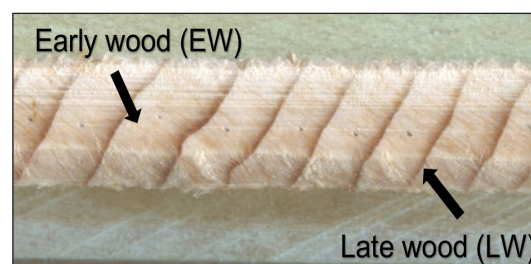When analyzing samples from trees of the same region, the variations in ring width are examined

Fig. 1. Tree sample with light early wood and dark late wood.

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and synchronously matched among the samples. This procedure is called *crossdating* and assures the correct placement of the growth layer and time. For crossdating it is necessary for the tree samples to show similar variation patterns. When variations among the sampled tree cores match the other cores collected, the year in which each ring was formed can be correctly determined (Fritts 2001). This procedure is of vital importance to further analysis, as chronologies produced by simply counting the rings can result in error-ridden data, due to the potential miscounting and misidentification of features, or the absence of rings (Fritts 2001).

The acknowledged founder of dendrochronology is Andrew E. Douglass, who observed similar patterns of variation in tree ring width in a large number of trees of the species *Pinus ponderosa*, a pine species in North America, and who drew up a chronology of 500 trees in 1914. However, there were scientists before him who recognized the potential of dating rings to a specific calendar year, such as the French naturalists Duhamel and Buffon in 1737, who observed narrow tree rings in a group of trees after a frost period. This was based on the number of tree rings matching the time that had passed since the frost period in 1709. Thus, the idea of dating tree rings in accordance with climatic extremes was established as early as the 18th century. Nevertheless, Douglass was the first to apply this procedure to the science of dendrochronology (Fritts 2001). He started setting up longer chronologies by overlapping sequences of living trees and sequences from trees that were used for construction wood, for example in houses or cathedrals, extending further and further back in time. With this procedure, he caught the interest of anthropologists striving to date prehistoric and historic native settlements in North America. Wood samples from these historic structures were then analyzed from different sites in the same region and were then arranged into one long sequence dating from 700 a.d. to 1929. Ever since, dendrochronology has been acknowledged as a powerful tool in the science of archaeology (Fritts 2001).

Douglass was also the first to establish the subfield called *dendroclimatology*, the study of past climates, by analyzing tree ring width, as he recognized that weather and climate must influence the ring width. For instance, he reasoned that narrow rings could be found after years with a lack of precipitation, as moisture stress limited the growth of the tree ring in that specific year. Subsequently, he recognized the potential of climatic information in the form of tree rings as a proxy for long-range climate records (Fritts 2001).

More technologically developed methods were introduced by Harold C. Fritts in 1960. Fritts was a pioneer in analyzing tree cores using statistical and later computer methods for studying growth patterns (Lamb and Gray 1978). Over time, dendrochronological studies have improved, based on increasingly reliable measurement techniques and statistical programs

and are considered a reliable source of climatic information on past decades and centuries, while helping to form a more close-knit picture of climate change and its effect on vegetation.

The principle of limiting factors plays a major role in dendrochronology. This states that the most limiting factor allows only a certain amount of growth (Fritts 2001). The degree and duration of this effect on biological processes varies from year to year. The limiting conditions are either of external or internal nature. The most significant external factors are water availability, temperature, light, atmospheric oxygen, and CO_2, as well as soil minerals. Internal regulators of growth, amongst others, include availability of nutrients, minerals, enzymes, and water. The internal factors, however, are usually the result of external factors, which limited tree growth during a previous time period (Fritts 2001). When a factor is no longer a limiting one (e.g., if enough water becomes available), the growth process will increase until a different factor becomes limiting, (e.g., temperature). Because of this effect on the width of the rings, narrow rings are recognized as containing more precise information on limiting climatic factors than wider rings. Tree ring widths can only be crossdated "if one or more environmental factors become critically limiting, persist sufficiently, and act over a wide enough geographic area to cause ring width [...] to vary the same way in many trees" (Fritts 2001). The limiting factors are also called "extreme weather conditions" (Schweingruber 2007), which occur suddenly, and are either of a short- or long-term nature, with severely damaging effects, such as wind-throws or hail-storms. The term "extreme" also refers to reactions to permanent changes in the environment, such as increasing temperatures. Because of limiting factors, such as decreased precipitation, a range of trees will be affected by this environmental situation. As a result, all, or at least most of the trees will likely show similar trends in wider or smaller ring width and then may be aligned more easily.

For this reason, analyzing tree rings of one tree specimen is insufficient. Also, a very small sample size is subject to random variation. The greater the number of samples from the same site that are analyzed, matched, and compared, the higher the probability of producing error-free dating as well as providing reliable information. A sample size of five or ten trees already leads to a reduction in random variation. For scientific research, a sample size of at least ten trees with two cores from each tree is recommended (Fritts 2001), however some studies require only a minimum sample size of five trees (Kaczka and Büntgen 2006).

On the excursion to the High Tatra mountains in June 2019, tree ring samples were taken from 15 Norway spruce, *Pieca abies* (L.) Karst, at each of three different locations. In this thesis, the focus will be placed on one location, that is, the Javorová valley, and on the growth variations of these 15 trees. Dendrochronological methods are used to determine the age structure and growth patterns of the selected trees.
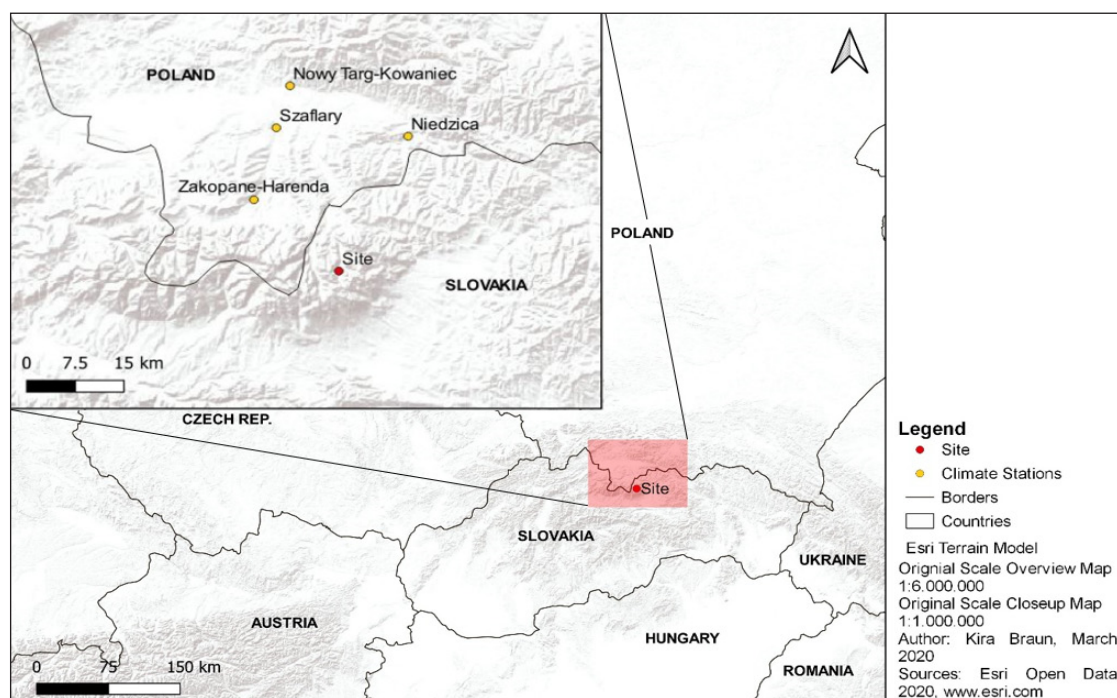
Fig. 2. Research site in a European context.

Site description

The samples were extracted in the High Tatra National Park, located in Central Europe (49° N, 20° E), on the border between Poland and Slovakia (Fig. 2). The Tatra Mountains are the highest range of the Carpathian arc, with Gerlachovský štít being the highest peak at 2655 m asl. The Carpathian mountain range is the smallest high mountain range in Europe and occupies the core of Central and Eastern Europe as the most eminent landmark (Kozak *et al.* 2013).

The Tatra mountains have a crystalline core, consisting of granitoids and metaphorphic rock. The core is covered by autochthonous Mesozoic sedimentary rock, of which limestones and dolomitic stones prevail in the research area (Gaweda *et al.* 2003).

Today the Tatra mountains are protected landscapes and consist of two National Parks, which are divided by the state borders of Poland and Slovakia. The Polish side comprises 25 % of the overall area with 21 164 ha and is called Tatrzanski Park Narodowy (TNP). The Slovak side makes up 75 % of the protected area with 113 221 ha and is referred to as the Tatranský Národny Park (TANAP) (Grodzki *et al.* 2003). The forest stands of Tatra National Park and in general the Carpathian forests, are among the best-preserved natural forests in Europe (Zielonka and Malcher 2009).

The samples for this study were taken from spruce in the Javorová valley on the north-eastern edge of the High Tatra mountains. The Javorová valley is characterized by water permeable limestone and is covered with Renzinas soil, which belongs to the group of the leptosols, from the greek *lepthos*, thin. Leptosols are characteristic of alpine regions (IUSS 2014). The research area is located next to the Javorinka mountain river at 1450 m asl. (Fig. 3). The site is on a north-eastern facing slope, and most of the trees were on a slight slope next
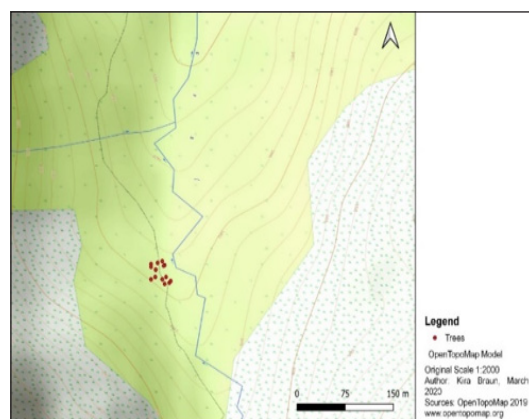

Fig. 3. Research site with individual trees.

to the path. A few samples were taken from trees on a steeper slope. The site was chosen close to the elevational limits of the ecological amplitude of the *Picea abies* (L.) Karst, because tree growth on the margins of the species' habitat tend to be most significantly influenced by external factors, such as temperature (Fritts 2001).

The climate in the Tatra mountains has the most diversified conditions in Central Europe. They are the result of the strong relief of the mountain massif meeting wide-open basins. Also, they serve as a climatic divide, limiting the free movement of north-south air masses (Niedzwiedz 1992). During the winter, polar-continental air masses arriving from the (north-)east affect the climatic conditions, while during the spring, summer and autumn, the influence of oceanic polar-maritime air masses from the west is predominant (Kaczka *et al.* 2016).

Since weather stations are distributed sparsely in the High Tatra National Park, climate data from Zakopane, a city on the Polish side of the park, are

presented in this study. The National Research Institute of Poland, the Institute of Meteorology and Water Management, provided the data, and has recorded daily measurements of precipitation, as well as maximum and minimum temperatures since 1951. As illustrated in the map above (Fig. 2), the Climate Station Zakopane-Harenda is on the north side of the Tatra Mountains, which corresponds most closely to the climate of the Javorová valley. The Slovakian climate stations are located in the south and west of the National Park and do not reflect the climatic conditions of the Javorová valley, as it is north-east facing, and as a result had to be excluded as a suitable data source. The data from the three climate stations: Niedzica, Szaflary and Nowy-Targ Kowaniec in Poland were not considered for correlation calculations and references, as they are further than 30 km from the research site, which is considered the maximum distance between a climate station and the sampling site that is acceptable for the accurate correlation of ring width and climate calculations (Fritts 2001). The Zakopane-Harenda climate station reflects the climate of the research area most reliably, because it is located 25 km from the research site and north of the mountain range. However, these climate records should not be considered a substitute for the climate at the sampling site. The climate station is situated at 834 m asl., while the sampling site is located at 1450 m asl. With increasing elevation the air pressure decreases, leading to overall cooler temperatures at the research site. However, the data provided from the Meteorological Institute are of great value for correlation analysis, as they include reliable daily data on the climate variables investigated, while values for the elevational belt of the sampling site are based on estimates. For this reason, the climatic analysis and the growth analysis both use the Zakopane climate data.

The climate diagram in Fig. 4 gives a graphic overview of the climate of Zakopane and of the research area. Temperature and precipitation are plotted on a scale of 1:2, so wet months are clearly recognizable. When the sum of precipitation for a certain month exceeds 100 mm, the scale is increased from 2 mm/° C to 20 mm/° C and displayed in a solid blue color. The months from April through September are considered wet months according to this definition. Months in which frost periods are likely are marked with a light-blue bar below the 0° C/0 mm line, and the months from November through March are frost periods. Over a year the precipitation adds up to 1179 mm. The wettest month is July, with 198 mm rainfall. The driest months are December and January, with approximately 45.5 mm precipitation, but no water stress. The diagram lists the daily maximum average temperature of the hottest month, as well as the daily minimum average temperature of the coldest month on the left side of the y-axis. For Zakopane, the average daily maximum temperature of the hottest month (August) is 21.0° C, and the minimum is recorded in January at -6.7° C. The annual average temperature is 6.4° C. This type of climate diagram is named after its inventors, i.e., the Walter and Lieth climograph and is used frequently for describing the climate at sites where vegetation is under investigation, because the most important values for vegetation are highlighted (Guijarro 2019).
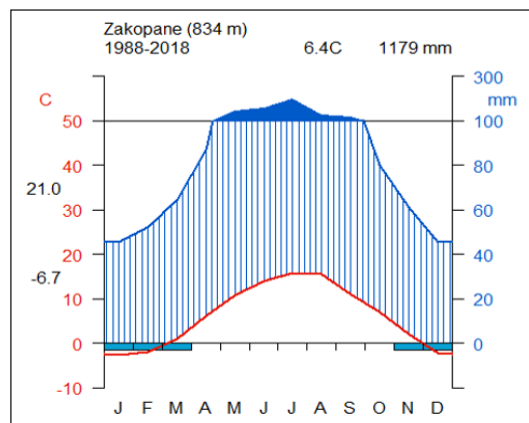

Fig. 4. Climograph from the Zakopane-Harenda climate station between 1988-2018, annual precipitation = 1179 mm, mean temperature = 6.4° C, mean maximum temperature August = 21.0° C, mean minimum temperature January = -6.7° C.

In sum, the climate in Zakopane is wet and temperate. The rainfall is high, even during the months that do not qualify as wet periods. Throughout the year, the climate can be classified as humid, as the precipitation curve is always above the temperature line, portrayed here in a blue striped pattern.

The classification of the climate is *Dfb* according to the climate categories of Köppen-Geiger. Köppen was a plant physiologist and used plants as a climate indicator, and Geiger was a climatologist. The *Dfb* classification describes a fully humid snow climate with warm summers, where during these four months, temperatures reach above 10° C (Kottek *et al.* 2006).

Species description

The focus of this study is on the Norway spruce (*Picea abies* (L.) Karst), which is the most dominant tree species in the High Tatra subalpine spruce forest. At the site, old trees were chosen, as they usually provide the most ring width variability and as a result maximize the amount of climatic information. The *Picea abies* is an evergreen conifer, reaching 50-70 meters in height with long shoots and skewed needle leaves. Its maximum age is approximately 300 years (Bartels 1993). It is a partial shade tree and can survive with minimum sun exposure during early growing stages. According to Leuschner and Ellenberg (2017), seasonal growth can be classified as follows:

"[The *Picea abies* belongs to the *Quercus* type of temperate tree species], which stops growing in height relatively early in the year, even when conditions are favorable, and is mainly driven by endogenous development processes. Shoot growth on these species pauses during the summer, whilst the growth in roots and girth continue even after the growth in height ceases."

At the age of 50-60 years, spruce reach their reproductive age and start having three to five seed cycles per year. Furthermore, characteristics such as very high drought sensitivity, very high susceptibility to wind breakage, high herbivore sensitivity, moderate waterlogging tolerance, moderate late frost sensitivity and low winter frost sensitivity are ascribed to *Picea abies*. Their seedlings are also very highly drought sensitive (Leuschner and Ellenberg 2017).

The Norway spruce is typical for boreal mountainous altitudes up to 1500 m asl. in three regions of Europe. It is the dominant species in the alpine southern European, the hercynian-carpathian and north-eastern European mountain ranges. In the High Tatra mountains, this spruce is the dominant species of the coniferous forest in the upper montane forest zone, which extends from 1250 to 1520 m asl. (Rączkowska 2019).

Because of its ability to regenerate in small gaps or amidst full grown, light-blocking trees, it prevails against larch (*Larix decidua*) in the subalpine zone (Zielonka and Malcher 2009; Kaczka *et al.* 2016). Its large distribution area, straight rapid growth, and minimal requirements in terms of habitat make the spruce the most important mainstay in European forestry (Bartels 1993). However, it was not only natural processes that influenced composition of forests in the research area. Selective replacement of larch with more shade tolerant species, such as the previously mentioned Norway spruce *Picea abies* or the European silver fir (*Abies alba* L.), was practised when changes in forest management shifted toward private and commercial land use (Zielonka and Malcher 2009). The processing of timber from spruce has a long tradition in the Tatra Mountains. As a result, the Norway spruce also predominates in the lower montane forest zone, up to 700 m asl., which is the natural habitat of mixed forests with deciduous beech (*Fagus sylvatica*) and coniferous fir (*Abies alba*) (Rączkowska 2019).

The land use changed in the 12th century when animal grazing and mining were first introduced in the Tatras. Mining activities peaked in the 17th and 18th centuries. Metallurgy followed in the early 18th century, with a smelting center in the Javorová village. This industry was resource-intensive, with an increased demand for charcoal as well as timber for mining infrastructure. The Javorová valley was a primary catchment area, resulting in large scale deforestation (Rączkowska 2019). The name of the valley derives from the Slovak term for the maple tree – *javor* – which highlights the land use change as well.

This monostructure has become even more problematic ever since the bark beetle infected the forest, spreading more quickly in the past decades. Since spruce is the bark beetle's favored habitat, it can spread more quickly than in a mixed forest. As a result, large spruce stands were felled during an outbreak in the 1990s (Grodzki *et al.* 2003). The bark beetle plague is an ongoing issue and will most likely affect large areas of the National Park.

Although the Tatra Mountain forests have been and are influenced by human activities, the high mountain region, where the sample site is located, is considered only slightly changed (Rączkowska 2019). Since 1959, the TANAP area has been officially registered as a National Park and its vegetation is protected (Grodzki *et al.* 2003). Today, human activity is largely limited to tourism, and although the Javorová valley is easily accessible, it is not the most frequently visited region of the National Park (Rączkowska 2019).

Material and Methods

Increment borer and sanding

The samples were extracted 1.5 meters above the ground at chest level with the help of an increment borer. This is a primary tool for collecting cores from living and dead trees for dendrochronological analysis and consists of three major parts: the extractor, the handle, and the auger (Grissino-Mayer 2003). Because of the sloped surface of the research area the samples were extracted by drilling two perpendicular holes on each side of the tree to reduce the probability of collecting reaction wood. The extraction of two radii per tree follows the *principle of replication* (Fritss 2001), assuring the analysis of variations of width within a tree. This procedure helps to avoid random variations and allows statistical comparisons of each tree. To prevent the cores from breaking, they were stored in a hardcover divider during transport in the field and glued into a clamp for more stability at the research base.

In the laboratory of the University of Passau, the surfaces were prepared for better readability by sanding the cores with a wood grinder. Each sanding was done for a few seconds to maximize surface clarity without diminishing the tree sample. For rough sanding a grain size of 60 was used, followed by a smaller grain size of 120 and finally a grain size of 600 was applied.

Measurement and preparation of the tree data

Measurement with CooRecorder and CDendro

After sanding, the tree rings were counted manually from the bark toward the core. Each decadal ring was marked with one small pencil dot, a semicentennial ring with two dots, and a century ring with three dots (Fig. 5). The dots could then be used as reference points. After that, both cores from one tree were scanned with a 2400 dpi (dots per inch) resolution and saved as TIFF format.

