

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

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**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<sub>2</sub>, 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:

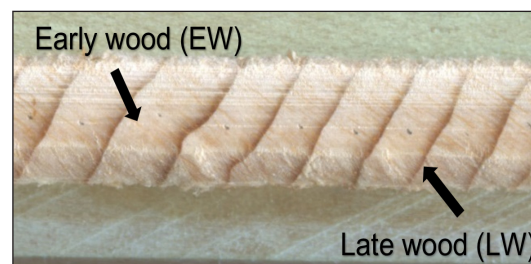
- How do trees at the margin of the elevational tree line in the Javorová valley respond to climate variables of air temperature and precipitation?
- How have these climatic variables changed over the past 70 years? Is a change in growth response due to shifts in climate visible at this site?

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 Institute of Poland, the Institute of Meteorology 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.

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 18<sup>th</sup> 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<sub>2</sub>, 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, *Picea 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.

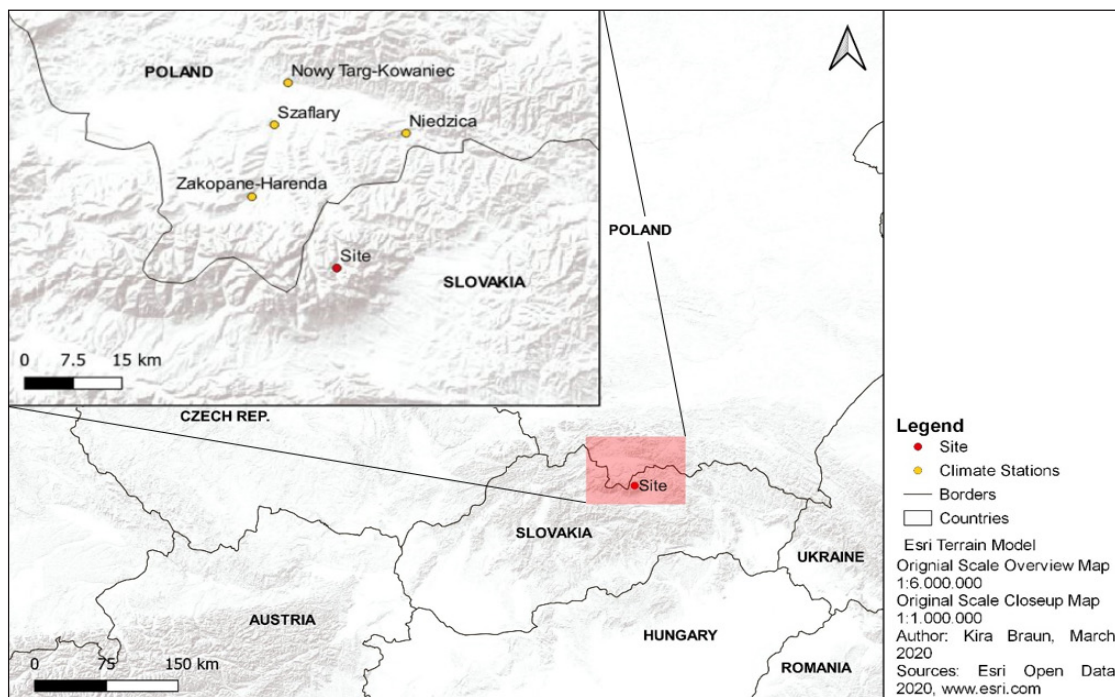


Fig. 2. Research site in a European context.

#### 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 metamorphic 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 Tatrzański Park Narodowy (TNP). The Slovak side makes up 75 % of the protected area with 113 221 ha and is referred to as the Tatranský Národný 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 *leptos*, 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

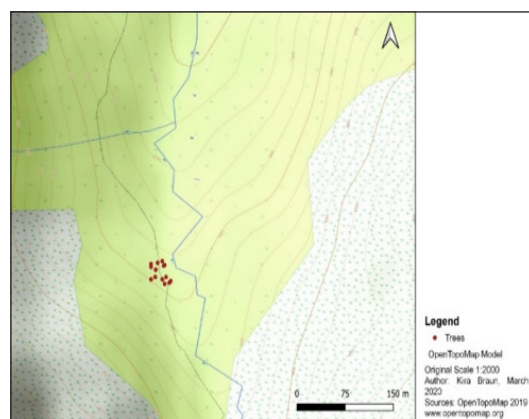


Fig. 3. Research site with individual trees.

