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Response of tree rings and NDVI of Central-European conifers to extreme climatic events

Odezva letokruhů a NDVI středoevropských jehličnanů na extrémní klimatické události

Doctoral thesis

Supervisor: Doc. Mgr. Václav Treml, Ph.D.

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Prohlašuji, že jsem předloženou závěrečnou práci zpracoval samostatně a že jsem uvedl veškeré použité informační zdroje a literaturu. Tato práce ani její podstatná část nebyly předloženy k získání jiného nebo stejného akademického titulu.

V Praze

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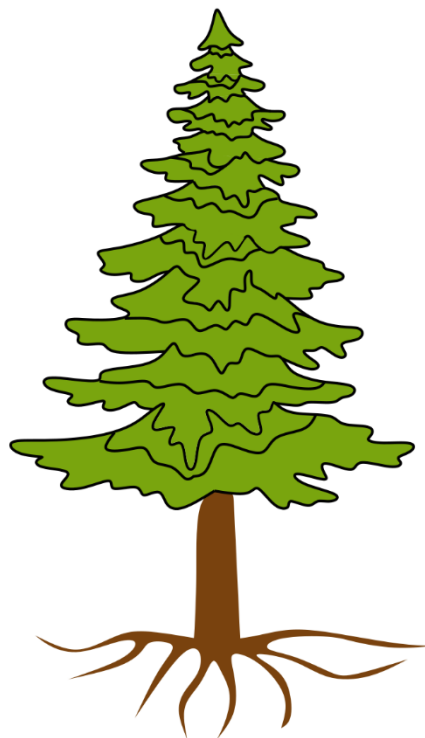
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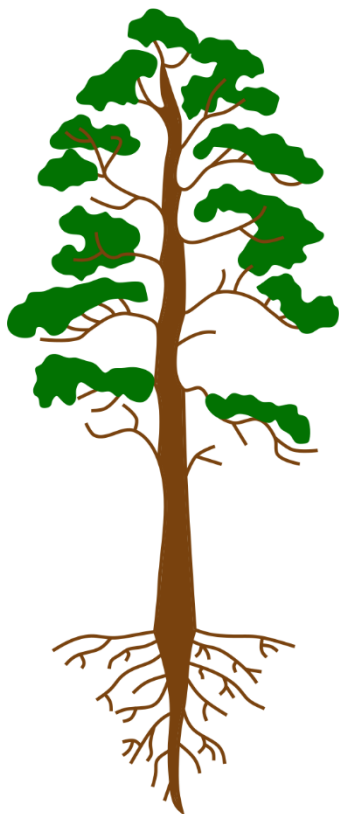
Pinus sylvestris   *Picea abies*

Abstract

Terrestrial ecosystems, mainly forests are important sinks of atmospheric carbon with high year-to-year variability driven by moisture availability. Trees store carbon in various compartments of the biomass, namely in stems, roots, and leaves. In this doctoral thesis, I investigated climate-growth responses of stem biomass (represented by tree rings) and leaf biomass (represented by normalized difference vegetation index; NDVI) of *Pinus sylvestris* and *Picea abies* in temperate forests of Czechia. I was interested in (i) general climate-growth responses and specifically, in reactions to drought and (ii) topographical factors influencing these responses at various spatial scales.

We demonstrated that climate-growth responses of both species' tree rings in the lowlands revealed a significant positive and negative influence of moisture and temperature, respectively, while in higher elevations the responses were opposite. At a landscape level, the topography of relief modulated responses of *Pinus sylvestris* tree rings, while at the large-scale level, the geographical position and elevation (temperature gradients) were the main factors for both species. Responses of NDVI were slightly weaker compared to tree rings and did not show the influence of topography at any scale probably because vegetation greenness (photosynthesis) is less climatically driven compared to radial stem growth. Overall agreement between the time series of tree rings and NDVI decreased with elevation, which is probably a result of their diverging climatic constraints.