Fig. 5. Scan of two tree samples from one tree with decadal, semicentennial and centennial marks.

The measurement of the cores and their dating were done using the software package *CooRecorder* and *CDendro* provided by Cybis Elektonik & Data AB from L.A. Larsson. Measurement of the tree ring width was done using the dendrochronology software *CooRecorder*. 7.7. The width was registered by zooming in to the scan and marking the distance between the end of the late wood (late summer/autumn) to the beginning of the early wood (spring/early summer) of each ring. The distance between each ring was recorded as a coordinate and saved in millimeters in a *.pos* file. The coordinates were then uploaded to *CDendro* 7.7. The software was used to convert the file to the Heidelberg format in order to visually crossdate them in another program.

Visual and statistical crossdating

The cores were visually crossdated against each other by applying the TSAP-Win™ (Time Series

Analysis Program) software. First, both series from each tree were aligned. Tree_6 had to be excluded because the single curves could not be aligned towards each other. The other pairs were successfully aligned, thanks to similar growth variations, which can, as previously mentioned, be attributed to the limiting factors which influence tree growth in a similar way. The measurements of the two series were then averaged to create a mean series for each tree.

Detection of negative pointer years was used to collate the visual crossdating. Because trees from the same species, such as the *Picea abies*, respond to climatic changes similarly in different regions, the search for negative pointer years in other data sets or scientific publications can be used for assuring the correct dating of the extracted cores. Narrow rings, which appear as negative pointer years, are considered to be the most reliable when aligning different cores for crossdating, because exceptionally narrow rings are the easiest to identify due to their pattern and are less susceptible to random variation (Fritts 2001). They are formed when a climatic variable is especially limiting, such as low temperature after a volcanic eruption. During an eruption, sulphate aerosols are injected into the stratosphere scattering incoming solar radiation and absorbing outgoing infrared radiation, which causes a warming of the stratosphere, while the Earth's surface cools down (Büntgen *et al.* 2015). A popular example is the Tambora eruption on the Indonesian Island Java in April 1815, which is the largest known volcanic eruption in recent history (Oppenheimer 2003). The amount of sulfur measured, approximately four times the average during the following years, caused a regional cooling and impacted temperatures on a global scale. Western and Central Europe as well as Eastern Europe, for example, had cooler temperatures of 1-2° C compared to the 1810-1819 average multiple for years. At the same time precipitation increased. This had catastrophic implications for the population. Agriculture was impacted significantly in 1816, which has been recorded as "the year without summer" (Oppenheimer 2003) in Irish, British, and Northern American folkloric tales. Snowfall was even recorded June 1816 in New York, Maine and Connecticut. This global cooling over several years is visible in most dendrochronological studies located in the Northern hemisphere (Briffa *et al.* 2004; Kaczka and Büntgen 2006; Büntgen *et al.* 2015) and narrow rings were also found in the samples of trees 3, 4, 13 and 14 at the Javorová site, as these trees are old enough (Fig. 6).
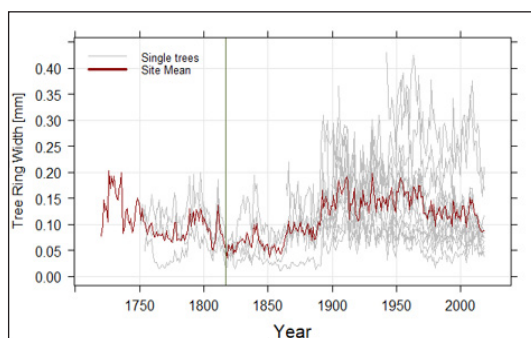

Fig. 6. Negative pointer year and narrow tree rings after the Tambora Eruption in 1815.

Further consistencies of narrow rings could be found in the following years: 1912 the Novarupta volcano erupted in Alaska, marking it the biggest eruption since Tambora, cooling down temperatures and causing narrow tree rings to form at the Javorová site, amongst several others (Briffa *et al.* 2004; Kaczka and Büntgen 2006; Neuwirt *et al.* 2007; Kaczka *et al.* 2016). More negative pointer years were found for the years 1934 and 1942/43 corresponding to the Neuwirth *et al.* study from 2007. In a study by Bijak (2006), the negative pointer years 1913 and 1980 are commonly found. The negative pointer year of 2004, following the hot and dry summer of 2003, is significantly visible at the Javorová site and can also be found in the study from Neuwirth *et al.* (2006).
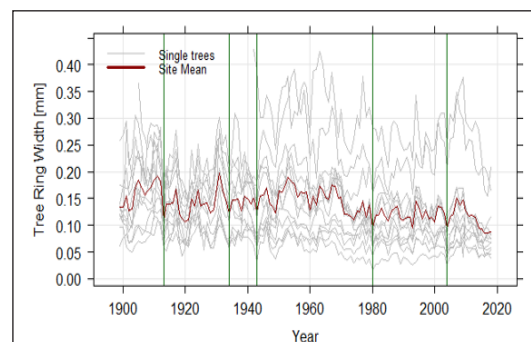

Fig. 7. Negative pointer years from 1900 to 2018 at the Javorová site at 1450 m asl. (Negative pointer years: 1913, 1934, 1943, 1980, 2004).

Extraordinarily wide rings, visible as positive pointer years, can also serve as orientation. Positive pointer years were detected in 1946 and 1961, which correspond to the Neuwirth *et al.* study from 2007. However, extraordinarily wide rings are more susceptible to random variation than narrow rings and should not be the only source of verification (Fritts 2001).

Further, statistical crossdating was performed using RStudio, which is an open-source software and a more user-friendly environment, in the programming language 'R' for statistical computing and graphics. Programming and analyses can be done with the help of R packages, which are a collection of R functions, compiled code, and data. Since RStudio is an open-source product, code and packages are provided by the RStudio team and third parties for free (Jones *et al.* 2014). In the following, the main analysis steps and the packages used will be introduced. The dplR-package, which stands for the "Dendrochronology Program Library in R" (Bunn *et al.* 2020), provides commands and coding for tree ring analyses such as crossdating and standardization. The results of statistical crossdating will be presented first. The dplR function *corr.rwl.seg*[1] was used for crossdating. This function correlates a particular tree series with the master chronology, which is comprised of all other series in the data set. Crossdating is achieved by overlapping segments; 50-year segments were used here. The segments are lagged by half the segment length; thus the 50-year segments overlap by 25 years. There

are two lines for each tree; the upper line represents the upper axis timeline, while the lower line represents the bottom timeline. As shown in Fig. 8, each segment is colored according to its similarity with the master, based on the p-value[2]. If the probability is less than 5 %, the correlation coefficient is significant. The blue color shows that the series are correlating well, having a p-value below 5 % (p < 0.05). Green signifies that the segments do not completely overlap the period, so no correlation was calculated. When the crossdating is not significant, the bar is red (Bunn *et al.* 2020). Tree 10 did not achieve the statistical crossdating and therefore has been excluded from the sample set.

[1]Corr.rwl.seg stands for correlation of ring widths (rwl) in segments (Bunn *et al.* 2020).
[2]The p-value describes the probability that a match is achieved by pure chance. The measure is calculated by deriving the probability of achieving an observed correlation coefficient from a single matching experiment. Then two series, the master series and the observed tree series, are compared by overlapping the segments. Correct matches should be characterized by a low p-value (Wigley *et al.* 1987).
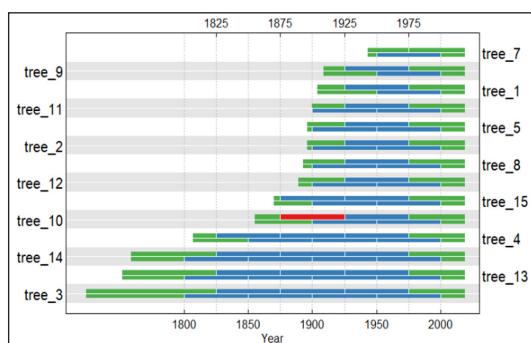

Fig. 8. Statistical crossdating using the corr.rwl.seg function of the dplR package.

Descriptive analysis of the tree data

Out of the 15 trees sampled at the site, 13 were included for further analysis. The average age is 166 years, while the age of the oldest sample, tree_3, is 299 years, dating back to 1720. The youngest sample is tree_7, which dates back to 1942, making it 76 years old. The mean annual width of all the trees included is 0.111 mm per year.

Boxplots (Fig. 9) give a graphical overview of the range of growth widths of the collected tree samples. Each boxplot represents one tree on the x-axis, numbered in ascending order. On the y-axis the growth is displayed in millimeters. The information is divided into quartiles and the whisker-lines represent the lowest and highest observations. The extension of the lower whisker represents the lower 25 %, and the upper whisker the upper 25 %. The box starts at the first quartile and ends at the third. The bold line in the box is the median, which divides the lower and upper 50 % of the data. The circles outside of the box-and-whisker-plot are outliers (Cann 2004). More condensed boxplots show less variation and thus more consistent growth patterns, whereas boxplots
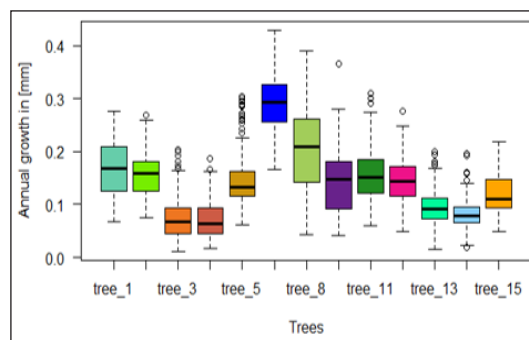

Fig. 9. Annual tree growth and variation of the sampled and included trees of the Javorová valley site at 1450 m a.s.l

with a greater range represent trees with rings that have a greater variation in ring width. Sites with high variability are frequently limited by environmental factors. The variability in ring width is referred to as *sensitivity* (Fritts 2001).

The width of tree rings in this study varies greatly. The mean annual growth of tree_3 and tree_4, for example, is 0.072-mm per year, while tree_7 grows 0.293 mm per year on average, which is approximately 4 times the annual growth of tree_3 and tree_4. This can be explained in part by its juvenility. As established before, trees tend to form broader rings at a younger stage (Fritts 2001). Tree_8 has the greatest variation in annual growth, ranging between 0.04- and 0.391-mm. Tree_4 varies the least, ranging between 0.016- and 0.186-mm annual growth. The mean growth of all trees ranges between 0.072- and 0.293-mm per year.

The mean of all correlations[3] between the 13 cores is 0.437. The measure of correlation between trees yields information about the similarity between the tree's variance (Fritts 2001). The value of the standard deviation[4] of the mean curve of the tree samples is 0.038 mm. The standard deviation shows that the rings that are narrower than the average of 0.111 mm are on average 0.073 mm wide and the wider rings measure on average 0.149 mm. The EPS (Expressed Population Signal) is 0.849, indicating a robust mean value function. The chronology signal expresses the degree to which the chronology portrays the hypothetically perfect chronology (Briffa and Jones 1992).

[3]In the dplR-package rbar.tot. (Bunn *et al.* 2020)
[4]The standard deviation is the square root of the "variance, which is a measure of the scatter of values about the mean" (Fritts 2001).

The *Gleichläufigkeit*[5], a conformance test, exhibits a value of 0.682. For this data set, the value means that in 68.2 % of the cases the tree rings in the respective trees behave similarly. The calculation is achieved by pairwise comparison of all records[6].

[5]The Gleichläufigkeits (wert) is the coefficient of parallel variation. It results from climatically determined pointer years and coincidental synchronous sections. Only when values of both components add up correctly, will the resulting Gleichläufigkeit coefficient exceed random variation (Eckstein and Bauch 1969).
[6]In R Studio the *Gleichläufigkeit* cannot be computed if two curves have less than three years overlap (Bunn *et al.* 2020).

19

*Growth respons-
es of Norway
spruce and cli-
mate change*

Detrending

Tree rings widths are the result of various factors, such as climatically related environmental signals, endogenous and exogenous disturbances, age-size-related trends, and an unexplainable year-to-year variability, which is not related to the signals mentioned (Cook and Briffa 1992). Non-climatic factors are also referred to as *noise* (Fritts 2001). While disturbances such as windthrows occur at a specific point in time, the age- related trends and the climatic influences are continuous components. To analyze the climatic information in the tree rings, the influence of the age of the tree needs to be considered. Younger, fast-growing trees produce wider rings, while at a later stage tree rings tend to become smaller. Because of this trend in tree growth, it is important to remove the age impact from the measurements. The correction of ring width between ages is referred to as *standardization.* The values produced are called *ring-width indices.* As a result of this process, the higher variability of the juvenile section and the more mature section of the tree with a smaller variability in ring width is made comparable (Fritts 2001). The process of standardization is described by Fritts as follows (2001):

"A growth function of some form is fitted to each measured radius by means of a curve-fitting computer-technique [...] Different curves from different specimens may be specified by using appropriate computer [methods]. Standardization is accomplished by dividing the ring width by the value of the fitted curve for the particular year, which removes the systematic changes in ring-width values associated with increasing tree age. The resulting indices from all rings formed in each year are averaged to obtain a mean index chronology for individual [...] sites."

For this study, the standardization functions of the dplR package were used. The removal of the natural growth trends in RStudio's package dplR is called *detrending*. A mean curve of all

trees was produced from the individual bi-weighted mean curves and then standardized. Out of the six available methods in the dplR package for detrending tree ring series, the following were implemented: Smoothing Spline, Negative Exponential Curve and Friedman's Super Smoother (Fig. 10). The standardization is accomplished by "dividing each [of the] series by the growth trend to produce units in the dimensionless ring width index" (Bunn *et al.* 2020). Different detrending methods highlight different characteristics, which will be explained in further detail in insights to the methods. In the top left the mean curve of the raw series is shown in grey and the detrended curves are assembled in one diagram. The mean curve shows that there are two groups of trees in terms of age. That is, mature and juvenile trees, affecting the shape of the curve. There are older trees, of up to 299 years of age. Trees number 3, 4, 13, 14 and 15 belong to this group. There is also a group of more juvenile trees, including samples 1, 2, 5, 7, 8, 9, 11 and 12. The variability in age of the samples explains the two segments of juvenile growth peaks reaching up to 0.2 mm, while the mature growth of the first group attains minimum values of 0.05 mm between the ages of 150 and 200 years. Thus, the trend of declining growth with increasing age is apparent from the mean curve. This is the common biological age trend of a tree. This trend is removed by standardization.

On the top right the implementation of the Smoothing Spline [7] (method = "Spline") is displayed. The method uses a spline with the frequency response of 0,5[8] at a wavelength 0,67* "series length in years" (Bunn *et al.* 2020). Such a spline reduces the amplitude of waveforms having a period of 67 years by 50 %. When wavelengths consist of cycles longer than 8 years, variations can be defined as a low-frequency variance. Such long-term
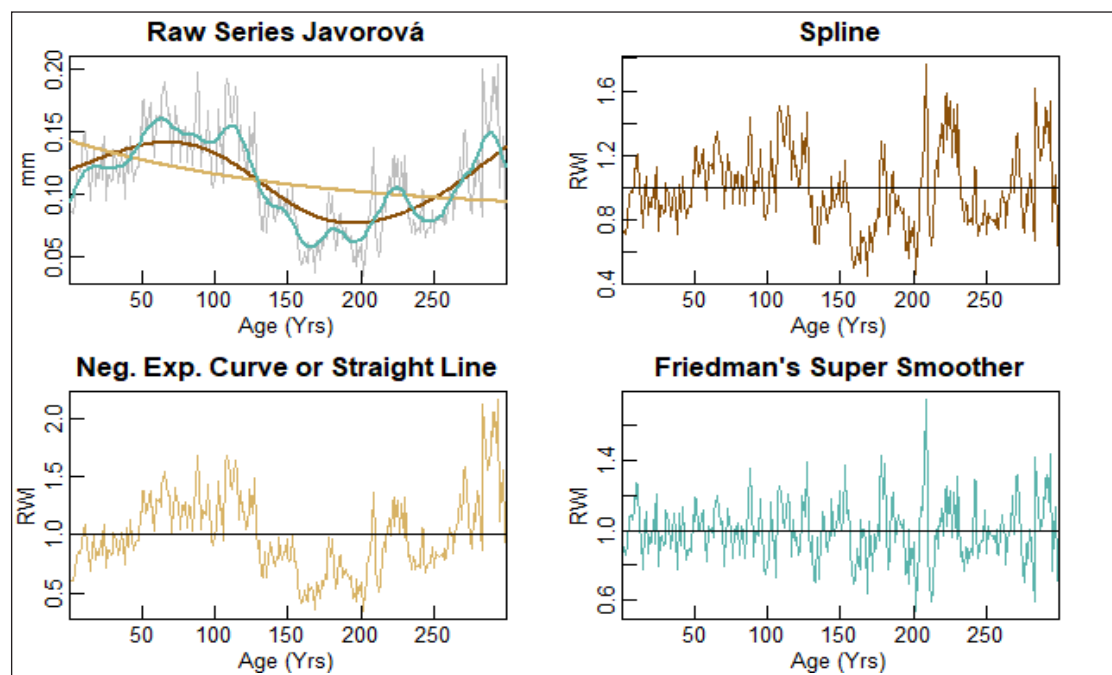

Fig. 10. Raw mean curve and tree width indices produced by applying three different standardization methods: Smoothing Spline (top right), Negative Exponential Curve (bottom left) and Friedman's Super Smoother (bottom right)

variations usually originate from changes in the environment, including long-term variations in climate (Fritts 2001). As a result, the standardized curve still contains the long-term variations in climate but has eliminated the short-term climate signals.

[7]Splines are used in statistics to mathematically reproduce flexible shapes. Points, where adjacent functional pieces join each other, are placed among the mean curve (Perperoglou *et al.* 2019).
[8]The frequency response filter determines the degree of smoothness of the filter. At a 0.5 (or 50 %) frequency response cut-off, 50 % of the amplitude of a signal, in this case the age impact, is retained (Cook *et al.* 1992).
[9]The wavelengths are cycles (Fritts 2001); here 67-year cycles are used for the detrending.

The detrending method with a modified negative exponential curve (method = "ModNegExp"), which can be found on the bottom left of Fig. 10, uses a deterministic growth trend model (Cook *et al.* 1992). The modified exponential curve has been found suitable for detrending conifers because it "approximates the various parabolic, hyperbolic, and logarithmic forms and resembles the declining rate in the conifer biological growth function" (Fritts 2001).

Friedman's Super Smoother (method = "Friedman") is the last method applied. The method uses a non-parametric regression estimator to remove the biological growth trend. In comparison to the Smoothing Spline method, not only the long-term but also the short-term climate signals are included in the resulting indices. As a result, more sensitive curve amplifications are not lost during detrending. Short-term climate signals are thus emphasized.

All the methods above produced indices that have no linear trend and a mean value of one. The detrending process is visible in the standard deviation values of the computed indices. The standard deviation values have decreased. Previously, the mean annual growth was 0.111 mm and the standard deviation was 0.038 mm. For the detrended curves indices, which are measured in dimensionless units and have a mean of 1, the following standard deviations were calculated: The Spline Curve has a standard deviation of 0.236, the Negative Exponential Curve Mean, 0.33 and the Friedman Curve, 0.166. However, it must be noted that standardization methods can over-filter. Due to the long period of time, over which climate changes, long-term effects of climate change may not be distinguished from increasing age. The standardization process will unavoidably "remove some of these long-term growth changes due to low-frequency variations in climate" (Fritts 2001). The Smoothing Spline, as a polynomial curve fitting option, is more flexible and thus more likely to fit and remove some effects of the long-term climatic changes, in contrast to the negative exponential curve fitting option.

These standardized curves now attain the mean chronology without the age impact of all trees, and will be used for further correlations with climatic signals in Section "*Minimum temperature*", "*Maximum temperature*" and "*Impact of precipitation on tree growth*". Before analyzing the growth responses to climatic variables, insight is provided into climatic changes at the Zakopane climate station and at the research site.