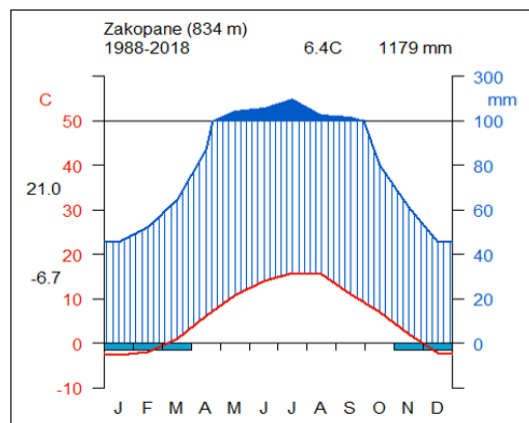
to the path. A few samples were taken from trees on a steeper slope. The site was chosen close to the elevational limits of the ecological amplitude of the *Picea abies* (L.) Karst, because tree growth on the margins of the species' habitat tend to be most significantly influenced by external factors, 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 12<sup>th</sup> century when animal grazing and mining were first introduced in the Tatras. Mining activities peaked in the 17<sup>th</sup> and 18<sup>th</sup> centuries. Metallurgy followed in the early 18<sup>th</sup> 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.

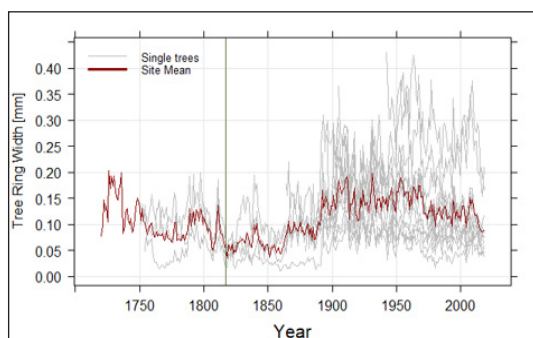
The measurement of the cores and their dating were done using the software package *CooRecorder* and *CDendro* provided by Cybis Elektronik & Data AB from L.A. Larsson. Measurement of the tree ring width was done using the dendrochronology software *CooRecorder* 7.7. The width was registered by zooming 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

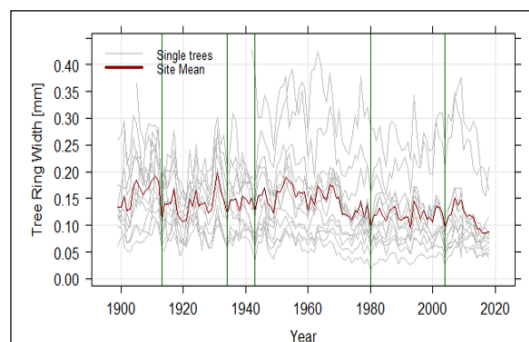
Analysis Program) software. First, both series from each tree were aligned. Tree\_6 had to be excluded because the single curves could not be aligned towards each other. The other pairs were successfully aligned, thanks to similar growth variations, which can, as previously mentioned, be attributed to 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; Neuwirth *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).

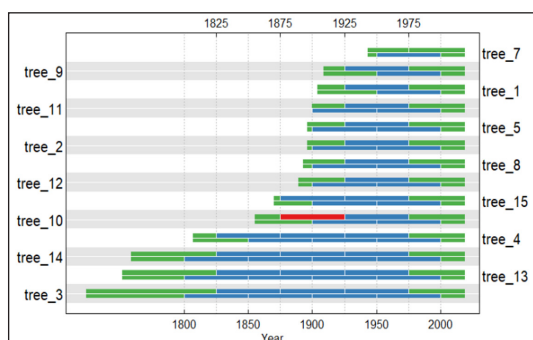
Extraordinarily wide rings, visible as positive pointer years, can also serve as orientation. Positive pointer years were detected in 1946 and 1961, which correspond to the Neuwirth *et al.* study from 2007. However, extraordinarily wide rings are more susceptible to random variation than narrow rings 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 dpiR-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 dpiR function *corr.rwl.seg*<sup>1</sup> 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<sup>2</sup>. 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.

<sup>1</sup>Corr.rwl.seg stands for correlation of ring widths (rwl) in segments (Bunn *et al.* 2020).