Climatic drivers of extreme growth reductions agreed with the general climatic signal, however, the importance of drought significantly increases for both species along the large-scale elevational gradient from mountains to lowlands. Tree rings showed growth depression up to two years after drought events, while NDVI increased, probably to gain more assimilates and buffer the damage. Responses to extreme events were not affected by topography at the landscape level, while at large scale the influence of elevation was obvious.

Our results suggest that climate-growth responses of stem and leaf biomass of two main Central European conifers are decoupled at specific spatial and temporal dimensions under ongoing climate change. These findings should be considered in studies forecasting the carbon storage in stems and foliage of boreal and temperate forest ecosystems and in attempts to extrapolate tree rings to the landscape level using remote sensing data.

Keywords: *Pinus sylvestris*, *Picea abies*, tree rings, NDVI, drought responses, topography

Abstrakt

Terestrické ekosystémy, především lesy jsou důležitým úložištěm atmosférického uhliku s vysokou meziroční variabilitou řízenou dostupností vody. Stromy ukládají uhlík v různých částech nadzemní i podzemní biomasy, hlavně ve kmeni, listech a kořenech. V této dizertační práci jsem studoval klimatické reakce růstu kmenové biomasy (reprezentované letokruhy) a listové biomasy (reprezentované normalizovaným diferenčním vegetačním indexem; NDVI) u smrku ztepilého (Pic*ea abies*) a borovice lesní (*Pinus sylvestris*). Zabýval jsem se (i) všeobecnými klimatickými reakcemi, specificky pak dopady suchých událostí a (ii) topografickými faktory, které tyto rekace ovlivňují na různých prostorových úrovních.

Výsledky ukázaly, že letokruhy obou druhů v nížinách vykazují signifikantní pozitivní vztah k dostupné vlhkosti a negativní k teplotám, zatímco ve vysokých nadmořských výškách byl tento vztah obrácený. Na krajinné úrovni byla reakce letokruhů borovice lesní ovlivněna topografií reliéfu, zatímco ve větším měřítku byla podstatná geografická pozice a nadmořská výška (gradienty teploty) u obou druhů. Reakce NDVI byla oproti letokruhům slabší. NDVI navíc nevykázalo jakékoli ovlivnění topografií, pravděpodobně, protože zelenost vegetace (fotosyntéza) je méně klimaticky závislá oproti růstu kmenové biomasy. Koherence mezi přírůstem dřevní biomasy a NDVI klesala s nadmořskou výškou, což je pravděpodobně výsledek jejich odlišných klimatických limitací.

Klimatické faktory extrémních snížení růstu se shodují s všeobecným klimatickým signálem, nicméně význam sucha se u obou druhů výrazně zvyšoval podél velkoplošného výškového gradient z hor do nížin. Letokruhy vykázaly snížení růstu trvající až dva roky po suché události, zatímco NDVI narostlo, pravděpodobně za účelem získání více asimilátů k opravení poškozených pletiv. Reakce na suché události nebyly ovlivněny topografií na krajinné úrovni, ovšem ve vetším měřítku se projevoval vliv nadmořské výšky.

Tyto výsledky naznačují, že klimatické reakce kmenové a listové biomasy dvou dominantních středoevropských jehličnanů jsou při probíhajících změnách klimatu prostorově a časově oddělené. Tato zjištění by měla být zohledněna ve studiích predikujících ukládání uhlíku do kmene a listové biomasy boreálních a temperátních lesních ekosystémů a při pokusech o extrapolaci letokruhových řad stromů do prostoru pomocí dat dálkového průzkumu Země.