Climatic trends

The climate system is complex and comprises the atmosphere, hydrosphere, cryosphere, lithosphere, biosphere, and the interactions amongst these components. To analyze the climate system, it needs to be reduced to a specific climate variable of the climate data corresponding to the parameters associated with tree growth. Conceptualizations in the form of mathematical equations[10] are employed and enable trends to be analyzed (Mudelsee 2019). For this study, minimum and maximum temperatures as well as precipitation were evaluated for the given period; January 1951 to December 2018. A central assumption was that because of global temperature trends, an increase in temperature occurred at the Zakopane climate station during this time as well. There are multiple methods for estimating trend values. In this study, the statistical method of linear regression[11] was applied. This is a common and well-accepted method for estimating, describing, and quantifying the linear component of climate trends. For instance, linear trend modelling is applied in most of the scientific reports included in the IPCC Physical Science Basis on Climate Change Report 2013 (Hartmann *et al.* 2013). In the following, the red trend line represents the regression model for the considered data.

[10]A simple climate equation (Eq.(1)) is described by Mudelsee (2019) as follows:
$$X(i) = X_{trend}(i) + S(i) \times X_{noise}(i) \qquad \text{Eq. 1}$$
where X(i) represents a climate variable, (e.g. temperature), which is decomposed into a trend and a noise component. The center of location for the climate variable X(i) is described via the time-dependent trend component $X_{trend}(i)$. The spread for the climate variable around the trend is described via the time depending scaling function S(i), the variability.
The noise component has a mean zero for E[$_{X_{noise}}(i)$] = 0 for i=1,...,n, where E is the exception operator. and a standard deviation unity.
[11]Mudelsee (2019) describes the linear regression as follows: $X_{trend}(i)$ is described by two parameters, the intercept, β_0, and the slope, β_1.
The model of the linear regression is given by
$$X(i) = \beta_0 + \beta_1 \times T(i) + S(i) \times X_{noise}(i) \qquad \text{Eq. 2}$$
In R Studio the lm() function was applied.

Temperature trends

Using the climatic data provided by the Zakopane station, temperature trends were calculated from the daily measurements for the years between 1951 and 2018. In general, an increase in temperature is evident. In comparison to the globally averaged land-surface air temperature increase between 1951 and 2012, which ranges between 0.18° C and ±0.04° C per decade, or 0.88° C [0.69° C-1.06° C] over half a century, according to the IPCC Report from 2013 (Hartmann *et al.* 2013), the increase in temperature is substantially greater at the Zakopane climate station. The minimum temperatures show a decadal increase of 0.37° C for the same reference period, and a semicentennial increase of 1.83° C. The increase in maximum temperatures is characterized by lower increase values compared to the minimum temperatures, which corresponds to the observation that minimum daily tempera-

tures increase faster than maximum daily temperatures (Hartmann *et al.* 2013). The decadal increase in maximum temperatures at the Zakopane climate station is 0.27° C, which equals a semicentennial increase of 1.37° C. Consequently, over a 50-year period, the mean temperature at the Zakopane climate station has increased 1.60° C, which is almost twice the global land-surface air temperature increase reported by the IPCC. The temperature change in minimum and maximum temperatures is illustrated in Fig. 11. In the following, temperature trends of selected months, seasons, and the growing season will be presented to highlight the finding that the increase in temperature does not occur homogenously throughout the year. The increase in temperature is more pronounced in certain months than in others.

Minimum temperature

The overall increase in minimum temperatures became apparent in the figure above. They increase more quickly than the maximum temperatures. The increase in temperature during the first three months of the year is particularly significant. Over a 50-year time span, the JFM (January, February, March) minimum temperatures increased by 2.65° C, which is equal toa decadal increase of 0.53° C. While the mean JFM minimum temperature was -8.39° C between 1951 and 1961, the mean between 2008 and 2018° C was -5.43° C at the Zakopane climate station (Fig. 12).

The increase in minimum temperatures during the summer months is not as pronounced as during the winter/early spring months. During June, August, and September (JAS) the minimum temperatures increased, having a decadal trend of 0.35° C or 1.75° C over half a century (Fig. 13).

In general the increase in minimum temperatures was found to be the greatest during the winter and spring months, followed by the summer months and the least increase was detected during the fall months. In November, for example, the decadal increase is 0.22° C, which is equal to an increase of 1.11° C over 50 years. In return, this means that the intensity of the temperature rise during JFM is almost double of the fall temperature increase.

Maximum temperature

Maximum temperatures are also increasing rapidly. As mentioned earlier, the total increase in annual mean temperature is 1.37° C over 50 years. In the following, the early year months (JFM), the growing season (GS), and autumn temperatures are going to be analyzed more closely.

From the climate data provided, it becomes apparent that maximum temperatures are increasing steadily during the early season in the time frame considered. While the mean maximum temperature of JFM was 1.57° C between 1951 and 1961, the mean between 2008 and 2018 was 2.74° C. The semicentennial increase in temperature is 1.53° C (Fig. 14).

Unlike the minimum temperatures, the maximum temperatures show the greatest increase during the summer. Here the maximum temperatures of the growing season, which lasts from May
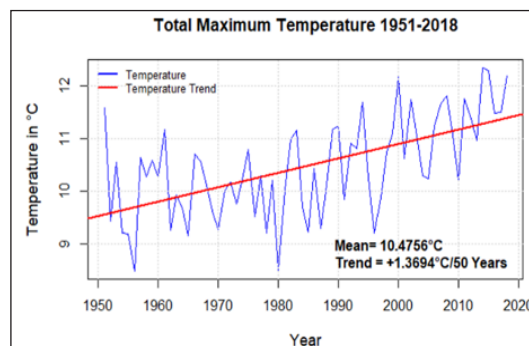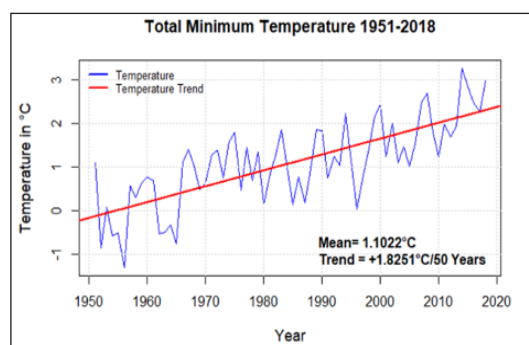

Fig. 11. Minimum and maximum temperature increase at the Zakopane climate station from 1950 to 2018.

Fig. 12. Minimum temperature increase for the months of January, February, and March between 1951 and 2018 at the Zakopane climate station.

Fig. 13. Minimum temperature increase for the months of June, August, and September between 1951 and 2018 at the Zakopane climate station

until August, including the initiation and post-xylem phase, shows the significant decadal increase of 0.36° C or 1.82° C over half a century (Fig. 15). The fall temperatures increased the least, similar to the minimum temperature rise. The decadal in-
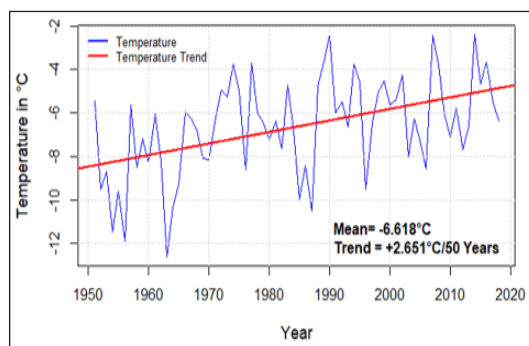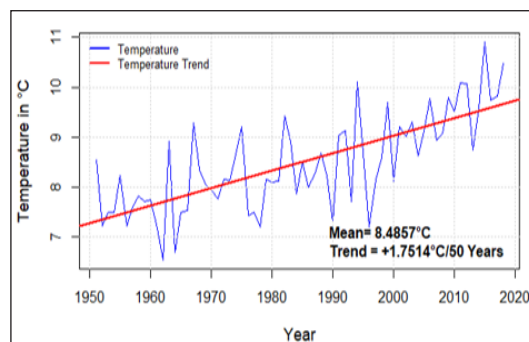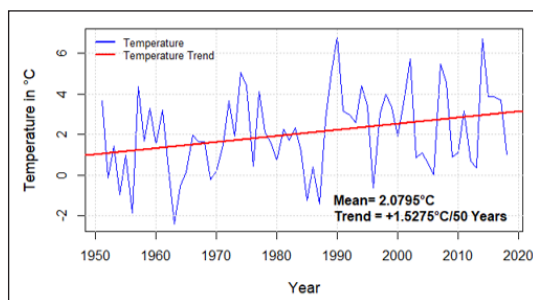
Fig. 14. Maximum temperature increase for the months of January, February, and March between 1951 and 2018 at the Zakopane climate station.
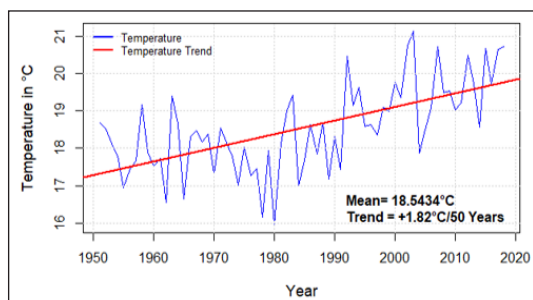

Fig. 15. Maximum temperature increase of the growing season between 1951 and 2018 at the Zakopane climate station.

crease for the months September, October, and November (SON) was 0.12° C, or 0.59° C in 50 years.

Precipitation trends

On a global scale, precipitation trends vary immensely. In the mid-latitudes of the Northern Hemisphere (30° N - 60° N) an increase in precipitation was documented for the period of 1951 to 2008, but the trends are non-significant for the majority of data sets (Hartmann *et al.* 2013: 201f).

The precipitation measures recorded at the Zakopane climate station follow a similarly insignificant positive trend (Fig. 16). The mean precipitation sum over one year is 1131 mm, and shows a decadal increase of +8.2 mm per decade, or +41 mm in 50 years.

In contrast to the temperature trends which were found to increase overall during each month of the year, the precipitation change shows negative trends during certain months. An example would be the month of December, during which the greatest decline in precipitation was found. A downward trend of -13.2 mm was recorded for a 50-year period, which equals a decadal decline of -2.6 mm. A decline in precipitation for the month of April was also found. However, the decrease is very slight, and measures only -1.9 mm in 50 years.

In contrast to rapidly increasing maximum temperatures during the growing season, the precipitation sum has not changed significantly during May through August.

Most months show a slight increase in precipitation, such as February, for which a decadal increase of +0.80 mm was documented. Overall, the Zakopane climate station recorded an insignificant positive increase in snow and rainfall.
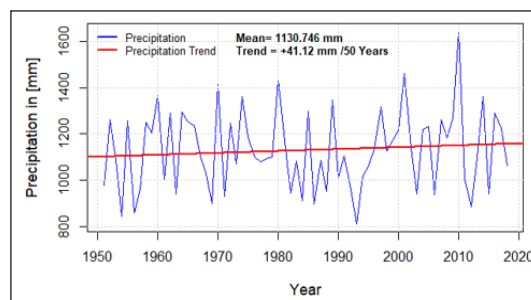

Fig. 16. Total precipitation change between 1951 and 2018 at the Zakopane climate station.

Results

In dendroclimatology, the statistical measure *correlation coefficient* is used to "measure associations between two series [...] such as a chronology from trees and a climatic sequence" (Fritts 2001) to analyze the relationship between tree growth and climatic variables. For this study, the correlation of ring width and the following climate factors were calculated: minimum temperature, maximum temperature, and precipitation. The climate data from Zakopane, presented in the previous point, covers the period from 1951 to 2018. Correlations can be calculated only for the time span for which both climate data and tree ring width measurements exists. Both the climate and tree series have a common axis for the entire 1951 to 2018 period. The growth response of the sampled spruce to climate variables prior to 1951, therefore, cannot be analyzed. For the correlation analysis, the daily data was transformed into monthly averages: monthly mean temperature and monthly sum of precipitation. Correlation calculations are established until 2017, because in addition to the same-year impact, the linkages between the effect of the climatic variables of the previous year on tree growth are considered. The climatic influences of a given year affect the ring width of the following year as well, as growth has a delayed reaction time. The climatic factors influence the level of water or sugar storage, which affects the shoot growth and thus the plant's ability to practice photosynthesis among other processes. In particular, the nutrient-storage and biological processes of the previous-year's growing season are believed to impact the current-year radial growth. This effect is also called the "carry-over effect" (Büntgen *et al.* 2007). This statistic relation is also referred to as *autocorrelation* and is calculated by moving the time axis back one year (Fritts 2001).

The correlation coefficient can range from an upper value of +1, which indicates perfect and direct agreement, to a value of -1, which indicates perfect and inverse agreement. If the two data sets are completely independent or random with respect to one another, the correlation coefficient takes the value zero (Fritts 2001). In the following figures the values of the correlations are displayed as colors. Red signifies a negative correlation, indicating a negative growth response and blue appears when a positive correlation was found, indicating a positive growth response. The color scale with the corresponding values can be found next to the figure. For significant correlations, the value is displayed within the field

23

*Growth respons-
es of Norway
spruce and cli-
mate change*

for which the correlation was found. As the calcula-tion increases in significance, stars are added. Three stars (***) signify very high significance (p < 0.001), two (**) are generated when the p-value is between 0.001 – 0.01, and one star (*) when the p-value is between 0.01 and 0.05 (Warnes *et al.* 2020).

The y-axis shows calculations for each month, starting with January at the bottom. Quarterly cor-relations were also calculated, e.g., for January, Feb-ruary, March (JFM), for April, May, June (AMJ), for July, August, September (JAS), and October, Novem-ber, and December (OND). Furthermore, the influence of a climate signal during the growing season (GS) from May to August, which is includes the initiation and post-xylem phase, is also analyzed. The "Total" bar shows the general response of tree rings to a spe-cific climate variable. The in-year impact is dis-played on the left half of the x-axis and the previous year impact on the right half. The calculations and their portrayal are visibly divided by a bold black line. Both sides show correlation calculations for the raw mean curve, which can be found on the far-left side of both segments, and for the individual de-trended curves, where the curve of the indices was correlated with the climate variable considered.

First, the growth response of the sampled spruces for the whole period, 1951 to 2017, will be presented. After that, the first 33 years and the sec-ond 33 years will be considered separately and put into context with the temperature and precipita-tion changes presented in Sections "*Temperature trends*" and "*Precipitation trends*".

Impact of temperature on tree growth

The ring width of trees at high elevation sites yield the most reliable information on temperature, as they have been shown to respond more sensitively to temperature than trees at low elevations. The cor-relation of temperature and growth tends to increase at high elevations and becomes directly correlated

with growth (Fritts 2001). Therefore, studies that in-vestigate the impact of temperature on tree growth are often located in mountain ranges, such as a study on growth reactions of multiple species in the Pol-ish and Slovakian Tatra Mountains (Büntgen *et al.* 2007), or temperature reconstructions for Central Europe using tree ring proxies from the Tatra Moun-tains (Büntgen *et al.* 2015), or high elevation studies in the Alpine region (Hartl-Meier *et al.* 2014).

In the following sections, the relationship be-tween minimum and maximum temperatures and tree growth at the Javorová site will be examined.

Minimum temperature

Low temperatures can be especially limiting to tree growth, as they impact the tree's ability to practice respiration and assimilation in the cambium as well as other biochemical processes that are essential for growth (Fritts 2001). Low air temperatures are in fact believed to be the most limiting factor of cell production at high altitudes (Solár 2013). At high el-evation sites, temperatures are cooler than at lower elevations for multiple reasons, one being the de-crease in air pressure. Cooler temperatures thus persist for a longer time at high elevation sites, which results in a shorter growing season (Fig. 17).

The limiting effect of low temperatures on growth is apparent in the samples taken at the Javorová site. As expected, low temperatures are generally limiting to tree growth, as evidenced by the fact that negative correlations with high and very high significance were calculated. The impact of the pre-vious year is found to be more significant than the same-year impact. The previous-year correla-tion reaches values up to -0.66*** and the same year up to -0.57***. Correlations using the Friedman Curve, which includes short-cyclical climate vari-ability, produce the least significant correlations. The month of March, especially the previous year correlation, returns values with very high sig-

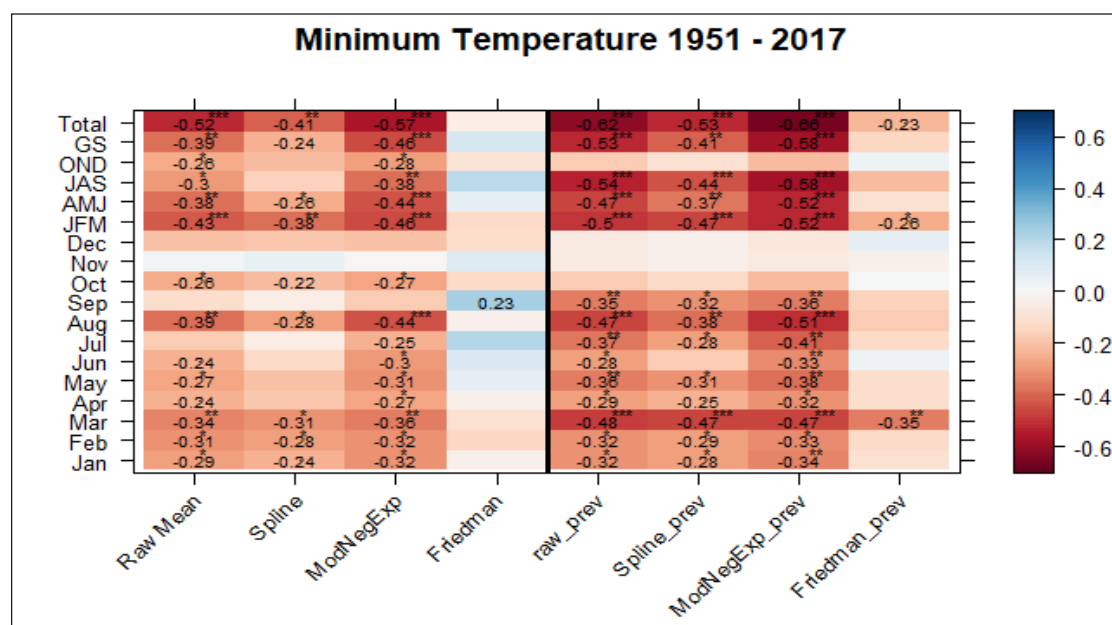

Fig. 17. Growth response to minimum temperatures in the period from 1951 to 2017, GS = growing season, OND = Oc-tober, November, December, JAS = July, August, September, AMJ = April, May, June, JFM = January, February, March.

nificance up to -0.48***. The same-year impact is of high significance and reaches values up to -0.36**. The tendency of chronologies from higher elevations showing negative responses to March and April temperatures is common and can be found in other studies of the Tatra region such as Büntgen *et al*'s study on multiple tree species of 2007.

Low temperatures during early spring affect the initiation phase of cambial activity, which is increased when the trees are located on a north-facing slope (Fritts 2001). The Javorová site is north-east facing, which suggests that the exposure to less sunlight during these early months may impact the initiation phase as well. The correlation results support this assumption.

For the month of August, tree ring width correlates significantly with respect to previous-year and same-year calculations, with previous year correlations up to -0.47*** and same year correlations up to -0.39**. The limiting effect of low temperatures to tree growth during the growing season becomes especially clear here. The growing season is short at high elevation sites, and during the growing season, low temperatures impact the radial growth significantly, producing narrower rings (Fritts 2001). During August, the growing season comes to an end at high elevation sites, as the tree is in the post-xylem phase. The correlation calculations between the GS and minimum temperatures highlight these points. The previous-year impact is particularly visible, and the same-year correlations show highly negative and significant responses up to -0.46***.

The only month for which a slightly positive correlation between tree growth and minimum temperatures was found is the month of November. Nevertheless, the correlation is insignificant.

In conclusion, with regard to minimum temperatures, the correlation analysis supports commonly accepted knowledge that low temperatures limit tree growth significantly. Because of this fact, some studies suggest that warming in the montane forest ecosystem might favor tree growth (Savva *et al.* 2006; Hartl-Meier 2014). As presented in "*Minimum temperature*", minimum temperatures are increasing rapidly in the High Tatras Mountain region.