<sup>2</sup>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).

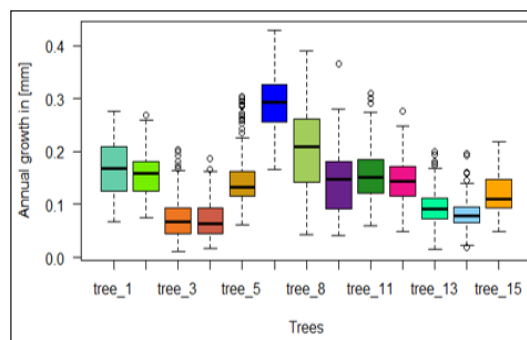


**Fig. 8.** Statistical crossdating using the `corr.rwl.seg` function of the `dplR` package.

#### 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<sup>3</sup> 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<sup>4</sup> 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).

<sup>3</sup>In the `dplR`-package `rbar.tot`. (Bunn *et al.* 2020)

<sup>4</sup>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*<sup>5</sup>, 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<sup>6</sup>.

<sup>5</sup>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).

<sup>6</sup>In R Studio the *Gleichläufigkeit* cannot be computed if two curves have less than three years overlap (Bunn *et al.* 2020).



## Detrending

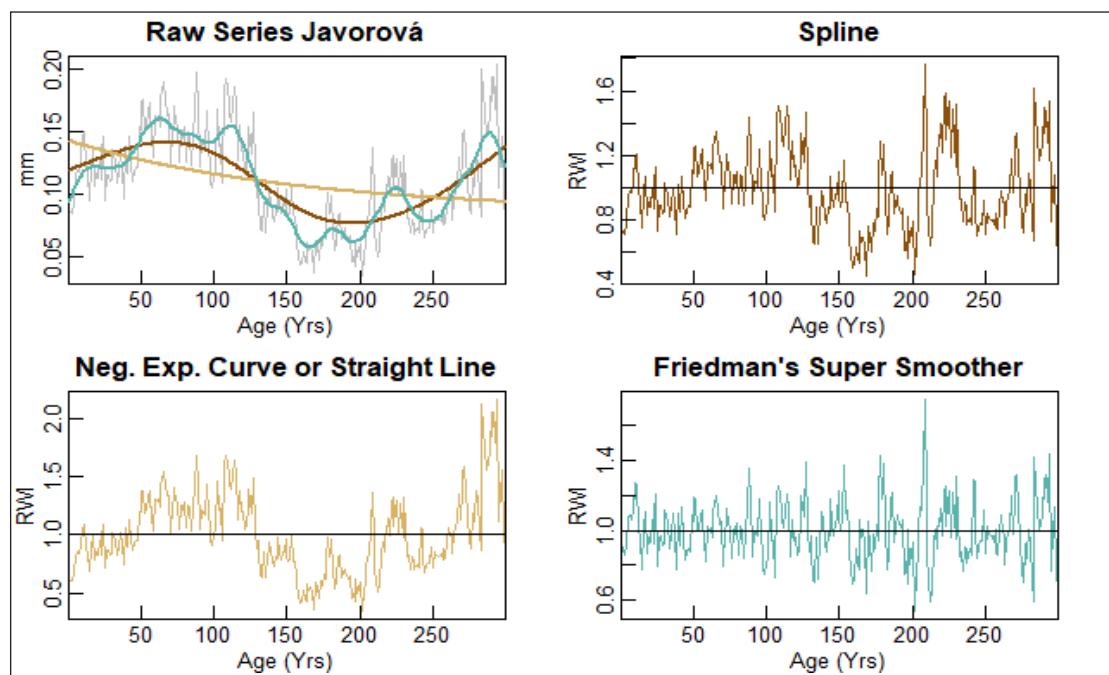
Tree rings widths are the result of various factors, such as climatically related environmental signals, endogenous and exogenous disturbances, age-size-related trends, and an unexplainable year-to-year variability, which is not related to the signals mentioned (Cook and Briffa 1992). Non-climatic factors 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 <sup>7</sup> (method = “Spline”) is displayed. The method uses a spline with the frequency response of 0,5<sup>8</sup> 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.

<sup>7</sup>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).

<sup>8</sup>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).

<sup>9</sup>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<sup>10</sup> 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<sup>11</sup> 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.