Klíčová slova: borovice lesní, smrk ztepilý, letokruhy, NDVI, odezvy na sucho, topografie

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1. Introduction

Forests cover a large part of the land (cca 38 %; Our World in data 2023) and are essential for the functioning of many natural processes including land-atmosphere interactions. They influence climatic conditions, the water cycle, bind carbon in biomass, and are also important for the economy (Durrant et al. 2016). Estimates of future forest functioning are uncertain due to the non-linear relationship of tree growth to climate and the spatial-temporally unstable responses of trees to climate (Norby et al. 2010). Such changes may affect carbon uptake and storage across terrestrial ecosystems (Babst et al. 2014), especially if temperatures rise without adequate precipitation increases, forests will suffer from drought and the supply of carbon to woody biomass will slow down (D'Arrigo et al. 2004). It is therefore important to understand the factors that influence forest productivity, and the associated intensity of interactions between trees and atmosphere, and soils.

Forest ecosystems are exposed to various factors that can potentially reduce their productivity (drought) or, conversely, enhance tree growth (extension of the growing season, so-called carbon and nitrogen fertilization), and these factors have not been constant in time and space (Babst et al. 2014). The climate is the main growth driving factor because it influences the availability of water which is necessary for turgor in cambial cells (Cabon et al. 2020). Thanks to warming in recent decades, trees are exposed to new climatic conditions (warmer and drier in most cases) with more frequent climate extremes (heat waves and associated droughts; Dannenberg et al. 2019, Sánchez-Salguero et al. 2017, Scharnweber et al. 2020). Climate-growth responses of trees to climate are therefore changing and may significantly differ between "normal" and "extreme" years. For instance, cold boreal forests were observed to lose their original sensitivity to temperature (D'Arrigo et al. 2004). Dry events in such ecosystems may likely have a high negative impact because the species growing there are not adapted to such conditions. While increasing concentration of CO_2 in the atmosphere leads to higher temperatures and associated droughts, with more CO_2, trees can also use available water more efficiently because of smaller losses while taking up the same amount of carbon dioxide (Körner et al. 2007). In theory, this increased efficiency in water use could at least partially reduce the negative impact of drought (Farrior et al. 2015). Fertilization of the landscape by nitrogen in small amounts may be beneficial for forest productivity, however in high concentrations it is a rather limiting factor since it leads to acidification (Kolář et al. 2015).

The results of the interaction between growth-promoting and growth-limiting influences are unclear and likely to be geographically variable. While increasing temperatures in lowland

temperate forests have a negative effect (Morales et al. 2020), a positive effect is observed in boreal forests and higher-elevation temperate forests (D'Orangeville et al. 2018). The more frequent and severe droughts associated with increasing temperatures have an increasingly negative impact (Allen et al. 2010). Besides elevation, the climate-growth responses of trees are influenced also by other spatial and environmental gradients such as bioclimatic zones, species composition, site fertility, or local topography (Montpellier et al. 2018, Schmied et al. 2023, Oberhuber and Kofler 2000). Therefore, it is necessary to study forest behavior at various spatial scales to understand at which level given factors become important.

Growth-promoting and growth-limiting influences are not only spatially-temporally variable but may also vary between tree biomass compartments such as leaves, stem, and roots (Bernoulli and Körner 1999, Kannenberg et al. 2019a, Anderegg et al. 2013). Each of these parts is physiologically different and has different functions, therefore it is likely, that also their climate-growth responses will vary (Fatichi et al. 2014). It was observed that the growth of leaf and wood biomass are both sensitive to slightly different time windows within a year (Seftigen et al. 2018). In drought conditions, trees seem to prefer the growth of leaf biomass since it is a crucial organ for the assimilation of carbon (Kannenberg et al. 2019a). These diverging responses might have important implications for answering the question of the higher importance of source (carbon assimilation in leaves) or sink (sequestration in wood) growth limitation (Anderson-Teixeira and Kannenberg 2022).

The main objectives of this doctoral thesis are (i) to discern the response of Scots pine (*Pinus sylvestris*; PISY) and Norway spruce (*Picea abies*; PCAB) to the climate and extreme events in Central Europe and then (ii) to identify spatial variability of these responses from landscape to regional-scale level. The final objective is to (iii) compare climate-growth responses of stem biomass (tree rings) and NDVI (leaf greenness and biomas).