In the following, the time series was split in half and correlated with the corresponding tree rings. The minimum temperatures during the period be-

tween 1984 and 2017 is tendentially higher than during the first period. While the mean minimum temperature during the period 1951-1983 was 0.56° C, the mean of the second period from 1984 to 2017 was 1.61° C. The comparison of the growth response presented in Fig. 18 gives an insight into the impact of climate change on the growth response of the sampled spruce at the highest elevation site of the Javorová valley. A general shift to more positive responses to minimum temperatures is evident. Tree ring widths correlated negatively with high significance (between -0.42* and -0.48**) with same-year minimum temperatures and even more distinctly with values of the previous-year impact (between -0.44** and -0.64***). However, overall, between 1951 and 1983, the overall impact of minimum temperatures is insignificant and only slightly negative for the period from 1984 to 2017. A similar shift in growth response was found for the winter/early spring months (JFM). During the first period, the previously mentioned negative response to early year JFM minimum temperatures is found to be strongly negative and significant, -0.49* and -0.52**. For the second period however, the correlation calculation yields insignificant values for the same-year and previous-year impact. These results, which yielded the most rapid increase (2.65° C in 50 years), suggest that the rapid increase in minimum temperatures during these months favors tree growth.

During the previously mentioned month of August, for which a negative growth response was found for the whole time span, the warming seems to positively impact tree growth response. The post-xylem phase might be less interrupted by low temperatures because of this warming.
However, the shift to more positive responses to minimum temperatures is not evident for every month. For instance, the tree ring widths correlated with November minimum temperatures were found to return positive values during the first period and slightly negative values in the second.

Overall, the findings suggest that the spruce sampled, generally respond positively to increasing minimum temperatures and will further benefit from increasing minimum temperatures. This assumption corresponds to the findings in a study on growth response of Norway spruce in the Polish Tatra Mountains (Savva *et al.* 2006).
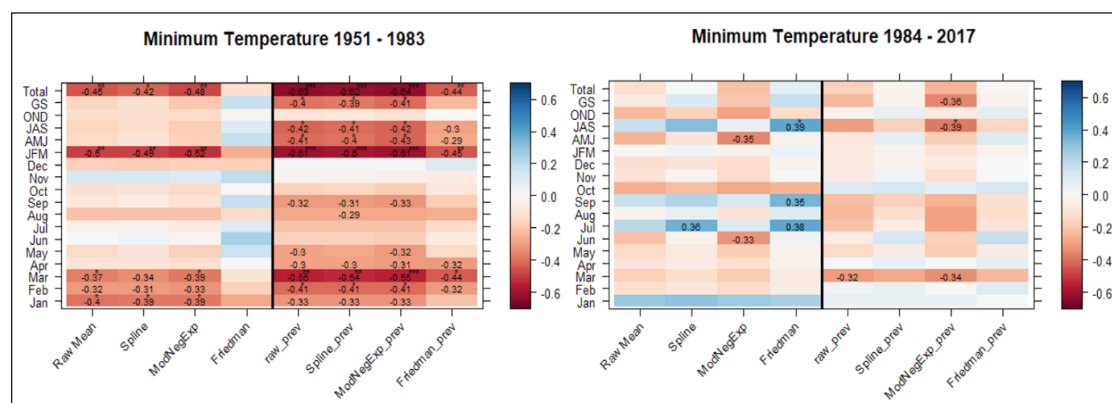

Fig. 18. Shift of growth responses to minimum temperatures from 1951 to 1983 and 1984 to 2017, GS = growing season, OND = October, November, December, JAS = July, August, September, AMJ = April, May, June, JFM = January, February, March.

However, certain studies (Büntgen *et al.* 2007) imply that snow cover has a protective function as well. Higher temperatures prior to the growing season may result in desiccation due to the shrinking of the protective snow cover from frost during later months and is considered as an important moisture source at the beginning of the growing season. Rising minimum temperatures may result in an increase in transpiration rates, which can also limit tree growth.

Maximum temperature

In the following section, the maximum temperature was correlated with tree ring width. The significance of the impact that previous-year temperature has on tree growth can be seen clearly on the right side of the diagram, indicating more significant correlations than found with the same-year influence. Like the analysis of the minimum temperature and growth response, the Friedman Curve shows the most positive correlation between tree ring width and maximum temperature. The general response of tree rings to maximum temperatures, which can be found at the top, shows significant negative values for each calculation of the previous-year impact, producing values between -0.25 and -0.45***. The same-year impact is not as significant but also points out negative correlations between maximum temperatures and the formation of tree rings, except for the detrended curve using the Friedman method, which is known to emphasize high-frequency, and thus short-cyclical variations.

Negative correlations can be found for the maximum temperatures, which are similar to the impact of minimum temperatures during the winter and early spring months on tree ring width. The correlation calculations yield values between -0.26* and -0.29* for the same-year, and -0.3* and -0.39** for the previous-year impact.

The correlation between tree ring width and maximum temperature was especially significant for the month of March. The previous-year impact was the highest for this month, with negative values between -0.36** and -0.42***. These results correspond to previous findings of negative correlations between tree ring width and early spring temperatures, and likely reflect the protective character of winter snow cover at high elevations (Büntgen *et al.* 2007).

At high elevations, trees commonly respond positively to temperatures during the summer months of June and July (Büntgen *et al.* 2007; Kaczka and Büntgen 2006; Kaczka *et al.* 2016). At the Javorová site, only the high-frequency indices generated using the Friedman method responded positively and with high significance (0.43***) to maximum temperatures during the month of July of the same year, in the period between 1951 and 2017 (Fig. 19). The positive effect of temperature in July of the same year can also be found for the remaining curves, but only the Spline curve yields a significant value of 0.23, while the other calculations are insignificant. The month of June does not show any significant positive response.

The extent to which these summer month temperatures correlate positively with tree ring width is far lower than comparable studies in the High Tatra Mountains, where positive correlations were found of up to 0.62 (Büntgen et al. 2007), 0.55-0.6 (Kaczka *et al.* 2016) and 0.5-0.6 (Kaczka and Büntgen 2006). Thus, the common growth response of *Picea abies* (L.) Karst to summer temperatures during the peak of the growing season (June-July), which was also observed in other Alpines regions (Frank and Esper 2005), cannot be observed to the same extent at the site in the Javorová valley for the period studied.

In August, when tree ring formation comes to an end, tree rings from the Javorová site respond negatively to maximum temperatures. Values from -0.22 and -0.25* occur for same-year and -0.27* to -0.3* for previous-year impact. This could be related to increasing water stress as temperature increases during summer months, but precipitation does not increase significantly. A different explanation could be the cooler conditions of north-facing
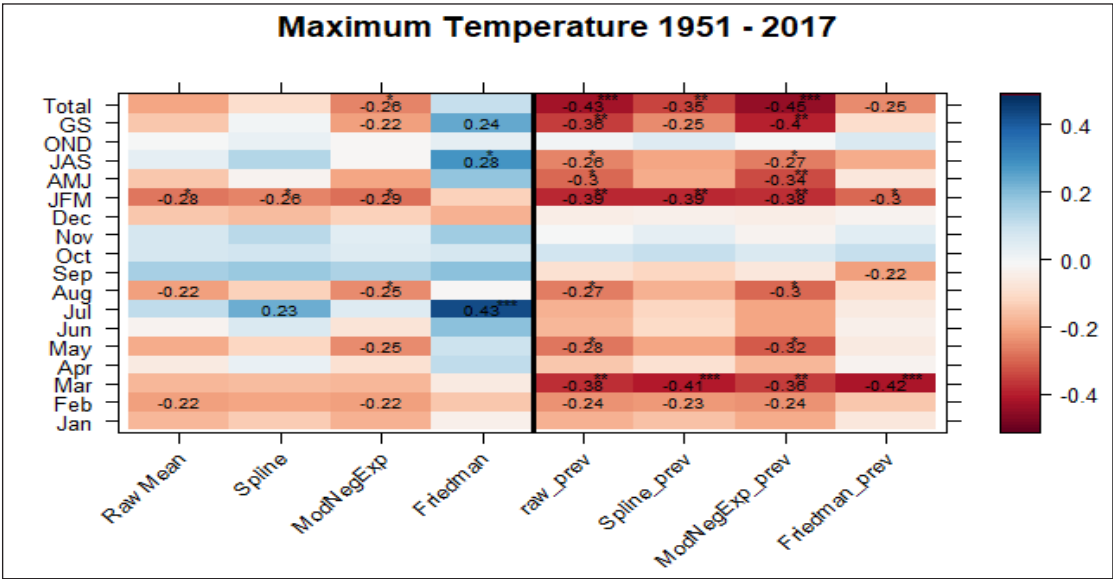

Fig. 19. Growth response to maximum temperatures in the period from 1951 to 2017, GS = growing season, OND = October, November, December, JAS = July, August, September, AMJ = April, May, June, JFM = January, February, March.

slopes, where maximum temperatures are not as warm as expected. This assumption was suggested in the Büntgen *et al.* study from 2007, in which August temperatures were not correlated positively with tree ring width in the Tatra Mountains.

Positive correlations were found for September through November of the same year. Although a positive impact of late summer and autumn temperatures is visible, it is not significant at this site and does not exceed a correlation value of 0.19. In other studies on coniferous mountain species, autumn temperatures of the previous-year impacted tree growth more significantly (Oberhuber 2004; Frank and Esper 2005; Kaczka and Büntgen 2006; Büntgen *et al.* 2007). The trees from the Javorová site respond only slightly positively to previous-year autumn temperatures. Growth reactions to autumn temperatures suggest mild conditions, and likely support carbon storage, and post-xylogenetic activities, while promoting root growth, as well as supporting the maturation of needles, shoots and buds, and preventing soil from freezing (Oberhuber 2004; Kaczka and Büntgen 2006; Büntgen *et al.* 2007).

The comparison of the first and second periods' response to maximum temperatures is in marked contrast to the response shift in minimum temperatures. While the response of these spruce was predominantly positive to same-year maximum temperatures from 1951 to 1983, the growth reaction was less pronounced or even reversed in the second period between 1984 and 2017 (Fig. 20). The change of the growth response to maximum June-July temperatures is particularly significant. The positive response of high elevation spruce trees to warm summer temperatures is very common earlier and can be found in various studies (Frank and Esper 2005; Kaczka and Büntgen 2006; Büntgen *et al.* 2007; Hartl-Meier 2014; Kaczka *et al.* 2016). During the first period, the trees responded positively to both June and July temperatures, yielding positive correlations between +0.29 and +0.45**. As presented in "*Maximum temperature*", the increase in maximum temperatures is especially pronounced during the summer months. For the months of June and July, the semicentennial trend measures 1.56° C. While the mean maximum temperature for June-July during the period from 1951 to 1983 was 18.8° C, it was 20.0° C during the period from 1984 to 2017. During the second period, the response to June tem-

peratures was found to be negative, and the response to July temperatures was less positive and significant. Only the correlation with the Friedman curve shows an increase, returning a value of +0.53**.

The shift of positive response to negative response over time is evident for the entire growing season. During the first period, positive responses were found for all curves, reaching values between +0.32 and +0.44*; during the second period, the correlations for the same-year impact are found to be less positive, insignificant, or even negative. Furthermore, during the first period, tree ring width responded without any significance to previous-year temperatures during the growing season, while during the second period they had a negative impact.

These findings suggest that spruce react negatively to rapidly increasing maximum temperatures, particularly during summer months, when temperatures increased steadily, while precipitation sums only increased marginally. This trend might cause water stress, thus limiting tree growth. These findings are in strong contrast to the findings of Savva *et al.* (2006), where increased radial growth was especially associated with an increase in summer temperatures.

On the other hand, a shift toward less negative or even positive response to early year maximum temperatures can be found as well. The same-year response of JFM temperatures yield values of up to -0.33 during the first period, but during the second period there is no significant or positive correlation for the month of January. The change in previous-year correlations is even more pronounced. While the response to previous year JFM temperatures and tree growth was found to be strongly negative and highly significant, with values from -0.48** to -0.5**, they are only slightly negative and insignificant for the second period. This finding corresponds to the results that were found for the change in minimum temperatures and suggest that spruce in the Javorová valley benefit from increasing early season temperatures. As mentioned in the analysis of temperature change, the maximum temperatures during the months of JFM increase significantly, with a semicentennial trend of 1.53° C.

Impact of precipitation on tree growth

The availability of water is an essential factor for tree growth. The more precipitation there is, the more
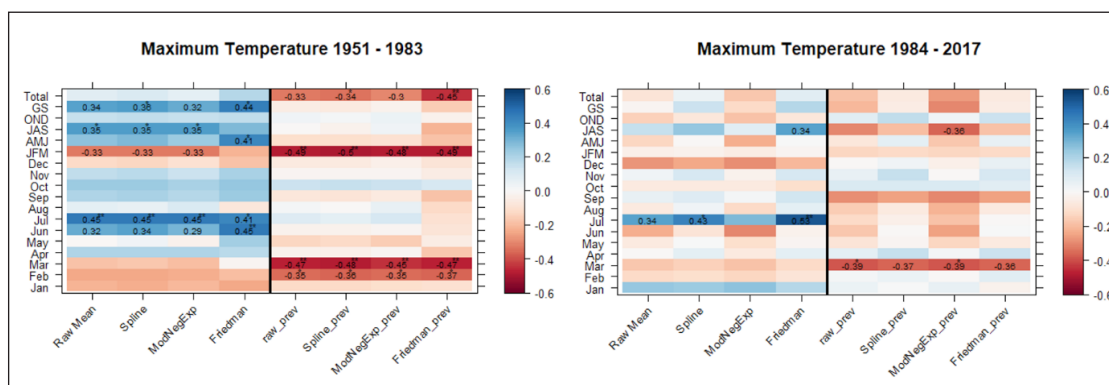

Fig. 20. Shift of growth responses to maximum temperatures from 1951 to 1983 and 1984 to 2017, GS = growing season, OND = October, November, December, JAS = July, August, September, AMJ = April, May, June, JFM = January, February, March.

saturated the soil becomes and thus a longer period may pass until water stress can impact tree growth negatively (Fritts 2001). As shown in the climate diagram (Fig. 4), the site is not affected by water stress at any given point in the year.

In contrast to temperature, precipitation tends to have a less significant impact on tree growth at high elevation sites (Fritts 2001). The correlation coefficient tends as a result to show less significant values. Fig. 21 below shows that the influence of the same-year availability of water has a greater effect on the tree's ring width than does the precipitation of the previous year greater effect on the tree's ring width than does the precipitation of the previous year.

Positive responses to winter precipitation (December and January) and early spring (JFM, consisting of snowfall), are apparent. This response is frequently found at high elevation sites. The snow that falls during the winter months is believed to protect the surface below from frost in the spring, and is an important water source during the initiation phase (Büntgen *et al.* 2006). The response to early spring precipitation in March was similarly positive, indicating the importance of water being supplied during the first part of the growing season. This is a common response of high elevation trees and can be found in a range of dendrochronological studies (Oberhuber 2007; Büntgen *et al.* 2007).

In contrast, the tree ring width and April and May precipitation correlated negatively. An explanation for this inverse relationship between precipitation and ring width may be that during these months, precipitation is generally expressed as snow at high elevation sites such as the Javorová site. Snow at this part of the growing season is shown to be limiting to tree growth, as it extends the length of the photosynthetically inactive period and delays the beginning of the growing season (Fritts 2001).

The response of tree ring widths to summer precipitation is ambiguous. While June and August precipitation correlates positively, July and September correlations are negative. From a quarterly perspective, April, May, and June (AMJ) correlated insignificantly negatively with an average of -0.08, while July, August, and September (JAS) correlated negatively with an average of -0.2. Negative correlations of summer precipitation are a feature found in other studies in the Tatra Mountains (Büntgen *et al.* 2007) and the Alpine region (Hartl-Meier *et al.* 2014). While the most limited amount of precipitation usually falls in June (Kaczka *et al.* 2016), the trees at the Javorová site responded positively to early summer precipitation and negatively to mid-summer precipitation in July. Precipitation at high elevation sites, can still occur as snowfall, and limit tree growth, even when maximum temperatures are reached in the summer months.

Overall, common feature of trees from high elevation sites responded negatively to precipitation during the growing season at the Javorová site, but during the studied period, between 1951 and 2017, only insignificant values (between -0.05 and -0.22) were found.

The response of tree ring width to precipitation is analyzed over time. The period from 1951 to 1983 is presented on the left and the period from 1984 to 2017 on the right (Fig. 22). As shown in Section "*Precipitation trends*", precipitation increases +41 mm over 50 years. During the first period, the trees responded more negatively to precipitation during the growing season, with values ranging between -0.31 and -0.41*, which is, as mentioned above, common for high elevation trees. However, during the second period, from 1984 to 2017, their response was insignificant. The precipitation sum did not change significantly during the growing season (May, June, July, and August); an increase of +6.9 mm was recorded for all months over the 50-year period. The shift toward a more positive response might be linked to increasing maximum temperatures during the summer, which promote evaporation.

The common positive response to snowfall during winter/early spring (JFM) can easily be de-
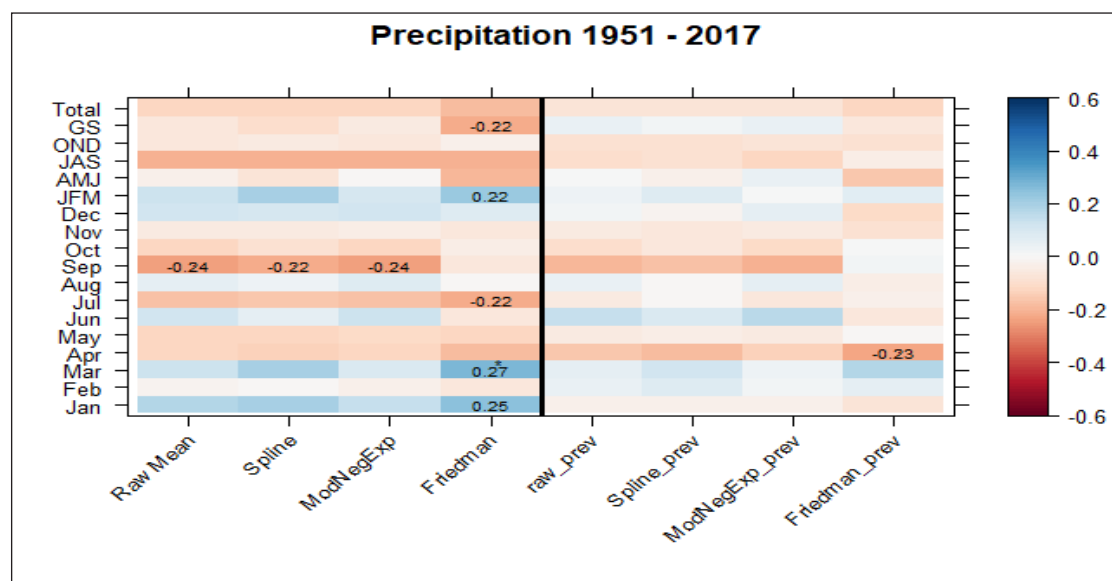

Fig. 21. Growth response to precipitation in the period from 1951 to 2017, GS = growing season, OND = October, November, December, JAS = July, August, September, AMJ = April, May, June, JFM = January, February, March.