<sup>10</sup>A simple climate equation (Eq.(1)) is described by Mudelsee (2019) as follows:

$$X(i) = X_{\text{trend}}(i) + S(i) \times X_{\text{noise}}(i) \quad \text{Eq. 1}$$

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  $X_{\text{trend}}(i)$ . 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  $E[X_{\text{noise}}(j)] = 0$  for  $i=1, \dots, n$ , where  $E$  is the expectation operator, and a standard deviation unity.

<sup>11</sup>Mudelsee (2019) describes the linear regression as follows:  $X_{\text{trend}}(i)$  is described by two parameters, the intercept,  $\beta_0$ , and the slope,  $\beta_1$ .

The model of the linear regression is given by

$$X(i) = \beta_0 + \beta_1 \times T(i) + S(i) \times X_{\text{noise}}(i) \quad \text{Eq. 2}$$

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  $0.27^{\circ}\text{C}$ , which equals a semicentennial increase of  $1.37^{\circ}\text{C}$ . Consequently, over a 50-year period, the mean temperature at the Zakopane climate station has increased  $1.60^{\circ}\text{C}$ , 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 homogeneously 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  $2.65^{\circ}\text{C}$ , which is equal to a decadal increase of  $0.53^{\circ}\text{C}$ . While the mean JFM minimum temperature was  $-8.39^{\circ}\text{C}$  between 1951 and 1961, the mean between 2008 and 2018 was  $-5.43^{\circ}\text{C}$  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  $0.36^{\circ}\text{C}$  or  $1.75^{\circ}\text{C}$  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  $0.22^{\circ}\text{C}$ , which is equal to an increase of  $1.11^{\circ}\text{C}$  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  $1.37^{\circ}\text{C}$  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  $1.57^{\circ}\text{C}$  between 1951 and 1961, the mean between 2008 and 2018 was  $2.74^{\circ}\text{C}$ . The semicentennial increase in temperature is  $1.53^{\circ}\text{C}$  (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

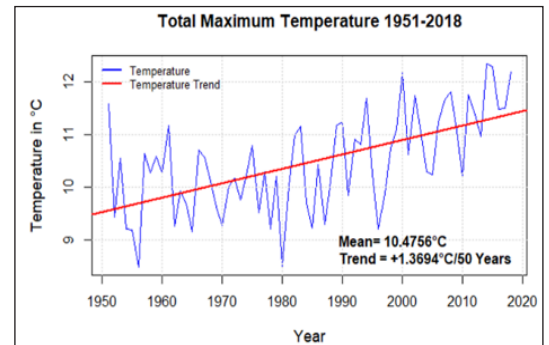
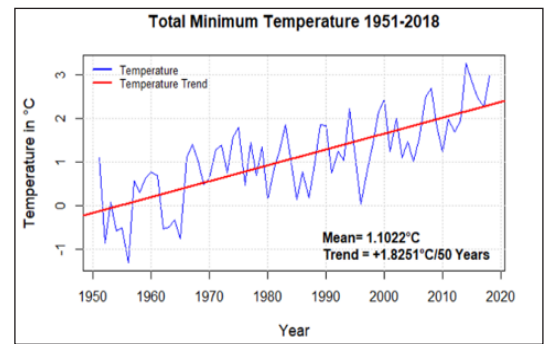


Fig. 11. Minimum and maximum temperature increase at the Zakopane climate station from 1950 to 2018.

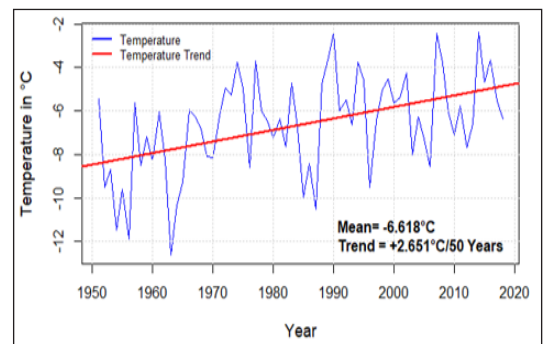


Fig. 12. Minimum temperature increase for the months of January, February, and March between 1951 and 2018 at the Zakopane climate station.