2. Stem biomass

2.1 Stem biomass formation

Stem biomass (xylem, wood) is formed by assimilated products of photosynthesis, which is the process by which plants convert sunlight, water, and carbon dioxide into glucose (a form of sugar) and oxygen. Formation of stem biomass (xylem, wood) is a crucial process for trees because it influences the amount of water and hence nutrients that they can transport and, most importantly, their competitive ability (Schweingruber 1988). In the seasonal climates, trees are changing wood structure within the year due to changes in meteorological conditions and solar angle (Schweingruber 1988). At the beginning of the growing season (spring), coniferous trees are producing mainly tracheids with large diameters and thin walls because they need to transport a lot of water (light earlywood) (Fig.1). Later in the summer, they create denser wood which is formed by smaller tracheids with thick walls (dark latewood; Fig. 1) with supportive function increasing the stability of the stem (Cuny et al. 2014). These changes in wood structure lead to the creation of tree rings, which might be used as a time series of wood biomass production with annual resolution (Cuny et al. 2016). The proxies derived from the tree rings, such as width and structure, store information about the conditions prevailing at the time of the formation of the tree ring. This makes the time series of tree rings an important tool for detecting environmental changes and reconstructing their trends (Fritts 1976). Several factors are involved in tree growth, as described by Cook's model:

$$G = A + C + D1 + D2 + E$$

Where G is the width of a given tree ring, A is the age trend, C denotes climatic factors, D1 is endogenous factors (genetics, disease), D2 describes exogenous disturbances, and E is random environmental effects. Physical-geographic factors are represented in this model by the variables C (climate), and D2, by which we mean factors such as slope movements, floods, fires, and other disturbances in the landscape (Cook 1985).

The climate is generally the most important factor in tree growth because precipitation and temperature affect available soil moisture, evapotranspiration, photosynthetic activity, growing season length, and tree phenology (Fritts 1976, Schweingruber 1988). The cross-dating principle represents evidence of the crucial effect of climate on tree stem growth (Douglas 1941).

In trees, water deficit leads to reduced growth, reduced cell wall thickness (especially in latewood), cell collapse, or failure to form a tree ring (often in the case of loss of foliage). False

rings, rows of resin ducts, or poorly lignified cells may also occur (Pallardy 2008). Hydrological influences such as long-term waterlogging are also reflected in the tree rings. In some locations, typically in the floodplain, there may be a problem of excess water. In such cases, soil aeration is reduced, which slows down the growth of the root system and, as a result, high groundwater levels can lead to an overall reduction in tree growth (Vaganov et al. 2006). In such cases, there is a reduction in vascularity because moisture is abundant and the tree does not need to invest as much in the formation of the conducting apparatus as it normally would (Kozlowski 1997).

Trees are also affected by external physical-geographical factors such as landslides, avalanches, debris flows, fires, and floods (Stoffel 2006, Seifert et al. 2017, Arbellay et al. 2012). Although these are very short events in the development of the tree ring, the energy exerted is very concentrated and can be reflected in the tree ring as a scar or other symptoms of physical damage to the stem (Arbellay et al. 2012, Krause and Křížek 2018).

While soil characteristics such as nutrient levels or moisture do influence the formation of tree rings (Schmied et al. 2023, Rabbel et al. 2018), they are more likely to be reflected in the overall productivity of the given site, whereas growth trends and significant years are climate-controlled (Fritts 1976).