Fig. 22. Shift of growth responses to precipitation in the period from 1951 to 1983 and 1984 to 2017, GS = growing season, OND = October, November, December, JAS = July, August, September, AMJ = April, May, June, JFM = January, February, March.
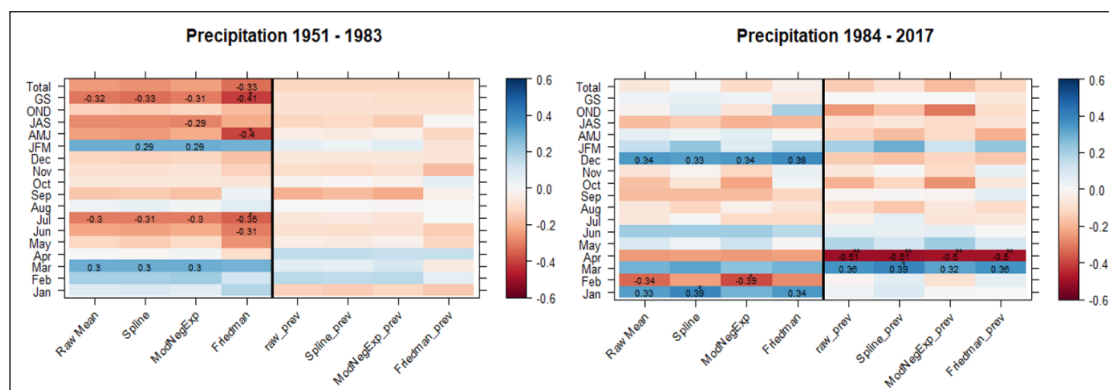
tected for the first period. This finding supports the assumption that the snow cover serves as protection from desiccation and increased transpiration rates of needles and shoots. During the second period the response is still positive but no longer significant. The temperatures during the winter and early spring (JFM) months increase rapidly, causing the snow to melt earlier during the year and diminishing this protective cover.

As shown in Section "*Precipitation trends*", precipitation sums have been declining in the month of December, while temperatures have increased. The correlation analysis shows that from 1951 to 1983, trees responded slightly negatively to December precipitation, but responded positively during the second period, between 1984 and 2017; reaching values between +0.33 and +0.38.

Another shift in the response over time is visible for the month of April. Precipitation sums decreased only marginally, by -1.9 mm in 50 years, however, the response turned highly negative for the second period, especially for the previous-year calculations. Increasing temperatures at the beginning of the year drive early snow-melt and prevent snow accumulation.

In general, the second period deviates from the usual pattern of growth response of high elevation trees to precipitation (Büntgen *et al.* 2007). However, the change in precipitation sums has changed only slightly. This finding suggests that the upcoming climatic changes have an uncertain effect on high elevation tree stands.

Discussion and Conclusion

The present analysis supports the commonly accepted knowledge on growth responses of high elevation trees to climate signals in a range of points, including high temperature sensitivity and medium responsiveness to precipitation.

Significant negative responses to winter and early spring (JFM) temperatures underline the high sensitivity toward temperature (Fritts 2001) and the suggestion that snow cover has a protective function for high elevation tree stands (Büntgen *et al.* 2007).

The positive response to June and July temperatures is consistent with previously published studies researching growth responses of mountain forest stands to temperature (Fritts 2001; Kaczka and Büntgen 2006; Büntgen *et al.* 2007; Kaczka *et al.* 2016). However, the response to summer temperatures was more pronounced in the period from 1951 to 1983 than in the period from 1984 to 2018. Findings (Savva *et al.* 2006; Hartl-Meier *et al.* 2014) that increasing temperatures benefit the subalpine spruce stands could not be recognized in the shift of growth response to maximum temperatures during the growing season at the Javorová site. In fact, the positive response to maximum summer temperatures was reversed for the second period, indicating that warming limits the tree's productivity in forming tree rings after a certain point. This observation supports the assumption that the growth of high elevation trees does not follow an upward linear trend corresponding to increasing photosynthesis and can even be reversed (Büntgen *et al.* 2007).

On the other hand, the shift to less negative impacts of minimal temperatures supports this proposition (Hartl-Meier *et al.* 2014) to a certain extent. Further observations are recommended to evaluate the impact that increasing temperatures have on the Javorová spruce stand.

Temperature is not the sole factor determining the productivity of high elevation tree ring formation. Precipitation influences the xylem formation as well, and the following common features of growth response to precipitation were found at the Javorová site:

Positive response to March precipitation supports previous findings on the importance of sufficient water the start of growing season (Oberhuber 2007; Büntgen *et al.* 2007). Additionally, the common observation that high elevation tree stands respond negatively to precipitation during the summer months was also found at the Javorová site (Büntgen *et al.* 2007; Hartl-Meier *et al.* 2014).

The High Tatra Mountains experience a distinct temperature increase that exceeds the global average surface air temperature increase. This analysis of the response of tree ring width to climate signals shows favorable and unfavorable developments regarding selected climate variables. On the one hand, a shift toward a more positive response to increasing minimal temperatures was found, but on the other hand, the trees at the Javorová site showed a shift toward a more negative response to increasing maximum temperatures.

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A simple prognosis for the future vitality of the sub-alpine spruce forest stand based on the growth response to certain climate variables cannot be given. For continuous healthy tree ring formation, a combination of temperature, precipitation and the timing of snow-melt needs to occur together (Büntgen *et al.* 2007). Even while positive effects on radial growth may be found due to increasing temperatures, the effects of climate change can impact the forest ecosystem in multiple biotic and abiotic ways. A higher frequency and intensity of insect outbreaks and windstorms are likely to occur (Hartl-Meier 2014).

Wind disturbances are one of the most destructive disturbances affecting European mountain forests. In the past 50 years, 1 million hectares of forest area was affected by windstorms in western and central Europe. However, disturbances are part of the natural regeneration cycle and a natural thinning can promote the regeneration of more light-demanding tree species such as the European larch (*Larix decidua*) in contrast to the overly represented Norway spruce in the forest ecosystem (Zielonka and Malcher 2009).

However, wind disturbances can affect spruce stands post-event, as windblown and windfallen trees are hotspots for bark beetles. From 1994 to 1997 there was a bark beetle outbreak in both Tatra National Parks, the Polish Tatrzanski Park Narodowy (TNP) and the Slovak Tatranský Národný Park (TANAP). Tree mortality was found to be linked to previous wind damage, as the damaged trees served as a breeding ground for bark beetles, which attacked the surrounding tree stands (Grodzki *et al.* 2003). The approaches to managing the outbreak were very different in the two national parks, as the Slovak management applied classical pest management techniques, such as pheromone traps and sanitary cutting as well as log debarking, while sanitary protection measures were not allowed in the TNP because of its nature protection status. The outbreak collapsed in 1997, not because of the measures taken on the Slovak side but because of a period of cold, wet summers, according to Grodzki *et al.* (2003). Nevertheless, the threat of bark beetles continues today. A more recent study on the effectiveness of pheromone traps in the TANAP blames the current bark beetle infestation partially on the lack of management action on the Polish side, where bark beetle populations are extremely high and human interference is prohibited (Galko *et al.* 2013). The Javorová valley in particular is primarily affected by two spruce bark beetle species: *Ips typographus*, also known as the European spruce bark beetle and *Pityogenes chalcographus*, the smaller European spruce bark beetle. The situation in the Javorová valley has reached an epidemic level according to Galko *et al.* (2013). Although 1.6 million insects were caught using 40 traps in 2012, the epidemic does not seem to be containable.

Continuous observations on tree vitality and further studies on growth responses should be supported to establish more knowledge on the effects of climate change on ecosystems. Further investigation on the change in the precipitation regime should be considered when analyzing water availability in connection with tree growth.

In addition to tree ring analysis, the upward expansion of mountain forests is an indicator of climate change and is reported from high mountain eco-systems around the world, as well as in the Southern Carpathians (Solár 2013). Further research in this area could focus on whether this trend is expressed in stands of Norway spruce (*Picea abies*) in the Javorová valley due to climate change.

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Appendix

Field notes.

Tree-ID	Species	Drilling hight (cm)	Circumfence (cm)	Included/Excluded
I 1	*Picea abies*	140	160	Included
I 2	*Picea abies*	141	146	Included
I 3	*Picea abies*	129	127	Included
I 4	*Picea abies*	133	107	Included
I 5	*Picea abies*	117	133	Included
I 6	*Picea abies*	119	155	Excluded
I 7	*Picea abies*	134	146	Included
I 8	*Picea abies*	74	184	Included
I 9	*Picea abies*	121	137	Included
I 10	*Picea abies*	109	168	Excluded
I 11	*Picea abies*	107	151	Included
I 12	*Picea abies*	109	132	Included
I 13	*Picea abies*	70	170	Included
I 14	*Picea abies*	150	140	Included
I 15	*Picea abies*	90	137	Included

Feral pigeon melanism may vary with local climate; an example from the West Carpathians

V. KINASOVÁ, M. JANIGA and J. SOLÁR

Institute of High Mountain Biology, Žilina University, Tatranská Javorina 7, SK-059 56, Slovak Republic; e-mail: solar@uniza.sk

Abstract. Local pigeon populations surveyed in Slovak towns are intricately linked to the anthropogenic environment of their particular habitat. In the past, this has generally been more limited to historical, commercial areas, and agricultural areas, but more recently, pigeons are also expanding into newly built neighbourhoods and housing estates. The group of melanic pigeons was largely dominant in terms of abundance in 1998 and 1999 (in 1998 its lowest abundance was 42 %, and in 1999, 49 %). The second most numerous was the blue-bar phenotype, whose abundance ranged from 15 to 40 % in 1998 and from 17 to 34 % in 1999. The group of red and brown pigeons was the least numerous. The relationship between altitude and the abundance of the individual phenotypes was statistically significant only in the case of the melanic group. When examining the influence of weather factors, it was statistically proven that more melanic pigeons were found in mountainous areas with lower temperatures, higher humidity and precipitation. On the other hand, the abundance of pigeons with red plumage is statistically significantly higher in conditions of warm but humid weather in lower-lying urban areas.

Key words: feral pigeons, phenotype, abundance, melanism, Slovakia

Introduction

In all places where feral pigeon populations exist, a feather polymorphism has developed (Murton *et al.* 1973). According to Dunmore (1968), at least 20 colours and patterns were recorded in populations of the rock pigeon *Columba livia* L., which were well described by Levi (1963). Domestic pigeons also have a large variability of colours and patterns, which are characterised by human selection. Therefore, the variability of colour and pattern in feral pigeons is the result of an interaction between repeated mutations, and stems directly from their domestic ancestors (Podhradský 1953;

Hollander 1983; Johnston and Janiga 1995) as well as selection pressure (Cole 1969). Variability in feral pigeon populations could be also partially affected by mixing with messenger pigeons (Leiss and Haag-Wackernagel 1999). Generally, feral pigeons have two or three times higher genetic variability than other bird species and likely have the highest known colour variability among wild birds (Johnston and Janiga 1995), as well as diversity, which results from the actions of pigeon breeders (Murton *et al.* 1973). Different colour and pattern variants are associated with different ecological and physiological properties (Murton *et al.* 1973, Janiga 1991a, Johnston and Janiga 1995) such as long-lasting conditions that have the effect of limiting the ability to form pigment in the body or fission of chromatophores (Podhradský 1953).

The default type for colour deviations is the plumage pattern of the wild rock pigeon *Columba livia* L. (Podhradský 1953; Malík and Štefka 1970; Havlín 1983; Tureček 1985). It has greyish-blue wings, the chest is medium grey, lighter on the abdomen, and the feathers on the neck have a green-violet metallic lustre. The lower part of the back (coccyx) is white. Two black parallel bands stretch across the wings and the tail feathers are bluish-grey with a black band. The claws and beak are black, and the leg feathers are bluish-grey. The iris is orange-red with a blue-grey orbital ring (Podhradský 1953). This default rock pigeon plumage colour pattern is called blue-bar or wild type among geneticists and breeders (Podhradský 1953; Lofts *et al.* 1966; Dunmore 1968; Cole 1969; Murton *et al.* 1973; Hollander 1975; Ferianc 1982; Hollander 1983; Janiga 1991a; Johnston and Janiga 1995; Leiss and Haag-Wackernagel 1999). It has a black pigment (eumelanin) deposited in the form of microscopic granules which are produced by specialized melanocytes (Hollander 1983).

The overall plumage of a pigeon is composed of three factors; basic colour, basic pattern, (Ferianc 1982; Johnston and Janiga 1995) and additional factors (Gibson 1995). According to Johnston and Janiga (1995) and Leiss and Haag-Wackernagel (1999), pigeons have three basic colours: dominant red, blue (black) and brown. In the United States, Dunmore (1968) performed the first analysis of phenotypes and gene frequencies, thus allowing a geographical comparison with other localities. His results from Syracuse in the state of New York are followed by Cole (1969), who compares

the number of basic phenotypes in the Arizona city of Tempe. In terms of colour, 96 % of Syracuse pigeons were identified as black. In Tempe, this colour accounted for just under 85 % of the total number (Cole 1969). Following these comparisons in two American localities, Cole (1969) assumes that the differences in the abundance of individual phenotypes are caused by unspecified environmental factors. In the 1990s, Glissmeyer (1996) investigated the abundance of individual phenotypes in the American cities of Boston, Los Angeles, and Salt Lake City. The feral pigeons that inhabited the Salford Shipyard in Manchester were dominantly melanic individuals (C, C^T, S), this wild type, or blue-bar represents only 21 % of the local population (Murton *et al.* 1973). A similar situation occurs in urban areas of many European cities. Meinertzhagen (1954) studied the polymorphism of pigeons and its distribution in London and found a decline in individuals with the blue-bar phenotype in favour of melanic pigeons until 1954. On the other hand, Lofts *et al.* (1966) found only 24 % of melanic phenotypes in the wild pigeon population in Flamborough Head in Yorkshire. The same author compared these results with the proportion of individual phenotypes of feral pigeons in Leeds and Liverpool, in which, on the contrary, he found a predominance of melanic individuals. In the Far East, the colour and pattern of pigeons plumage are different from those in Western Eurasia (Johnston and Janiga 1995). In Russia, polymorphism in feral pigeon populations was observed by Obukhova and Kreslavskii (1984), who determined that the proportion of melanic individuals was 87 % out of 1500 studied individuals in Moscow in 1979-83. Similar proportions were observed by Pechenev (1984) in Moscow in 1978-82. In Slovakia, Podhradský (1953) investigated the influence of various factors on the plumage of the feral pigeon in Bratislava. He also determined the ratio of phenotypes in a group of 497 individuals. Later, between 1981 and 1985, Janiga (1991a) determined the proportions of selected phenotypic groups (wild type, melanic group, group of "red" pigeons and group of white pigeons) in Bratislava, and compared these data with parameters of weight, wing length and other properties for each phenotypic group. The phenotypic composition of feral pigeons was also determined in Vienna in 1989 by Leiss (1989) and later in Vienna and Basel by Leiss and Haag-Wackernagel (1999). In the cities of southern Europe, Ballarini *et al.* (1989) found that 56 % of individuals identified as blue-bar phenotype, along with a much smaller percentage of melanic individuals in Piacenza. This was also confirmed by Ragionieri *et al.* (1991) in both Fertilia and Barcelona. Both authors also studied the proportion of phenotypes in the city of Bolzano, where the melanic group significantly predominated. The phenotype data from all mentioned sites was summarized by Johnston and Janiga (1995), who, based on the comparison of the phenotype ratios, tried to determine the factors influencing their changes.

According to Goodwin (1976), environmental factors can be different in various natural environments, which may eventually create different types of selection pressure affecting feral pigeons. According

to Podhradský (1953) and Ferianc (1982), the same genotypes produce different phenotypes in changed conditions. Podhradský (1968) dealt with the way factor changes affect the plumage of the feral pigeon in experimental conditions, in addition to Johnston and Janiga (1995) who showed that the adaptation of melanin expression can be caused by experimental conditions influencing the environment.

The abundance of some phenotypes in local populations is influenced by certain abiotic environmental factors, but in particular by their interconnected complex. Podhradský (1968) experimentally found a change in the colour of some phenotypes during moulting due to changes in external factors like temperature and humidity. In urban environments, this would mean that local populations of feral pigeons are affected by local climatic characteristics, which in a small area of Slovakia, depend on orographic conditions. This issue of the influence of altitude and altitude-based climatic factors was raised by Johnston and Janiga (1995), who found a statistically significant deviation in the number of melanic individuals with declining northern latitudes in the alpine Italian town of Bolzano and in some Eurasian localities. The ideas of these authors lead to the assumption that climatic factors related to altitude can replace the influence of latitude. Therefore, the main aim of this paper is the determination of the possible dependence of individual phenotypic groups' abundance on altitude as well as specific climatic factors.

Material and Methods

Study sites

Polymorphism and regional differences in plumage colour and pattern of feral pigeons was studied in nine Slovak cities (Trnava, Leopoldov, Piešťany, Trenčín, Nové Mesto nad Váhom, Žilina, Martin, Ružomberok and Liptovský Mikuláš) during the winter (February and March) in 1998 and 1999 (Fig. 1). In both years, local populations of pigeons were observed in the same parts of the cities and their outskirts. An SVHS video camera recorder (Panasonic, Japan) or binocular was used to record footage.

In Trnava, the aggregation of 99 individuals was observed on the buildings close to as well as inside the Figaro complex in 1998. Video of these pigeons was easily captured by a video camera, as the pigeons gradually settled on the roofs of the objects in the evenings. In 1999, the observation area in Trnava extended to populations of pigeons nesting on the rocky river bank of the Trnávka river, at the buildings close to the sugar factory, and in the recesses of old buildings on Schneidera-Trnavského Street. As such, the number of pigeons observed in Trnava increased to 156 individuals. After several surveys in Leopoldov, we identified one local group of feral pigeons on the roof of the railway station. Similarly to Leopoldov, in Nové Mesto nad Váhom, Trenčín and Žilina, the local population of pigeons was concentrated at one site. In Nové Mesto nad Váhom, pigeons were largely observed at a silo close to the railway station. In Trenčín, pigeons were concentrated at Mierové námestie
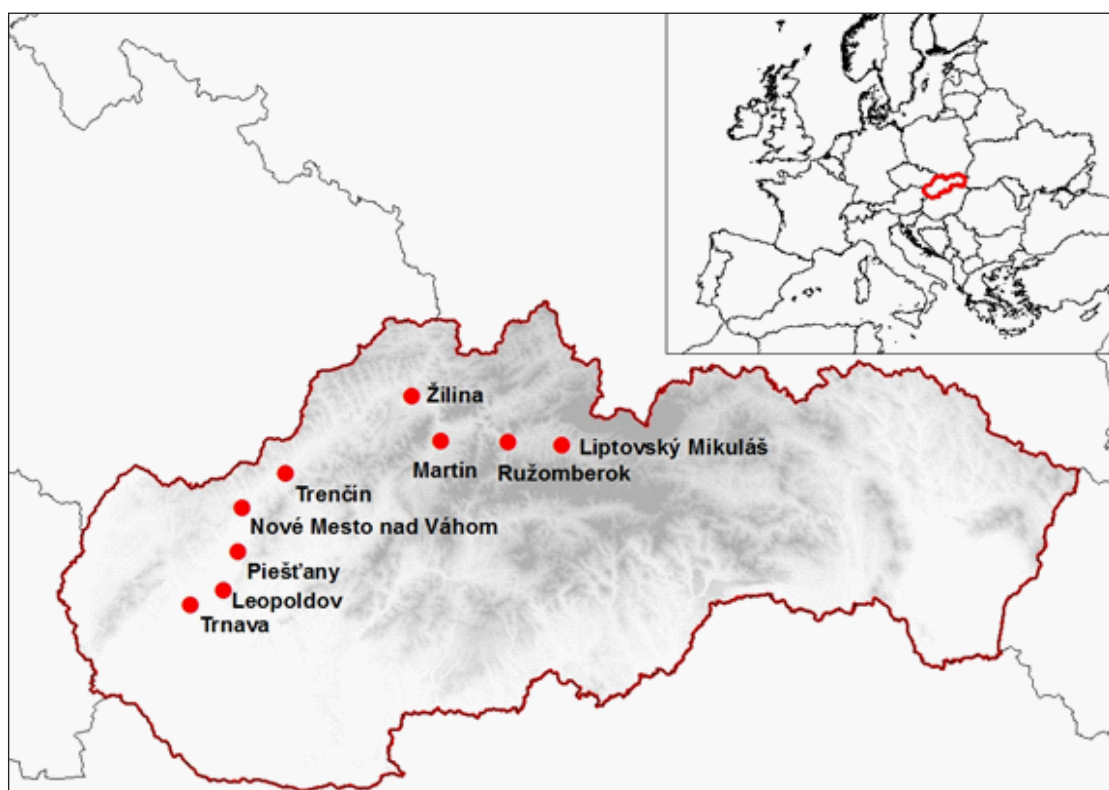
Fig. 1. Studied cities of Slovakia, where proportions of individual phenotype of feral pigeon were counted.

in the historical city centre, and in Žilina they resided in the main square in the commercial and historical part of the city. In Piešťany, several scattered aggregations of pigeons were observed during both years. The most abundant one was found in the city centre on the bank of the Váh River and surrounding buildings, where pigeons were fed as a result of people feeding seagulls and swans. Two other relatively large groups were observed in two housing estates on the outskirts of the city. In Martin, more groups were recorded; in the commercial centre of the city, in a housing estate on the outskirts of the city, and also at a silo where the number of pigeons was the largest, but access was not granted during either year of the study. In Ružomberok and Liptovský Mikuláš, pigeons were concentrated in several groups, but only in the historical and commercial centre of the city.