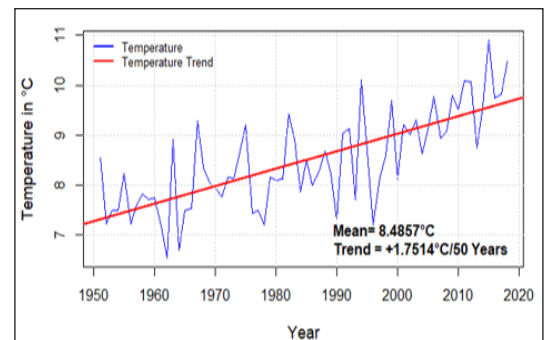
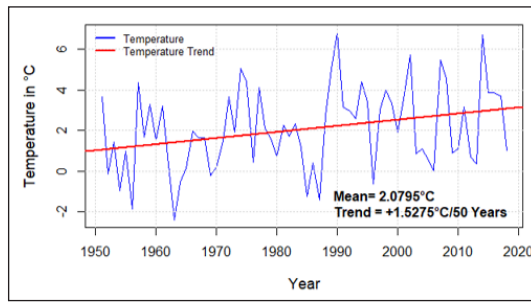
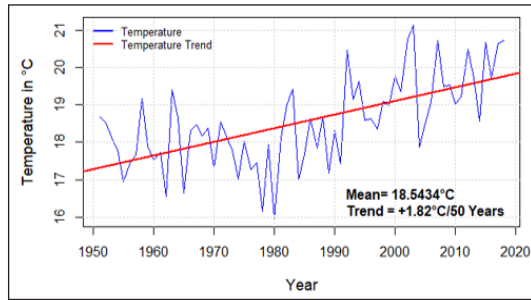


Fig. 13. Minimum temperature increase for the months of June, August, and September between 1951 and 2018 at the Zakopane climate station

until August, including the initiation and post-xylem phase, shows the significant decadal increase of  $0.36^{\circ}\text{C}$  or  $1.82^{\circ}\text{C}$  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  $0.12^{\circ}\text{C}$ , or  $0.59^{\circ}\text{C}$  in 50 years.

#### Precipitation trends

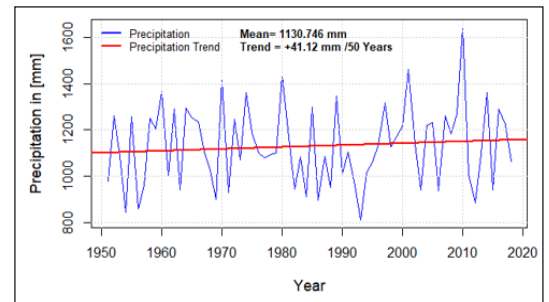
On a global scale, precipitation trends vary immensely. In the mid-latitudes of the Northern Hemisphere ( $30^{\circ}\text{N}$  -  $60^{\circ}\text{N}$ ) an increase in precipitation was documented for the period of 1951 to 2008, but the trends are non-significant for the majority of data sets (Hartmann *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

for which the correlation was found. As the calculation 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 correlations were also calculated, e.g., for January, February, March (JFM), for April, May, June (AMJ), for July, August, September (JAS), and October, November, and December (OND). Furthermore, the influence of a climate signal during the growing season (GS) from May to August, which includes the initiation and post-xylem phase, is also analyzed. The “Total” bar shows the general response of tree rings to a specific climate variable. The in-year impact is displayed 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 detrended 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 second 33 years will be considered separately and put into context with the temperature and precipitation 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 correlation of temperature and growth tends to increase at high elevations and becomes directly correlated