Figure 1: Transverse section of coniferous tree rings (by Hana Kuželová).
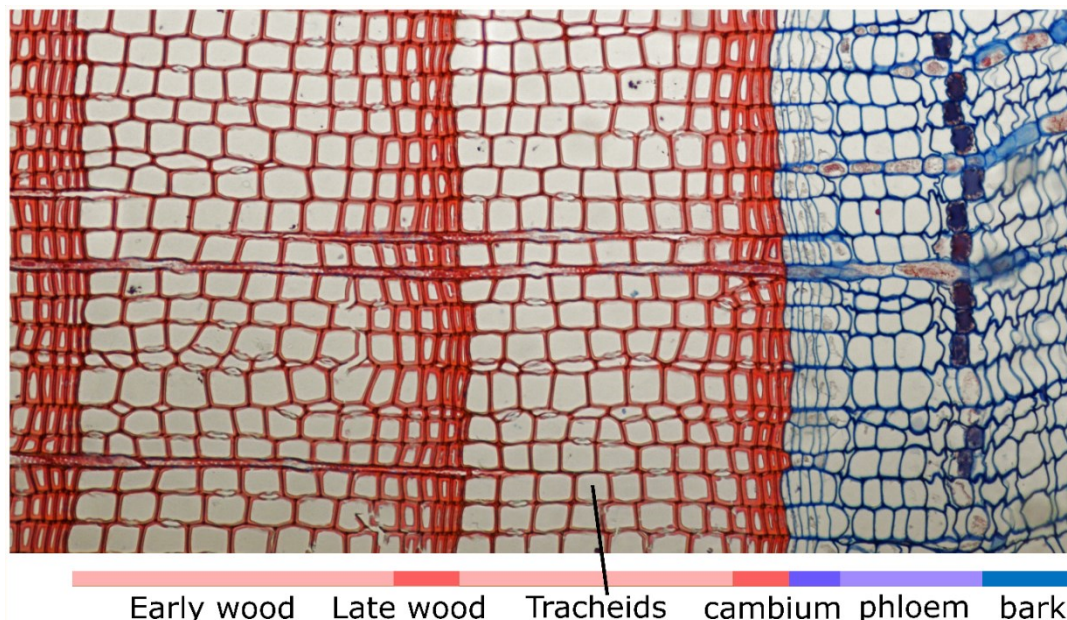
2.2 Response of stem biomass to drought

Radial growth of the stem is strongly dependent on available moisture because it influences turgor and hence the ability of cambial cells to divide (Fatichi et al. 2014). Stem expansion caused by dividing and enlarging wood cells in the cambium is an irreversible process. However, there is also reversible shrinking and swelling of stems which is caused by tree water deficit (Fig. 2; Zweifel 2015). During drought, the stomata are closed in order to reduce water loss by transpiration and therefore there is small carbon uptake which in a longer period may lead to carbon starvation. In such a case, the tree may allocate less carbon to wood formation, leading to reduced radial growth, narrower tree rings, and higher vulnerability to mortality (Wang et al. 2021).