The above descriptions of pigeon habitats show that feral pigeons are closely linked to the anthropogenic environment, populating mostly historic parts of the city suitable for nesting and with a high concentration of people. Other locations include silos and food processing facilities, representing an important food source. However, they are already expanding to the surrounding newly built parts too, as is it in the case of Martin and Piešťany.

Determination of phenotypic composition of local populations

Descriptions and classification using Leiss and Haag-Wackernagel (1999) was used to distinguish the most common phenotypes occurring in urban populations. Pigeons were divided into four phenotypic groups (blue-bar, melanic, red, pied) based

on the pattern and colour of their plumage. These groups were chosen so that the number of melanic (dark) individuals and their ratio to other groups was immediately apparent.

The first group includes pigeons with a plumage pattern similar to wild rock pigeons. This is called wild type or blue-bar phenotype. The second group is a group of melanic individuals with blue-checker, blue-T-pattern and spread phenotypes. The third group consists of pigeons that have plumage that is primarily red and brown. Pigeons that have varying degrees of their body covered with red or brown colours were also added to this group. Pigeons assigned to this group belong mainly to the following phenotypes: ash red-bar, ash red-checker, ash red-T-pattern and recessive red. The fourth group consists of white pigeons. This group includes all-white individuals or individuals with plumage containing white colour. The presence of white is conditioned by a complementary factor (Gibson 1995) to the main colour and pattern. These are the phenotypes: pencilled, grizzle, tiger-grizzle and recessive white. Not reliably categorized phenotypes were included in the fifth group of unidentified phenotypes.

Statistical evaluations

For each studied city, the relative abundance of each of the four main phenotype groups of feral pigeons were evaluated and statistically processed with factors of environment, especially altitude and weather conditions. The list of weather factors measured during the study can be found in Table 1. The relationship between abundance of phenotype groups and altitude was evaluated by correlation using linear regression. Alti-

tude with weather variables converted to factors by principal component analysis (PCA). Resulting component scores were correlated with the data reflecting abundance each phenotype group.

Results

The total number of individuals and the relative percentage within each phenotypic group (see methodology) recorded in 1998 and 1999 in selected Slovak cities is shown in Table 2. The group of melanic (hyperchromatic) pigeons (Fig. 2a,b) was significantly dominant in all cities and in both years. The prevalence of this melanic group was 42 % at minimum in the first year, and 49 % at minimum in the second year (Table 2). Individuals from this phenotype group represent more than half of the local population in most cities. Their higher abundance occurred mainly in cities at higher altitudes (except Liptovský Mikuláš).

The second most abundant phenotype group was the wild type/blue-bar pigeons. The abundance of this group was less in cities with higher altitude (except Žilina, Martin and Liptovský Mikuláš). Values representing the relative abundance of this phenotype range from 15 %

to 40 % in the first year and from 17 % to 34 % in the second year of the study (Table 2). Pigeons with basic red and brown patterns were merged into the phenotype group of red pigeons. This group had low relative abundance in all examined cities.

Pigeons with basic red and brown patterns were merged into the phenotype group of red pigeons. This group had low relative abundance in all examined cities. In the examined Slovak cities, their average relative abundance was only 4.5 % in 1998 and 3.7 % in 1999, meaning that pigeons with red and brown patterns were relatively rare in urban populations (Fig. 2a,b). White or partially white pigeons (pied) were also rare or moderately rare (Fig. 2a,b).

Using linear regression, we observed statistically significant dependence on altitude in the case of the melanic phenotype group (Fig. 3). The correlation coefficient (Table 3) indicates a close connection between the above variables. In cities at higher elevations there was an increased abundance of melanic pigeons. Blue-bar and red pigeon abundance was not significantly correlated to altitude (p > 0.05).

The weather factors and altitude were processed by analysis of principal components. The resultant factors, especially PC 1, describe different weather conditions in mountainous areas (humid, rainy with low temperature) and in lowland areas (warmer and

| | Average air temperature in °C | | | | | |
| | year 1998 | | | year 1999 | | |
	February	March	1998	February	March	1999
Trnava	4.9	4.3	10.8	-0.2	6.9	10.9
Leopoldov	4.0	3.7	10.6	-0.4	6.7	10.6
Piešťany	3.7	3.4	10.0	-0.4	6.6	10.0
Nové Mesto nad Váhom				-0.6	6.2	9.8
Trenčín	2.9	3.0	9.4	-0.8	6.1	9.7
Žilina	2.0	1.4	8.0	-1.3	4.5	8.5
Martin	2.0	1.5	8.2	-1.6	4.0	8.6
Ružomberok	2.4	1.4	8.0	-1.5	3.4	8.7
Liptovský Mikuláš	1.0	0.5	7.2	-2.7	3.4	7.6
	Average air humidity in %					
Trnava	60	54		65	60	
Leopoldov	61	59		78	65	
Piešťany	72	67		84	72	
Nové Mesto nad Váhom				82	73	
Trenčín	78	70		82	73	
Žilina	81	74		84	76	
Martin	83	76		87	78	
Ružomberok	69	75		77	75	
Liptovský Mikuláš	77	71		92	90	
	Monthly and annual total precipitation in mm					
Trnava	0	10	493	34	12	522
Leopoldov	1	15	516	50	26	632
Piešťany	2	14	626	38	20	615
Nové Mesto nad Váhom				67	37	706
Trenčín	2	27	627	60	31	689
Žilina	18	38	756	59	29	763
Martin	25	44	804	61	31	743
Ružomberok	13	42	764	59	30	604
Liptovský Mikuláš	12	46	644	59	19	719

Table 1. Values of weather factors used in the study.

| Cities | lat. | alt. | Total number of individuals | | Phenotype groups | | | | | | | | | |
| | | | | | year 1998 (II,III) in % | | | | | year 1999 (II,III) in % | | | | |
	N	m asl	1998	1999	Blue	mel.	Red	Wht	ndf	Blue	mel.	Red	Wht	ndf
Trnava	48°	146	99	156	33	42	4	10	11	34	49	4	10	3
Leopoldov	48°	151	130	217	33	50	4	11	2	32	50	2	11	5
Piešťany	49°	162	73	91	30	51	3	8	8	29	51	7	11	2
Nové Mesto nad Váhom	49°	195		198						19	51	9	16	5
Trenčín	49°	211	60	140	22	53	8	10	7	17	53	7	13	10
Žilina	49°	344	45	45	27	60	2	11	0	27	58	0	15	0
Martin	49°	390	86	66	40	51	6	3	0	30	62	2	6	0
Ružomberok	49°	490	41	77	15	63	7	15	0	18	65	1	14	1
Liptovský Mikuláš	49°	590	60	197	30	52	2	6	10	21	59	1	8	11

Table 2. Relative abundance of pigeons according phenotype in selected Slovak cities with regards to altitude (lat. = latitude, alt. = altitude, Blue = blue-bar, mel. = melanic, Wht = white, ndf = non defined).
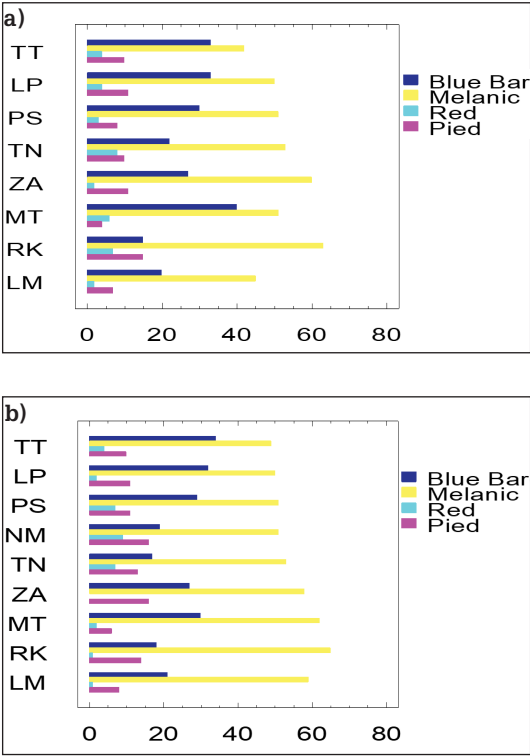

Fig. 2. Relative abundance of pigeons according phenotype in selected Slovak cities; **a)** 1998, **b)** 1999; TT = Trnava, LP = Leopoldov, PE = Piešťany, NM = Nové Mesto n. Váhom, TN = Trenčín, ZA = Žilina, MT = Martin, RK = Ružomberok, LM = Liptovský Mikuláš.

| | Altitude | | | |
	r	P	F	n
Melanic	0.68	0.002	13.2	17
Blue-bar	-0.31	0.23	1.6	17
Red	-0.39	0.1	2.76	17

Table 3. Results of testing the relationship between altitude and the abundance of phenotypic groups.
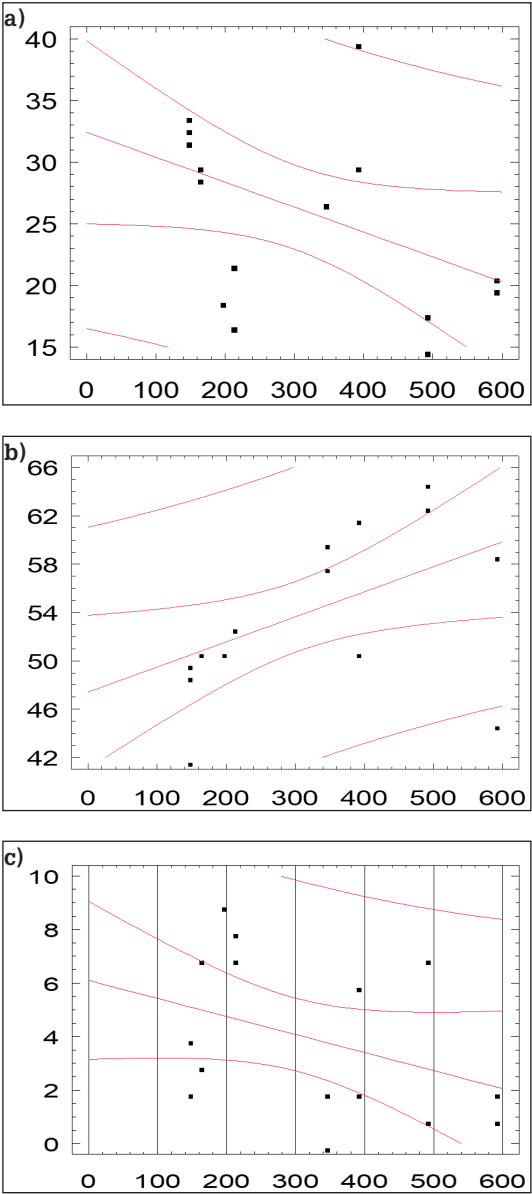

Fig. 3. Statistical dependence of phenotype groups abundance with altitude; **a)** - melanic, **b)** - blue-bar, **c)** - red.

drier conditions) of Slovakia (Table 4). The component score (Table 5) of PC 1 was considered as an independent variable in linear regression, when changes in the abundance of individual (melanic, blue-bar and red) phenotype groups with weather factors were examined. The significant correlation (Table 6) was found in the case of the melanic phenotype group, which indicates that, in mountainous areas of Slovakia with predominantly lower temperature, high humidity and higher precipitation, melanic pigeons are more abundant (gen. symbol C, C^T). Blue-bar and red phenotypes did not have a significant correlation with PC 1. None of the phenotype groups were significantly correlated with principal components PC 2 and PC 4. However, PC 3 correlated strongly with an abundance of the red phenotype group. The PC 3 component separates cities with warmer weather and higher precipitation in the lowlands from those with colder weather and low precipitation in mountainous areas. The abundance of pigeons in the red phenotype group was significantly higher in lowland cities with warmer weather and higher precipitation (Table 6).

Discussion

In all studied Slovak cities, a melanic (hyperchromatic) group of pigeons prevailed in both years, as well as in the cities listed in Table 7, with the exception of London in 1921. Even in this case, representation of the blue-bar phenotype decreased in favour of melanic individuals towards 1954 (Table 7), and in 1954 up to 81 % of pigeons at this site were identified as melanic (Meinertzhagen 1954). More recent data from eastern Slovakia (Košice 53.5 %, Svidník 56.4, Stropkov 59.6 %) has also confirmed melanic phenotypical dominance in terms of abundance (Čanády and Mošanský 2013, 2016). From a broader perspective, sites compared in Table 7 (g), at Flamborough in Yorkshire (a peripheral coastal area), show that blue-bar phenotypes (70 %) were more abundant than melanic phenotypes (24 %) in wild pigeon populations (Lofts *et al.* 1966). Podhradský (1953), Murton *et al.* (1973) and Janiga (1991a) also suggest that phenotypes showing varying degrees of melanism tend to dominate in cities. According to Johnston and Janiga (1995), there are also more melanic pigeons in the cities of European Russia and northern Central Europe. According to Goodwin (1954), the most common colour among feral pigeons in Great Britain is the blue-checker and blue-T-pattern phenotype, which belong to the melanic group. In 1951, Podhradský (1953) observed 497 pigeons in Bratislava, of which 20 % had the wild pigeon pattern and 63 % were melanic (Table 7). In 1981-85, the number of wild phenotype pigeons rose to 23 % and the number of melanic pigeons remained unchanged (Janiga 1991a). The phenotypic composition of pigeons in Brno is similar to Bratislava (Podhradský 1953). In the Gdansk wild, Hetmański and Jarosiewicz (2008) found that blue-bar pigeons were the dominant phenotype, especially in the old city centre, while melanic birds were most common in buildings constructed after WW II. This is not

the case in most southern European cities, where the blue-bar phenotype predominates over others (Table 8) (Johnston and Janiga 1995). Compared to others, "red" phenotypes are usually less common in Slovak cities, as well as in other European and American localities. In Syracuse, the "red" group (ash red-bar, ash red-checker, ash red-T-pattern and recessive red) represented less than 4 % of the total population (Dunmore 1968), which

	PC 1	PC 2	PC 3	PC 4
Altitude	0.36	0.22	-0.52	0.27
Annual temperature	-0.39	-0.26	0.18	-0.01
February temperature	-0.27	0.45	0.25	-0.27
March temperature	-0.18	0.56	0.14	0.07
Annual precipitation	0.38	0.05	0.52	-0.24
February precipitation	0.23	-0.50	0.00	0.31
March precipitation	0.32	0.22	0.55	0.58
February humidity	0.37	-0.24	0.14	-0.45
March humidity	0.41	-0.09	-0.17	-0.40
Total variability %	**56.7**	**28.5**	**7.2**	**4.7**

Table 4. Vectors (component weights) of the first four components derived from the correlation matrix of altitude and weather factors (average).

local.	year	PC 1	PC 2	PC 3	PC 4
TT	1998	-4.40	1.06	-0.47	0.01
TT	1999	-3.07	-1.53	-0.63	0.63
LP	1998	-3.64	1.10	-0.38	0.03
LP	1999	-1.17	-1.84	0.66	0.42
PE	1998	-2.10	0.90	0.02	-1.15
PE	1999	-0.70	-1.79	0.09	-0.60
NM	1999	0.57	-1.80	1.18	0.52
TN	1998	-0.90	1.09	0.32	-0.76
TN	1999	0.37	-1.75	0.70	-0.22
ZA	1998	1.40	1.66	0.68	-0.04
ZA	1999	1.72	-1.05	0.21	-0.93
MT	1998	2.03	1.58	1.11	-0.02
MT	1999	2.09	-1.04	0.003	-0.63
RK	1998	1.34	2.43	0.28	0.48
RK	1999	1.17	0.49	-1.24	0.98
LM	1998	1.83	2.57	-0.65	1.07
LM	1999	3.47	-1.10	-1.86	-1.08

Table 5. Component scores of weather conditions for individual cities where feral pigeons were recorded (the score determines each of the listed cities in the vector matrix described in Table 11) TT - Trnava, LP - Leopoldov, PE - Piešťany, NM - Nové Mesto nad Váhom, TN - Trenčín, ZA - Žilina, MT - Martin, RK - Ružomberok, LM - Liptovský Mikuláš.

	PC 1			
Melanic	r	P	F	n
	0.73	0.001	16.9	17
	PC 3			
Red	r	P	F	n
	0.55	0.02	6.5	17

Table 6. Results of testing the relationship between weather factors and the abundance of phenotypic groups.

Author	Locality	year	lat.	alt.	wild	melanic			other		SUM
					Bb	Bch	BT	S	Red	Wht	
Dunmore (1968)	Syracuse	?	42°	?	29 %	28 %	21 %	13 %	4 %	1 %	647
Cole (1969)	Tempe	1963	34°	?	20 %	38 %	24 %	1 %	13 %	2 %	93
Cole (1969)	Tempe	1968	34°	?	18 %	33 %	26 %	3 %	15 %	4 %	273
Glissmeyer (1996)	Los Angeles	?	34°	103	26 %	42 %	27 %			5 %	?
Glissmeyer (1996)	Salt Lake City	?	41°	?	10 %	38 %	23%			7 %	?
Glissmeyer (1996)	Boston	?	42°	?	16 %	59 %	18 %			7 %	?
Meinertzhagen (1954)	London	1921	51°	?	37 %	12 %	2 %	?	?	?	100
Meinertzhagen (1954)	London	1954	51°	?	14 %	36 %	45 %	?	?	?	100
Lofts *et al.* (1966)	Liverpool	1963	54°	?	23 %	37 %	27 %	7 %	3 %	1 %	305
Lofts *et al.* (1966)	Leeds	1963	54°	?	24 %	27 %	31 %	9 %	2%	5 %	265
Lofts *et al.* (1966)	Flamborough	1963	54°	?	70 %	16 %	8 %	0	4%	1 %	102
Murton *et al.* (1973)	Manchester	1966	54°	?	21 %	26 %	35 %	7 %		11 %	2843
Podhradský (1953)	Brno	?	49°	227	12 %	19 %	33 %	29 %	1%	3 %	89
Podhradský (1953)	Bratislava	1951	48°	133	20 %	20 %	32 %	11 %	11%	6 %	497
Janiga (1991a)	Bratislava	1981	48°	133	23 %			63 %	2%	12 %	276
Leiss (1989)	Vienna	1989	48°	171	30 %	23 %	22 %	5 %	5%	7 %	?
Leiss and Hague-Wackernagel (1999)	Vienna	?	48°	171	24 %	25 %	18%	7 %	?	?	7682
Leiss and Hague-Wackernagel (1999)	Basel	?	48°	259	25 %	22 %	16 %	6 %	?	?	327

Table 7. Frequencies of phenotypes of feral pigeon coloration from various European and North American localities (lat. = latitude, alt. = altitude, Bb. = blue-bar, Bch = blue-checker, BT = blue-T-pattern, S = spread, Red = red, Wht = white).

is comparable with the ratios presented in our survey of Slovak cities. This finding was not confirmed in Tempe, Arizona, where the number of red pigeons were 13 % and 15 % over the two years of the study Cole (1969). These outliers could be explained by environmental factors related to latitude.