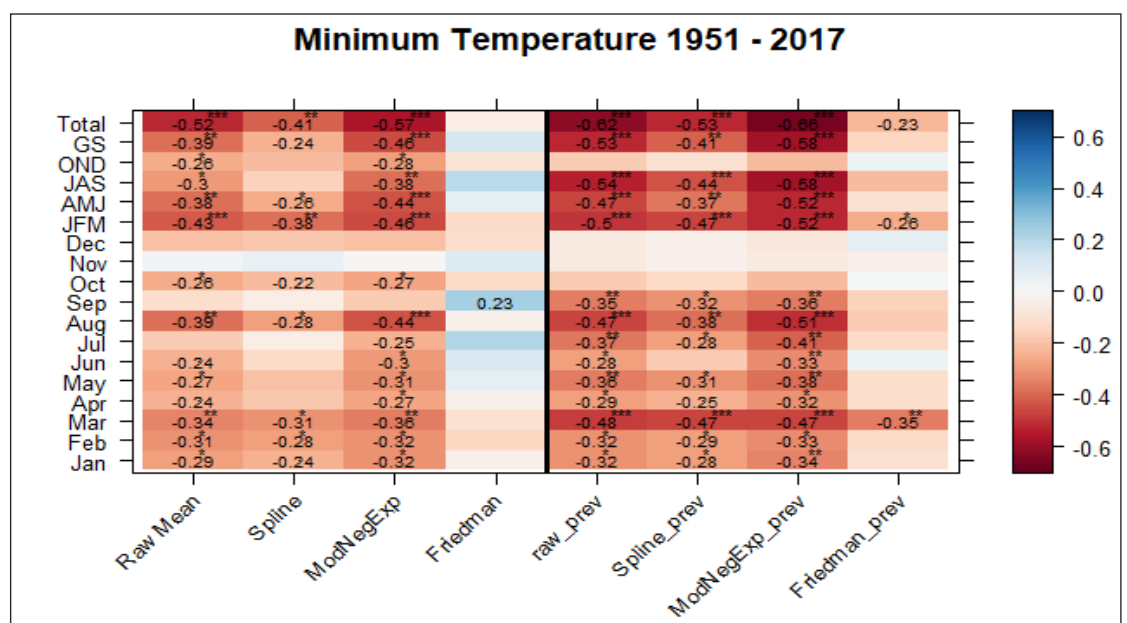
with growth (Fritts 2001). Therefore, studies that investigate the impact of temperature on tree growth are often located in mountain ranges, such as a study on growth reactions of multiple species in the Polish and Slovakian Tatra Mountains (Büntgen *et al.* 2007), or temperature reconstructions for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

In the following sections, the relationship between 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 elevation sites, temperatures are cooler than at lower elevations for multiple reasons, one being the decrease 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 previous year is found to be more significant than the same-year impact. The previous-year correlation reaches values up to  $-0.66^{***}$  and the same year up to  $-0.57^{***}$ . Correlations using the Friedman Curve, which includes short-cyclical climate variability, 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 = October, 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  $0.56^{\circ}\text{C}$ , the mean of the second period from 1984 to 2017 was  $1.61^{\circ}\text{C}$ . 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 ( $2.65^{\circ}\text{C}$  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).

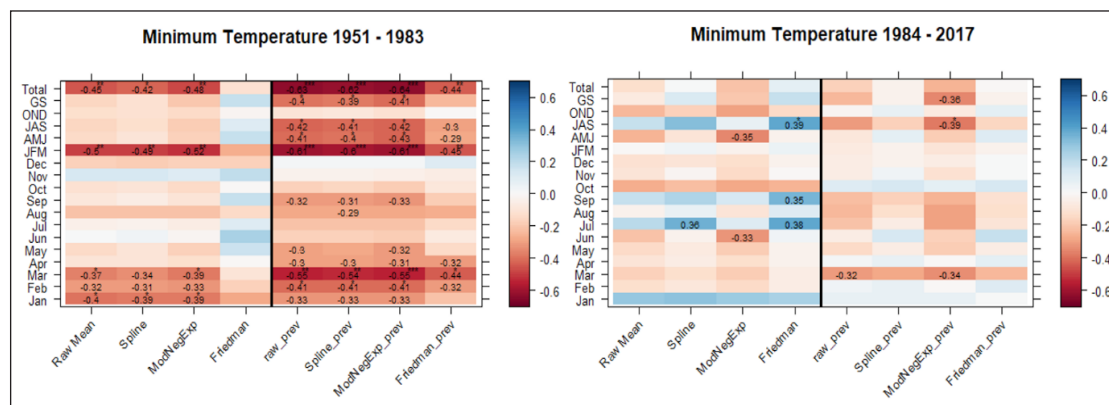


Fig. 18. Shift of growth responses to minimum temperatures from 1951 to 1983 and 1984 to 2017, GS = growing season, OND = October, November, December, JAS = July, August, September, AMJ = April, May, June, JFM = January, February, March.

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.