Figure 2: Stem radius fluctuations (SR, black line) divided into the stem growth (GRO, red line, and areas) and stem shrinkage at tree water deficit (TWD, blue line) from dendrometer data (Zweifel 2015).
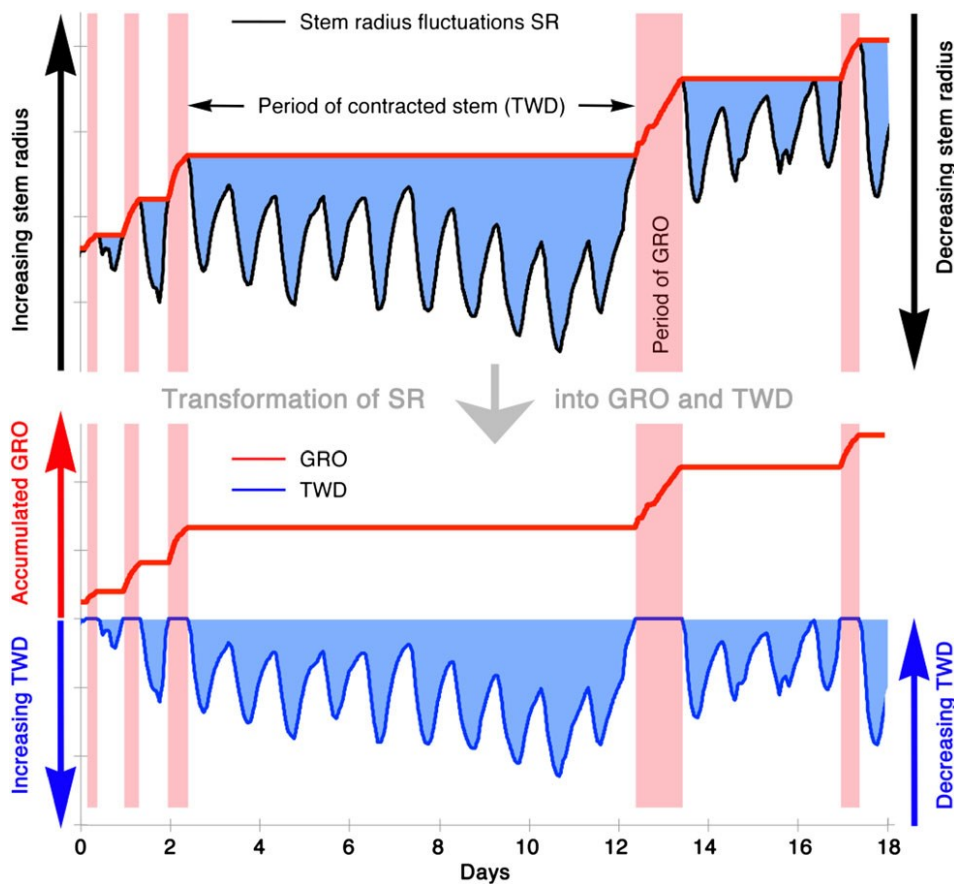
During periods of low water potential (bellow cca -2.5 MPa; Mayr et al. 2020) and hence a large tree water deficit in the stem, the negative pressure created by transpiration can lead to air being drawn into the xylem and cause embolisms (presence of air bubbles in tracheids). These embolisms block the flow of water and can result in hydraulic failure (Mayr et al. 2020). Woody plants have developed a mechanism for embolism repair, so-called "cavitation refilling" when neighboring living cells surrounding the embolized vessel can actively transport water and sugars into the affected xylem, pushing out the air bubble and re-establishing water continuity (Klein et al. 2018).

Climate change in temperate forests is manifested by the increasing frequency and impact of extreme climatic events such as droughts and heat waves (McDowell et al. 2020). Droughts have serious impacts on tree growth (Sánchez-Salguero et al. 2017, Scharnweber et al. 2020, Morales et al. 2020), mortality (Camarero et al. 2015, Allen et al. 2020, Vanoni et al. 2016, DeSoto et al. 2020) and overall ecosystem productivity (Kolus et al. 2019). On the contrary, warming in a cold environment is reflected by increasing growth trends (D'Orangeville et al. 2018, Ponocná et al. 2016). A lower frequency of growth depressions caused by a cold growing season or frost events in spring can be expected (Vitasse et al. 2019), however, it is a matter of time before the temperatures will be too high even in boreal and cold montane forests.

In common European conifers, approximately 35–50% of tree biomass is located in the stem (Bernoulli and Körner 1999, Reich et al. 2014), with annual wood production representing approximately 15–20% of total assimilated carbon (Klein and Hoch 2015). The amount of carbon stored in stem during the growing season is determined by available resources, climate-driven cambial cell division activity, and allocation strategies into stem, foliage, roots, non-structural carbohydrates, and respiration (Fatichi et al. 2014, Cuny et al. 2015, Rossi et al. 2016). As a result, the time series of annual stem increments are closely related to climatic factors, including extreme events, as demonstrated by the use of extremely narrow annual rings (negative pointer years) as indicators of sudden cooling (Battipaglia et al. 2010) or significant drought events (Cook et al. 2015). In temperate parts of Europe, extreme reductions in tree growth (so-called pointer years; Schweingruber 1988) have significantly contributed to declines in ecosystem productivity (Trotsuik et al. 2020). In Central Europe, the years 1992/1993, 1996, 2003, 2015, and 2018 are often cited as having been recorded in lowland areas throughout Western and Central Europe (Neuwirth et al. 2007, Lebourgeois et al. 2010, Rammig et al. 2015, Vitali et al. 2017, Vitasse et al. 2019). All of these years were very dry in various parts of season, but in some cases, there was an additional effect of low temperature during the