Lichard (1981) claims that the hyperchromatic portion of the population in Bratislava is developmentally the oldest, which is also confirmed by the results of Podhradský (1952, 1953), but domesticated individuals are mixed into the group. It is predominantly a group of white phenotypes, which according to Podhradský (1952) and Goodwin (1957), represent immigrants from domestic farms. White-coloured pigeons are more abundant than red in most Slovak cities and their numbers are close to the values found in Bratislava by Janiga (1991a). In terms of the overall ratio, they are usually under-represented, which is in agreement with Johnston and Janiga (1995), but they are not uncommon, and can be observed in other cities (Table 7) where they make up 1 % -3 % of the total population.

According to Obukhova and Kreslavskii (1985a, 1985b), plumage polymorphism in feral pigeons largely reflects their abilities, and particularly their adaptability to changes in conditions. According to Murton *et al.* (1973), adaptation played an important role in the phenomenon of increased melanism in most European cities compared to the wild type phenotype that persists in natural (native) habitats. Lofts *et al.* (1966) also states that melanic phenotypes are selectively favoured in urban habitats. The authors give several reasons why this trend is generally valid in many cities. According to Obukhova and Kreslavskii (1985a), the melanic individuals have a survivability rate twice as high among urban biotopes, when compared to the wild-type phenotype; and therefore, higher presuppositions that they will reach adulthood (Murton *et al.* 1973; Janiga 1991a). Dunmore (1968) determined that there is statistically, the blue-T-pattern phenotype, belonging to the melanic group, constitutes the majority, and there is a significant decrease in "blue-bars" during the winter months (December and January) compared to the summer

Author	Locality	year	lat.	wild	melanic			other		SUM
				Bb	Bch	BT	S	Red	Wht	
Ragionieri *et al.* (1991)	Barcelona	?	41°	75 %	6 %	0	3 %	2 %	?	405
Ragionieri *et al.* (1991)	Fertilia	?	41°	84 %		6 %	?	0	?	17
Ballarini *et al.* (1989)	Piacenza	?	45°	56 %		29 %	1 %	4 %	3 %	?
Ballarini *et al.* (1989)	Bolzano	?	47°	8 %			85 %	2 %	1-2 %	%
Ragionieri *et al.* (1991)	Bolzano	?	47°	17 %			64 %	1 %	?	102

Table 8. Frequencies of colour phenotypes of some southern European cities (lat. = latitude, Bb = blue-bar, Bch = blue-checker, BT = blue-T-pattern, S = spread, Red = red, Wht. = white).

or autumn. This demonstrates the selection advantage of the blue-T-pattern phenotype during winter. The increase in the number of melanic individuals in the winter months of the year was also confirmed by Johnston (1984). Burley (1977) discusses the preference for dark phenotypes when pigeons choose partners, and according to Murton *et al.* (1973), melanic phenotypes have a higher chance of forming pairs with other phenotypes. The blue-bar phenotype is most prone to disease in cities (Obukhova and Kreslavskii 1985b). In a later study, Jacquin *et al.* (2011) found that melanic pigeons were less likely to be parasitized due to better immunocompetence. Therefore, a hypothesis exists that immune capacity and pathogen pressure play a potential role in maintenance colour polymorphism in bird species (Gangoso *et al.* 2011). These are likely the main factors contributing to the dominance of melanic phenotypes. The phenomenon of adaptation of melanic phenotypes to urban conditions and their advantage in such an environment is indicated by the opposite tendencies of these individuals in rural populations, where melanic individuals have a higher mortality rate than blue-bar phenotypes (Petersen and Williamson 1949). Lofts *et al.* (1966) state that in rural localities, individuals that experience regression of gonads in winter are mostly melanic. Corbel *et al.* (2016) observed a higher corticosterone response in melanic pigeons from rural habitats; but not in urban habitats, due to adaptation.

The plumage patterns of feral pigeons do not only reflect the phenomenon of urbanisation (Jacquin *et al.* 2013), but also domestication, or its elimination (Johnston and Janiga 1995). Albino pigeons, and partial-albino pigeons, which are present in greater numbers in cities than in native habitats, will likely grow extinct in subsequent generations (Podhradský 1952). They face decreasing numbers in Slovakian cities, as well as others (Table 7,8). Janiga (1991a) found a decreased similarity between young and their parents in white individuals in Bratislava, which indicates a decrease in the population of pigeons that were originally domesticated. Alleles for white plumage persist for a long time as recessive (Johnston and Janiga 1995). White nestlings had empty crop more often than the nestlings of other phenotypes (Janiga 1991b). Their white plumage, attracts the attention of predators, likely due to its uniqueness (Mueller 1975), and attacks of predators on pigeon aggregations with white plumage has been experimentally confirmed by Pielowski (1961).

One of the factors explaining the differences in the abundance between pigeon phenotypes found in European cities is the climatic characteristics caused by latitude. According to Johnston and Janiga (1995), there is a statistically significant relationship between rising northern latitudes and rising numbers of melanic individuals in the populations of 21 Eurasian localities (n = 22, r = 0.745, P = 0.001). An exception to this trend is the southern Italian city of Bolzano (Table 8), where a larger group of melanic individuals (85 %, 64 %) was recorded, compared to other Italian cities (Table 8). According to Johnston and Janiga (1995), the reason for this deviation could be the high altitude of this city.

The effect of altitude and associated climatic factors on the plumage pattern phenotypes of feral pigeons is not well covered in current studies on pigeon polymorphism. Findings of our study support the possible relationship between altitude and weather with the abundance of individual phenotypes of feral pigeons. Higher altitude often determines the specifics of climatic conditions in Slovak cities, and affects the ratio of individual phenotypes in favour of melanics. However, similar altitudes in different European cities determine different climatic characteristics. For example, in Basel (259 m asl.), it was found that the proportionate abundance of phenotypes (Table 7) is not identical to Slovak cities with a similar altitude (Table 2). On the other hand, in Vienna, the relative abundance of melanic phenotype individuals did not differ significantly, though it shares a similar altitude and climate with the Slovakian cities studied (Table 7). This phenomenon would be clearer if abundance phenotype data from European cities could be compared to weather characteristics.

C-series alleles determine the distribution of eumelanic (black) pigment or pheomelanic (red) pigment (Johnston and Janiga 1995). Derelle *et al.* (2013) by sequencing the melanocortin 1 receptor gene (MC1R), and showed that feral pigeon polymorphism is most likely not attributable to amino acid variation at the MC1R locus, as it is in case of some wild bird populations (Theron *et al.* 2001; Mundy *et al.* 2004; Baiao *et al.* 2007; Johnson *et al.* 2012). Later, Vickrey *et al.* (2018), discovered through whole-genome scans, that the NDP gene drives polymorphism, and post-domestication introgression supplies potentially advantageous melanistic alleles to feral pigeons. Podhradský (1953) compared the effect of the environment to changes in pigmentation in pigeons from both domestic farms (n = 430), and feral pigeons (n = 497) in Bratislava. He found that hyperchromatic individuals are predominant in cities and hypochromatic ones are predominant in domestic farms. Podhradský (1953) noticed that, although feral pigeons originate from domesticated pigeons, they are affected by significantly different biological and ecological conditions (changes in climate, food, nesting). He comments that factors such as heat, light, humidity, etc. affect plumage phenotype. Podhradský (1968) verified his claims by conducting experiments on pigeons that originated from the Bratislavan population of feral pigeons, with an unknown genetic disposition that he interbred panmictically. He kept the pigeons under variable temperature and humidity conditions. Blue-bar and ash red-bar phenotypes did not change plumage colour under the stress of these experimental conditions. However, the blue-checker and blue-T-pattern phenotypes reacted significantly, and while their plumage pattern changed by getting more intense or fading, the basic pattern did not change. Johnston and Janiga (1995) concur with Podhradský, that the feather pattern of some feral pigeons may depend on the environmental conditions at the time of moulting. Our findings of the statistical significance of the dependence of rising melanism on rising altitude and the relation of weather factors are in accord with Podhradský (1968). Increased hu-

midity and decreased temperature support an increase in the number of melanic individuals in areas characterized by this trend in the weather; predominantly in Slovak highlands and mountainous areas.

The possible effect of climatic factors on the abundance of some phenotypes or phenotypic groups is also mentioned by Dunmore (1968), who observed feral pigeons in Syracuse, New York State. blue-bar phenotype was the dominant group of individuals there. Cole (1969) suggests that cold winters played a role in the selection of resistant genotypes. However, Dunmore (1968) found decreasing abundance of "blue bars" when compared to other phenotypes during the coldest months. On the other hand, the success of melanic phenotypes (C, C^T) in the coldest months was confirmed by their reduced mortality during this period, and thus, their greater resistance to cold (lower temperatures).

Pigeons belonging to a 'red' phenotype group were also subject to the effect of environmental factors. The number of red-coloured pigeons may increase from north to south (Dunmore 1968, Cole 1969, Johnston and Janiga 1995). Pigeons with ash red base colour were rare in Syracuse (Dunmore 1968), but accounted for more than 12 % of all individuals in Arizona, which Cole (1969) claims could reflects Arizona's mild climate. The increase in abundance of red pigeons from north to south (Johnston and Janiga 1995), including n in Slovak cities, may confirm their sensitivity to some weather factors.

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Influence of car traffic on lead contamination in tissues of juvenile *Parus major* during postnatal development

M. KOČVARA, M. JANIGA and M. HAAS

Institute of High Mountain Biology, Žilina University, Tatranská Javorina 7, SK-059 56, Slovak Republic; e-mail: martina.haas@uniza.sk

Abstract. The main objective of our research was to identify the impact of external factors (spatial and time) on the amount of lead in the tissue great tit nestlings (*Parus major*) during ontogenesis in the submontane region of the High Tatra mountains. The research was carried out in the vicinity of several roads in the municipalities of Štrbské Pleso, Tatranská Lomnica, and Starý Smokovec in 1995-1996. The results confirmed that the amount of Pb found in tissues of great tit nestlings were different between studied sites, likely due to variation in traffic density. The size of each clutch also affects the amount of Pb in tissues. Lead content in tissues of nestlings from nests with a larger number of siblings (a larger clutch), is lower than in the tissues of individuals from a smaller clutch. The amount of lead rises with age; however, it does not depend on individual size predisposition. An insignificant increase in Pb levels were recorded during periods of bone growth (ulna/radius and tarsometatarsus). The amount of lead increased with increasing weight and with growing feathers. This means that Pb is taken up through the process of ontogenesis, mainly via feeding and it quickly accumulates into soft tissues and rapidly growing feathers. The lead level increased with rising weight and growing feathers, which points to accumulated lead derived mostly through feeding. The nestlings at sites with lower intensity traffic exhibited accelerated growth of feathers, as more metabolism was invested in plumage growth. This is considered a positive trend, as plumage growth correlates to an earlier departure from the nest.

Key words: Parus major, lead, ontogenesis, automobile transport

Introduction

There are many studies with a focus on lead poisoning in wild bird populations. However, they primarily focus on lead poisoning in birds caused by lead bullets. It is estimated that annually, lead kills up to one million wild birds in Europe, and results in sublethal poisoning in another three million (Johnson *et al.* 1982). Birds can be poisoned by ingesting lead. Often this occurs when they are struck by a lead bullet, or through fragments of ammunition present in their food. Symptoms of lead poisoning in birds can include lethargy, loss of muscle mass and fat stocks, anaemia, green droppings, a dropped wing, loss of balance and coordination, and other neurological symptoms such as paralysis or twitching in legs (e.g. Wobester 1997; Friend *et al.* 1999; Pattee and Pain 2003). Any or all of these symptoms may occur as a result of lead poisoning.

Lead gradually accumulates in bones throughout the life of the individual. Based on the level of lead present in bones, we can determine whether the individual has been chronically exposed to lead toxication or exposed to a single strong dose of lead toxication. Lead is gradually released from bones into the bloodstream, as a result of bone remodelling; a long-term process over a bird's lifespan. The lead content present in bone is generally considered to be an average lifelong exposure. High levels such as 5 mg.kg^{-1} in bones indicate a lead-polluted environment (Kelly and Kelly 2005).

Bones are one of the best and most reliable indicators of lead content in animals, as the level of lead detected serves as a cumulative dosimeter of lead exposure over many years. Bones are an important sample and indicator of lead exposure in bird bones because they contain 90 % of total lead. Accumulation is not always the same in each bone but may differ between bone types (Scheuhammer 1996).

Bone marrow plays an important role in absorption of lead by bone tissue. Lead deposits in bones through the bloodstream, and bone marrow receives blood from outside the bones. Therefore, bone provides valuable information on lead exposure and can be a very useful tool in investigating mortality from lead poisoning (Llacuna *et al.* 1995).

The great tit (*Parus major* L.) is a small bird. Their reproduction period takes place between March and August. Nesting begins during March and April, and if conditions are favourable, reproduction can occur up to two times per year. Tits build nests in various cavities, so they are a suitable species for settling nest-boxes. The typical clutch size can vary; however, it is most often 6 to 12 eggs. After hatching, both parents feed the chicks until they leave the nest (or longer!), up to 990 times per day (Vilček 1984).

Both the size of the clutch and the size of the eggs themselves are expressions of the quantity

of energy invested by the female great tit into the reproductive process (Pikula 1976; Nilson and Raberg 2001). Individuals that nest in highly urban environments such as city parks, must invest much more energy to provide nourishment due to the poor quality of the habitat; both in terms of food availability and proximity. Therefore, nesting pairs in these environments invest less energy in the clutch (Hinsley *et al.* 2008).

In studies evaluating the influence of several factors on the development of anorganism, it is more appropriate to use the physiological age of the young (expressed by changes in size) than the chronological age. The overall body size is preferable as an estimate of biological age because it is more directly tied to growth than chronological time (Strauss 1987). Because individual birds have a remarkable capacity to vary their mass and volume depending on their nutritional status (Emlen *et al.* 1991), it is biologically most meaningful to define size from skeletal measurements, independent of nutrient reserves (Piersma and Davidson 1991).

The fact that larger and heavier tits also yield larger and more viable eggs, can also be considered crucial (Schifferli 1973; Nager and Zandt 1994; Hegyi 1996). A factor that influences egg size significantly is the dominant status of the female, as well as her age (Desrochers and Magrath 1993; Báldi and Csörgö 1994). Additionally, egg size is also affected by the size of the clutch itself (Batt and Prince 1979). It is known that up to 80 % of eggs are conditioned hereditarily. Nevertheless, the rule that the larger the female, the bigger the eggs, can still be applied (Horak *et al.* 1995). It has been found that chicks hatched in years with a poor food supply exhibit a shorter tarsus than those that hatched in years when there was sufficient supply (Horak 1994).

Our research was conducted between 1995 and 1996 when lead-based fuel in Europe was still prevalent. This kind of fuel had a destructive impact on ecosystems and animals with close proximity to major roads. Therefore, the focus of this research was on birds nesting and reproducting near roads in the Tatras. We focused on the three most wide-spread municipalities in the High Tatras region in terms of vehicle traffic, which are situated directly under the High Tatras. Close attention was paid to the level of lead with respect to the location, the annual period, the number of eggs, the length of the feathers, and the length of the tarsometatarsus. We compared the amount of transport occurring in the selected locations (largely tourist municipalitie). Throughout the year these municipalities experience an influx of many tourists and associated traffic.

Material and Methods

Study area and sampling

In order to investigate the direct impact of car traffic on young birds in the nest, wooden nest boxes were placed in trees near the road in selected localities during early spring. The research was carried out from May to July during the years 1995 and 1996 in three localities: Tatranská Lomnica (850 m asl.; GPS: 49.16472° N, 20.28222° E), Starý Smokovec (1010 m asl.; GPS: 49.14097° N, 20.22102° E), Štrbské Pleso (1350 m asl.; GPS: 49.11889° N, 20.06361° E) in the foothills of the High Tatra Mountains, Slovakia.

In longitudinal transects at an average distance of about 10 m from the road, about 15 nest boxes were placed at each site. The boxes were placed at a height of 2.5-3.0 m above the ground. At Štrbské Pleso the first nesting box was placed at the following GPS coordinates: 49.1067853° N, 20.0755453° E. Every other nesting box was placed 100 meters from the previous one over a distance of 1.5 km. In the village of Starý Smokovec, the first nest-box started at the GPS site: 49.802412° N, 20.1412263° E. In the municipality Tatranská Lomnica the first nest-box was placed at GPS coordinates: 49.917627° N, 20.1901498° E. Nest boxes were placed in each location and arranged in the same way (Fig. 1).
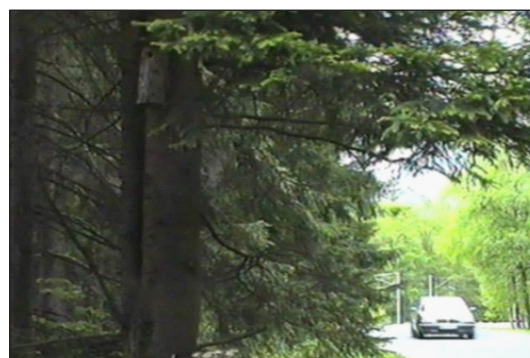

Fig. 1. Placement of wooden nest-boxes near roads in selected locations (Author: Marián Janiga 1995).

From May to July boxes were monitored regularly during the nesting period, and after hatching they were monitored every 2-3 days. Dates corresponding to egg laying and hatching, the number of eggs (clutch size), as well as measurements of egg length and maximum width were recorded consistently during the monitoring period.

The clutch size was determined when no additional eggs accumulated in the box (Gosler 1993). Hatchlings were sampled, and the following parameters were measured: length of tarsometatarsus, wing length (length of ulna / radius), and weight. Juveniles selected for analysis were killed by chloroform inhalation after measurement, then stored in plastic bags and frozen at -18° C.

Laboratory analysis

The samples were thawed at room temperature and were prepared for additional laboratory analysis. In the PTFE autoclave vessel, 0.5–1 g of each sample was weighed and 5 ml of 65 % HNO_3 and 3 ml of double-deionized water were added. The sample was decomposed for 5h in the autoclave (Autoclave ZA-1, Zahnašovice, Czech Republic) at 14° C in a drying box. The cool sample was put in a 25 ml volumetric flask and set up to 25 ml with double-deionized water.

Perkin-Elmer Model 1100B atomic absorption spectrometer (AAS) was used for flame atomic

absorption analysis of lead in tissue samples. For graphite furnace atomic absorption spectroscopy (GFAAS) analysis, the same spectrometer was used equipped with a Perkin-Elmer HGA 700 graphite furnace. Samples were introduced into the furnace with a Perkin-Elmer AS 60/70 autosampler and the results were recorded with a Perkin-Elmer EX-80 printer. The instrumental conditions for lead measurement were: lamp current (HCl) 10 mA, wavelength 283.2 nm, slit width 0.7 nm, gas air-acetylene. For GFAAS determination of lead, the pretreatment temperature of 700° C and atomization temperature of 2000° C were used. Ammonium dihydrogenphosphate ($NH_4H_2PO_4$) 0.2 mg was used as a chemical modifier for the measurement of Pb. Deuterium background correction was used throughout the work.

In each nest box, the maximum length and width of each laying egg were measured. The average length and width of an egg per clutch were calculated as the sum of all lengths and all widths and divided by the number of eggs. From this value, the theoretical average volume of eggs was calculated using the Hoyt´s constant (Hoyt 1979):

$$V = Kv. \, LB^2$$

Where:

Kv = 0.5228

L = length

B = breadth or maximum diameter

Energy investment of the female in the brood

The size and quantity of eggs in each clutch are not constant and differ among females and between nesting cycles year over year. To better understand the relationship between the energy investment of females and the postnatal development of nestlings, we calculated a female's energy investment in elation to each brood by multiplying the average volume of eggs and the number of all eggs in the clutch.

Car traffic during a typical day

To determine the correlation between the number of cars (emission load) and postnatal development of juveniles, the number of cars in the monitored localities on a typical day of the season (month). Each month (May-July), a random day was selected, in which all cars passing through the location were counted within a time unit (1 hour). The measurement was performed continuously for several hours on the same day and was divided into 2-3 consecutive days.

Statistcal analysis

Data from field observations was further processed using a spreadsheet table in Microsoft Excel. The data included species, place, date of the clutch, month, year, nesting box number and description, number of eggs in the clutch, average length, average width, egg volume, energy investment of the female, sampling date, sample mark, amount of lead, age, and measurements of wings, wing-vane, tarsometatarsus, and weight. Statistica, Ver. 8 was used for data analysis, and one–way ANOVA was used for statistical comparison between selected parameters (95 % confidence level p < 0.05).