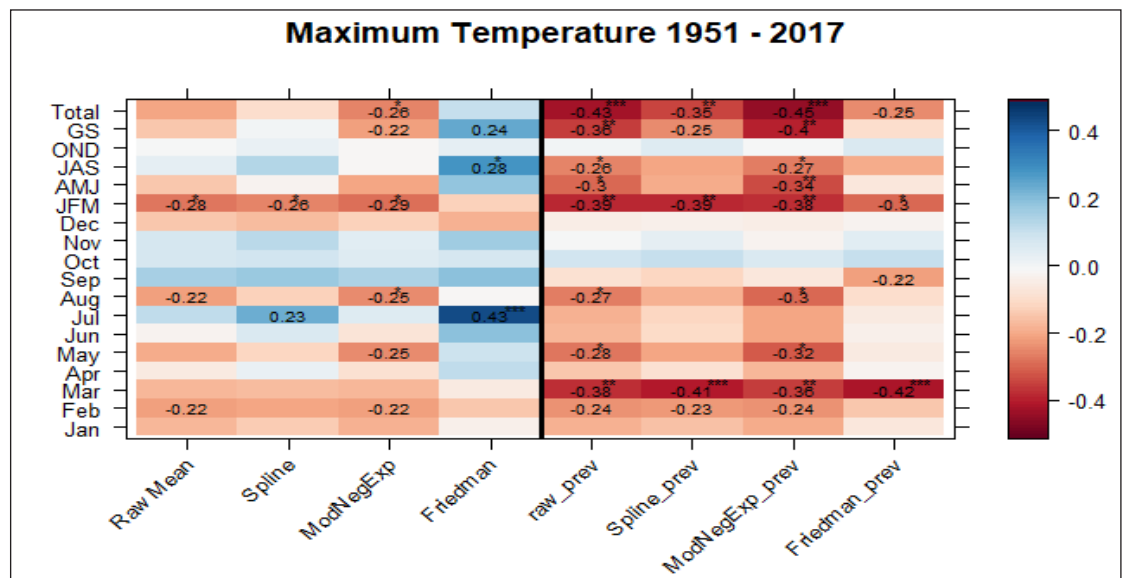
The correlation between tree ring width and maximum temperature was especially significant for the month of March. The previous-year impact was

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\*\*.

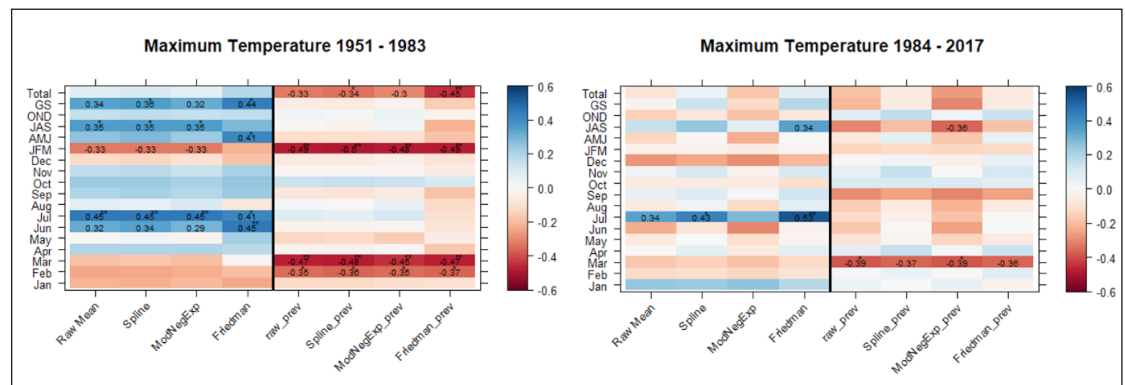
The shift of positive response to negative response over time is evident for the entire growing season. During the first period, positive responses were found for all curves, reaching values between +0.32 and +0.44\*; during the second period, the correlations for the same-year impact are found to be 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).