growing season or severe frosts at the beginning of the growing season (1948, 1956, 1976, 1996) (Neuwirth et al. 2007, Bauwe et al. 2013, Kolář et al. 2017). Other years, typically 2003, were the result of a very pronounced heatwave, and its impact on tree growth can be observed in the Czech Republic (Kolář et al. 2017), Germany (Bauwe et al. 2013), Switzerland, and northern Italy (Lévesque et al. 2013). The growth-reduction effect of the year 1976 has probably the largest areal extent, a consequence of a very pronounced and long drought, additionally supported by frosts during May. Growth declines this year are reported in northern Italy, Switzerland (Lévesque et al. 2013, Neuwirth et al. 2004), Benelux, Germany, Czech Republic (Babst et al. 2012), and northern Poland (Koprowski et al. 2012).

Differences in climatic conditions between high- and low-elevation forests have often resulted in opposite responses to drought, determined by their relative position to the ecological optimum of the species (Neuwirth et al. 2007, Zang et al. 2014, Trotsuik et al. 2020). Hot and dry events were negative in the lowlands (formation of a narrow annual ring) and positive in the mountains (formation of a wide annual ring) (Rolland et al. 2000, Neuwirth et al. 2007, Lebourgeois et al. 2010, Charru et al. 2017). From the mountainous regions of central and eastern Europe, the years 1913, 1942, 1954, 1974, and 1992 are reported as narrow tree rings (Hartl-Meier et al. 2014, Treml et al. 2015, Rammig et al. 2015). This basic overview suggests that towards the present day, growth reductions are becoming more frequent. Sidor et al. (2019) recorded the increasing frequency of extremely narrow tree rings of *Pinus sylvestris* in Romania since 1980. The increasing impact of negative pointer years has also been observed in *Picea abies* and *Abies alba* in eastern France (Rolland et al. 2000). In central Europe, temperatures have increased by 1 °C since the beginning of the 20th century (Allen et al. 2018), leading to higher evaporation (Mozny et al. 2020) and soil water deficits (Hanel et al. 2018). Superimposed recent summer heat waves (2003, 2015, 2018, Scharnweber et al. 2020) manifested in extreme reductions in growth followed by an overall decline in forest health across large areas of Europe (Etzold et al. 2019, Sidor et al. 2019, Schuldt et al. 2020). However, whether the current frequencies of extreme growth reductions represent a continuation of a long-term trend or are unprecedented in the context of an entire century remains unknown. In addition, there is limited information available on species-specific trends in extreme growth reductions and differences in these trends between warm and cool parts of a species distribution range.
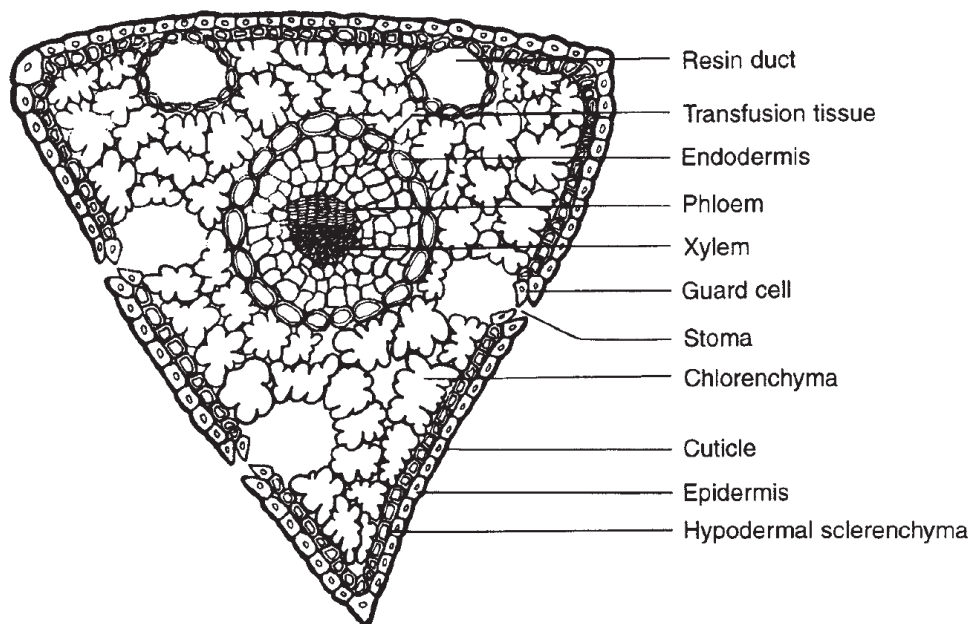
3. Leaf biomass