Results

Lead concentration in great tit tissues collected from the research sites (Štrbské Pleso, Starý Smokovec, Tatranská Lomnica) varies (Fig. 2). The highest levels of lead were recorded in the tissues of jueniles from the Starý Smokovec site (F (2.45) = 3.4, p = 0.04*). The amount of lead (Pb) in bodies of tit chicks in nests depends on each site and its corresponding traffic density (Fig. 3).
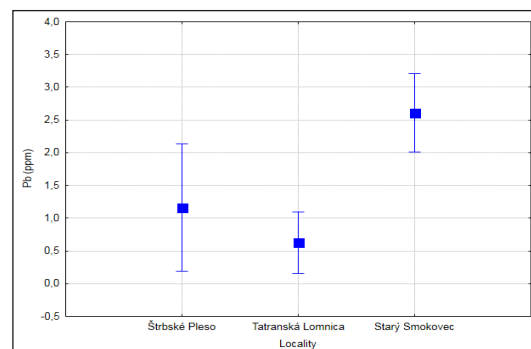

Fig. 2. Mean (± SE) concentrations of lead (ppm; dry weight) in the tarsi of nestlings of great tits from nest boxes located near the roads in the submountain region of the High Tatras. Nestlings were at the age of 6 to 20 days. Chicks from Starý Smokovec contained higher amounts of lead than birds from Tatranská Lomnica or Štrbské Pleso (F (2,45) = 3.4, p = 0.04*). The density of traffic was between two and three times higher in Starý Smokovec than in Tatranská Lomnica or Štrbské Pleso (Fig. 3).
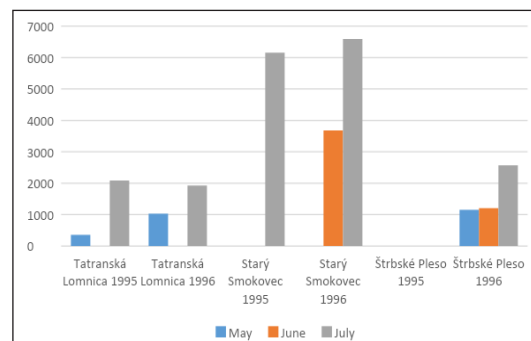

Fig. 3. During the period under review, the lowest car counts were recorded in Tatranská Lomnica and the highest in Starý Smokovec.

Comparison of the first nesting season (spring) and second nesting season (summer) (Fig. 4) indicates that the amount of lead in sampled tissues increases in the summer (F (1.46) = 3.3881, p = 0.7212). However, the differences between the seasons were not statistically significant. This phenomenon is also related to an increased amount of automotive transport in the summer months (Fig. 3).

When examining the dependence of the number of eggs and the level of Pb in the tissue of the nestlings tissues, we recorded a trend that with a larger number of eggs (10-16) the amount of lead in juveniles is lower (F (1.44) = 4.8301, p = 0.3328) (Fig. 5). However, this difference is not statistically significant.
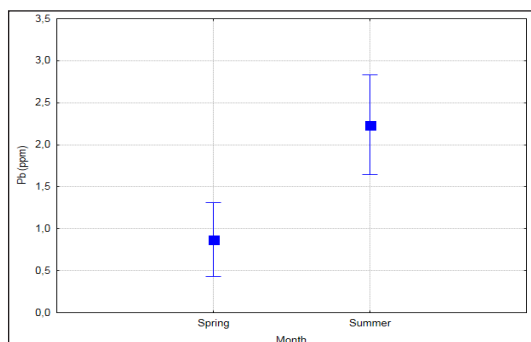
Fig. 4. Mean (± SE) concentrations of lead (ppm, dry weight) in the tarsi of nestlings of great tits from nest boxes located near the roads in the submountain region of the High Tatras. Nestlings were at the age of 6 to 20 days. Nestlings did not differ between summer and spring season (F (1,46) = 3.3881, p = 0.7212).
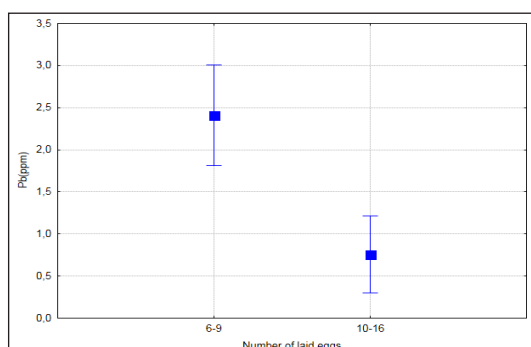

Fig. 5. Mean (± SE) concentrations of lead (ppm, dry weight) in the tarsi of nestlings of great tits from nest boxes located near the roads in the submountain region of the High Tatras. Nestlings were at the age of 6 to 20 days. The clutch size had no significant effect on Hg levels in nestlings (F (1,44) = 4.8301, p = 0.3328).

The same trend was also recorded in the energy investment by females in their eggs (transformed into the total volume of eggs). The energy investment of a female into a clutch may vary depending on the size of the eggs and the number of eggs in a clutch. Higher energy investment correlated to lower lead levels in nestling tissues (Fig. 6; F (1.27) = 3.2690, p = 0.8175). Nevertheless, this phenomenon is not statistically significant.
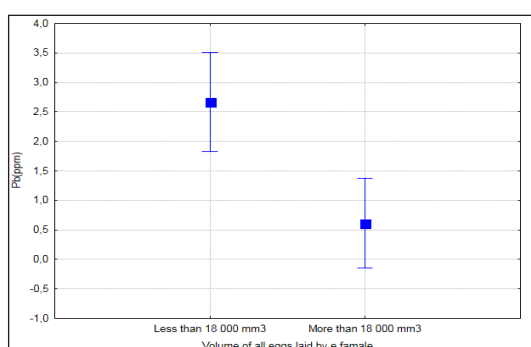

Fig. 6. Mean (± SE) concentrations of lead (ppm, dry weight) in the tarsi of nestlings of great tits from nest boxes located near the roads in the submountain region of the High Tatras. Nestlings were at the age of 6 to 20 days. Pb levels in nestlings did not depend on the total volume of eggs (F (1,27) = 3.2690, p = 0.8175).

We compared lead levels in tissues and physiological age and individual growth factors (plumage growth on the wing and length of tarsometatarsus). Lead levels increased significantly in older nestlings (Fig. 7; r = 0.6273, p = 0.0005). a similar situation was observed when comparing the lead levels and wing plumage growth. As growth of wing plumage increase, lead levels also increased (Fig. 8; r = 0.5331, p = 0.0497). We recorded the same trend in tarsometatarsus growth, although this correlation was not statistically significant (Fig. 9; r = 0.3362, p = 0.1167).

Physiological age of birds and density of traffic

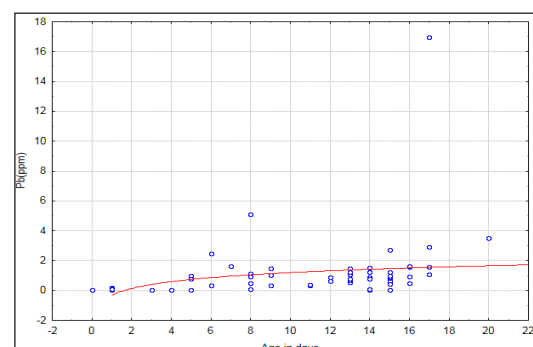The density of traffic near roads was divided into two categories: less than 2000 cars per day and

Fig. 7. Concentrations of lead (ppm, dry weight) in the tarsi of nestlings based on age (Pb = 0.3152 + 0.9833 * log10(x), r = 0.6273, p = 0.0005).
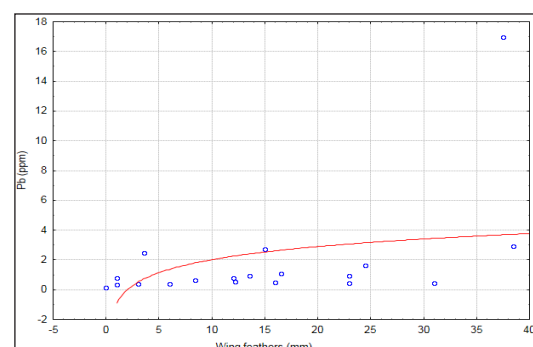

Fig. 8. Concentrations of lead (ppm, dry weight) in the tarsi of great tit nestlings based on wing feather length (Pb = 0.89 + 2.9079 * log10(x), r = 0.5331, p = 0.0497).
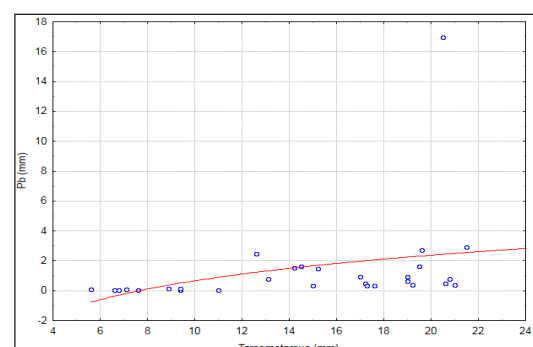

Fig. 9. Concentrations of lead (ppm, dry weight) in the tarsi of great tit nestlings based on tarsus length (Pb = -5.0211 + 5.6849 * log10(x), r = 0.3362, p = 0.1167).

more than 2000 cars per day. Traffic patterns did not appear to impact the physiological growth of young birds' bones (Fig. 10) or soft tissues (bodyweight – Fig. 11).

Taking into account that the amount of Pb in the growing wing feathers of young tits increases (Fig. 8) more quickly than Pb levels in leg bones (Fig. 9), we can state that the physiological growth of young from nests with heavy traffic was delayed. As a result, they stayed in the nest longer (i.e. they were fed longer) and were exposed to lead in the given locality for a longer duration (Fig. 12).
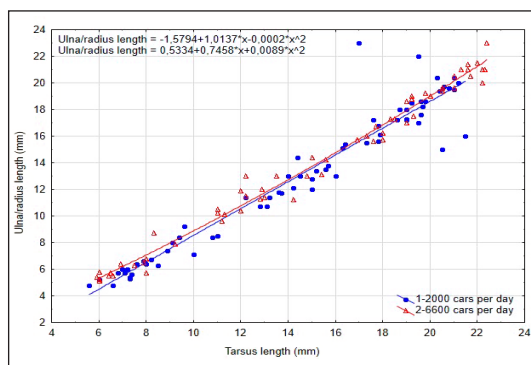

Fig. 10. Growth pattern of great tits (skeleton) in connection to traffic density. Pattern of growth of young did not differ on the number of cars at nearly roads.
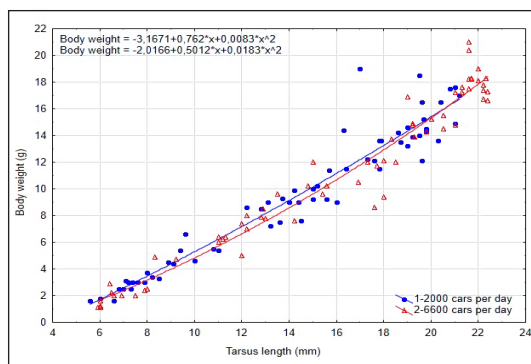

Fig. 11. Growth pattern of great tits (body weigh) in connection to traffic density. Pattern of growth of young did not differ on the number of cars at nearly roads.
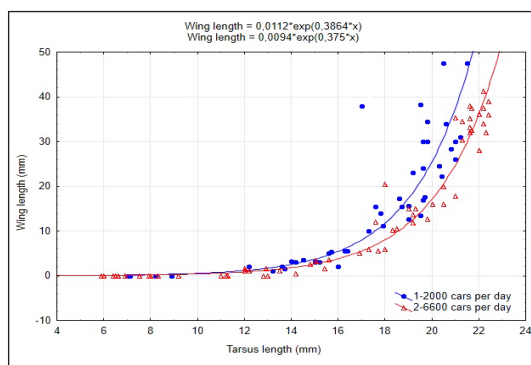

Fig. 12. Growth pattern of great tits (feathers) in connection to traffic density. Wing feathers of young grew relatively faster when related to tarsus bones in localities with less traffic than feathers of nestlings from localities of heavier traffic.

Discussion

To determine the heavy metal load of an environment, different species of birds are often used dependent on their position in the food chain. A potential animal species needs to comply with various requirements in order to be a reliable and contiguous biomonitor (Van Eeden and Schoonbee 1996). Great tit (*Parus major*) is often used as suitable model in behavioural and ecological research and are very useful as biomonitors for local contamination (e.g. Eens *et al.* 1999; Masahiko and Noriko 2001; Brnušáková and Janiga 2014). Due to the fact that tits readily use man-made nesting boxes, breeding populations can be easily established to monitor and study them in an area of interest, where it is possible to identify and evaluate local heavy metal pollution (Janssens *et al.* 2003). In our research, nesting boxes installed at selected sites were inhabited by tits during the first year of study in 30 % of cases. Species included *Parus major, Periparus ater* and *Lophophanes cristatus*. The dominant species was *P. major*.

Pb levels in young tit tissues varied between the three localities. Great tit nestlings from the site closest to the pollution source have significantly higher concentrations of metals (Dauwe *et al.* 2004). In our research, the highest concentration of Pb in tissues of tit juveniles was found in Starý Smokovec. This road is the most frequented, as it runs directly between Poprad, the largest foothill town and the town administrative center of the High Tatras, St. Smokovec. This location was observed to have the highest number of vehicles per day (Fig. 3).

The natural environment has been gradually contaminated by various forms of pollution, mainly as a consequence of urbanization and the increasing use of fuels by households, vehicles and industry (Swaileh and Sansur 2006). Lead remains a frequent contamination of vertebrates, especially in alpine habitats (Kompišová Ballová *et al.* 2020). The mobility of European Union residents has been growing as well, generating a substantial increase in the number of vehicles on the roads. According to Schafer and Victor (2000), the total mobility of the world's citizens at the turn of the millennium was 23 billion km, and will reach 105 billion km in 2039. In recent years, traffic congestion is becoming a significant problem for the majority of large cities all over the world, resulting in a reduction in transportation efficiency as well as increasing traffic exhaust emissions (Pan *et al.* 2018, 2019). Increased tourism in mountain areas results in increasingly toxic levels of lead in the environment as well as the growing prevalence of noise pollution; one of the most significant adverse factors disturbing a given habitat. The continuous movement of vehicles on roadways results in disturbing effects on nearby fauna and flora (Reijnen *et al.* 2002).

One of the consequences of increased traffic is an increase in emissions. As part of our research, we found that lead levels in the bodies of tit chicks are influenced considerably by the density of automotive transoport at a given site. Our research took place in 1995-96, when emissions from cars contained lead in addition to CO_2, due to additives in combustion mixtures. Current standards include

construction and operation of low-emission vehicles and improvement of traffic flow (building ring roads, viaducts and gradeseparated junctions) (Szwalec *et al.* 2020), but road transport remains detrimental to soil ecosystems along roadways. Heavy metals (Cd, Pb, Zn and Cu) with cumulative coefficients of 10–600 are among the substances emitted by vehicular traffic (Xu *et al.* 2014). Leaded gasoline is not the only source of rising lead concentrations in the environment. Other human activities, such as fuel combustion, industrial processes and solid waste combustion are also contributors.

In summer, measured Pb levels were higher than in spring. This phenomenon can also be attributed to an increased number of cars during tourist season. An interesting hypothesis is presented by Markowski *et al.* (2014), who observed higher concentrations of heavy metals in nestlings indirectly related to precipitation. According to Leech and Crick (2007), heavy rain decreases the number of available invertebrates by washing them out of vegetation. Such conditions may cause food limitation for canopy feeders and force them to forage for their young on the ground where food is more contaminated.

Lead is one of the most widely distributed toxins in our environment. It cannot be broken down, only converted to other forms. Studies on lead contamination in birds conducted in industrial areas showed a definite influence of environmental pollution on the levels of metals accumulated by birds (Dmowski 1993; Adout *et al.* 2007; Berglund *et al.* 2010). Lead can be accumulated in the bodies of soil organisms. Soil functions are disturbed by lead intervention, especially near highways and farmlands, where extreme concentrations may be present. Soil organisms suffer from lead poisoning and subsequently, these organisms can influence entire food chains (www.lenntech.com 2021). Tits as a nidicolous bird spend their first days of life inside nest boxes. Their main source of heavy metals exposure is through food supplied by their parents (Furness 1993). The great tit is versatile and often forages in bushes and even on the ground (Lack 1971). It is known to prefer caterpillars as the main food source for nestlings (Cholewa and Wesołowski 2011).

Diet may be an important variable in the manifestation of metal concentrations. The juvenile great tits are good indicators of lead toxicity from automobile transport, because these individuals easily absorb and retain thie pollutant due to an extremely rapid metabolism. Food provided by parents from the environment surrounding the nest had a high level of lead, resulting in an increase in lead levels in the chicks during the growth stage. Chicks that exhibited greater so-called 'selfish activity' did not receive food in larger quantities. Interestingly, tit can precisely determine the quantity of food required by a particular individual depending on its size. According to a study by Neuenschwander *et al.* (2003), tit of higher biological age also exhibit a greater intensity of begging behaviour and higher competition for food. However, development quality and the ability to leave the nest often decreases in these individuals.

This organism is characterized by a specific ability to discharge toxic elements of lead to their fast growing feathers, bones, or faeces (Dauwe *et al.* 2002, Deng *et al.* 2007). The liver discharges lead into feathers and bones in a way that prevents distribution to other body parts (Nybø *et al.* 1996). Lead content present in the body increases with rising age in nestlings, based on contamination levels present in the food supply. This phenomenon is also confirmed by the gradual increase in Pb levels with age, and both feather and tarsometatarus growth (Figs. 8-10). The same trend was observed in study by Brnušáková and Janiga (2014).

We concluded that nestlings from nests with more eggs tended to have lower Pb levels in their tissues. Taking into account the female's energy investment in laying, we found that in nestlings where the female had a higher energy expenditure (larger total egg volume), Pb levels were also lower. It can be assumed that a tit living during the nesting period in a biotope with higher lead concentrations will be much more contaminated, and therefore, can pass a higher percentage of lead to the clutch than a tit that lives in a less contaminated environment. Reproduction is usually described as one of the most energetically costly phases in the life cycle of an organism (Stearns 1992; Charnov 1993). In birds, reproduction is divided into nest construction, egg laying, incubation and chick rearing (Hansell 2000; Heenan 2013). Females occupied by taking care of a larger number of young tits are less able to effectively collect food than a tit caring for a smaller number of chicks. A larger number of young individuals results in a higher energy investment by the female into care but cannot compete with a tit that uses a lower energy investment in more frequent and intense feeding intervals. Therefore, young birds from large clutches leave the nest at a lighter weight and have a substantially reduced post-fledging survivorship. Evidence exists for this in a population of great tits, that varied their average clutch size from eight to twelve over a 17-year period, likely in response to crowding and the resulting changes in the density of the caterpillar population; their primary food source (Pianka 2008). In their study, Fritsch *et al.* (2019) found that *Turdus merula* showed a correlation between Pb levels and nesting success, where the breeding success of females decreased with increasing exposure to Pb. This research indirectly confirms our finding that higher levels of Pb are found in less successful clutches, with lower numbers of chicks and smaller eggs (Figs. 6-7).

Lead levels did not increase with body or bone growth. Weight and growing feathers proved to be the most important factors. In these two cases, the increasing curve of the lead level in the body of tit chicks was significant. Wing feathers of young grew relatively faster when related to tarsus bones in localities with less traffic than feathers of nestlings from localities with heavier traffic. It is possible that this is a detoxification method where Pb is deposited more readily in growing feathers. Condition parameters (body mass and hemoglobin concentration) were not related to heavy metal concentrations in the nestlings' excreta of *Sylvia communis*, which may correlate to the ability of young to detoxify their body, according to Turzańska-Pietras *et al.* (2018).

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