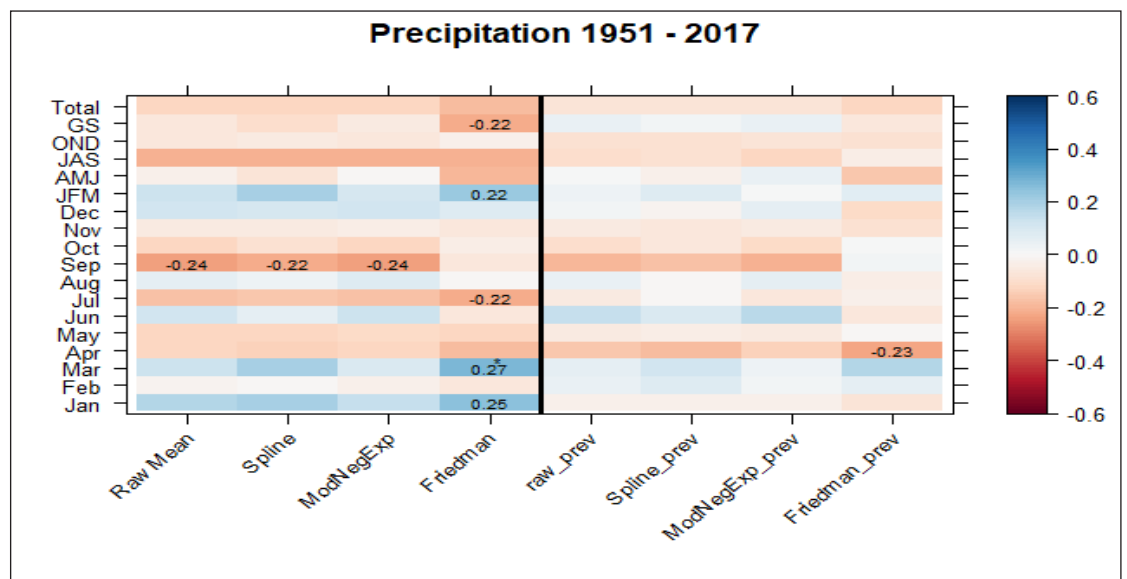
The response of tree ring widths to summer precipitation is ambiguous. While June and August precipitation correlates positively, July and Sep-

tember 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.

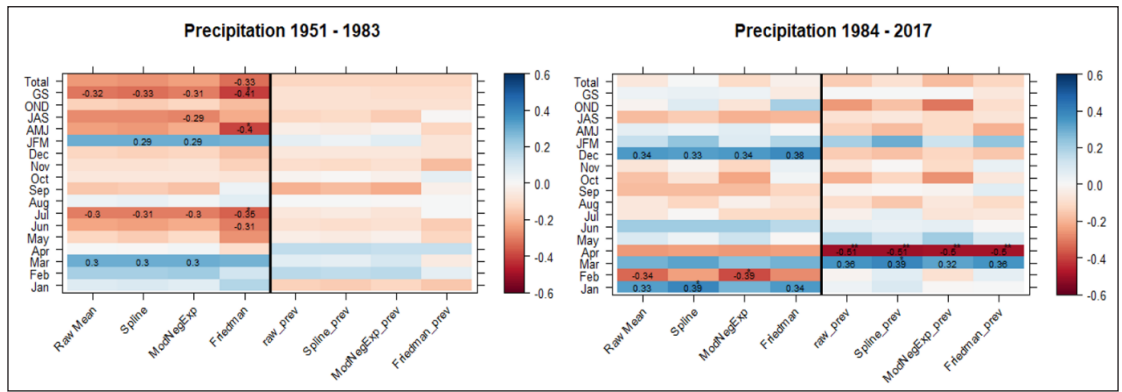
Overall, common feature of trees from high elevation sites responded negatively to precipitation during the growing season at the Javorová site, but during the studied period, between 1951 and 2017, only insignificant values (between -0.05 and -0.22) were found.

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.

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 Tatrzański 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 height (cm)	Circumference (cm)	Included/Excluded
I 1	<i>Picea abies</i>	140	160	Included
I 2	<i>Picea abies</i>	141	146	Included
I 3	<i>Picea abies</i>	129	127	Included
I 4	<i>Picea abies</i>	133	107	Included
I 5	<i>Picea abies</i>	117	133	Included
I 6	<i>Picea abies</i>	119	155	Excluded
I 7	<i>Picea abies</i>	134	146	Included
I 8	<i>Picea abies</i>	74	184	Included
I 9	<i>Picea abies</i>	121	137	Included
I 10	<i>Picea abies</i>	109	168	Excluded
I 11	<i>Picea abies</i>	107	151	Included
I 12	<i>Picea abies</i>	109	132	Included
I 13	<i>Picea abies</i>	70	170	Included
I 14	<i>Picea abies</i>	150	140	Included
I 15	<i>Picea abies</i>	90	137	Included