3.1 Leaf biomass formation

Needles of coniferous trees are well adapted to survive cold conditions and have several advantages over broad leaves found on deciduous trees. Needles have a smaller surface area compared to broad leaves, which helps to reduce water loss through transpiration. This adaptation is crucial in regions with cold winters, where water availability may be limited due to frozen soil (Bijlsma and Loeschcke 1997). The needles of coniferous trees often have a thick waxy coating (cuticle; Fig. 3) on their surface, which helps to reduce water loss through evaporation and protects the needles from freezing temperatures and damage caused by harsh weather conditions (Eckenwalder 2009). Moreover, the needle shape allows conifers to efficiently capture sunlight from various angles, maximizing their ability to carry out photosynthesis in low light conditions which helps them to thrive in areas with less sunlight, such as dense forests or regions with long winters (Zarter et al. 2006). Most coniferous trees are evergreen (they retain their needles throughout the year) which is possible due to the abovementioned needle adaptations. This allows them to continue photosynthesizing during the winter when deciduous trees have shed their leaves (Zarter et al. 2006). By maintaining their needles, coniferous trees can take advantage of any available sunlight and carry out photosynthesis even in the colder months. Moreover, the needle-like structure is changing along the temperature gradient to help them survive in a cold climate and unfavorable environmental conditions (Jankowski et al. 2017). Needles of conifers in cold environments tend to be shorter, have thicker cell walls, narrower and more resistant tracheids, and wider resin ducts. Moreover, such needles live longer and in general have higher leaf density and leaf mass per area (Jankowski et al. 2017, Savolainen and Hurme 1997).

The beginning of needles' growth at spring in lower latitudes is driven by photoperiodism (sensitivity to daylight hours increase), while in higher latitudes (cold areas) it is sensitive rather to temperature rise (Zohner et al. 2016). Buds on branches begin to swell and expand until they burst to open and the new needles start elongating (Rossi et al. 2009). During the peak summer, the newly formed needles reach their maximum size and develop their characteristic shape. The needles contain chlorophyll, hence they are freshly green, and actively involved in photosynthesis, which is reflected in their spectral properties by reduction of reflectance in the red part of the spectrum and increase in the near infra-red part (Knipling 1970). In autumn, the needles undergo physiological changes in response to decreasing daylight hours and colder

temperatures. The main change is the accumulation of energy (carbohydrates and other essential compounds) in the medullary rays, cambium, roots, and needles, which will be used during the winter months (Langenfeld-Heyser 1987). In winter, coniferous trees face harsh conditions such as freezing temperatures, reduced sunlight, and limited water availability due to frozen soil. Although their metabolic activity slows down, they continue to photosynthesize to a certain extent if the threshold temperature is exceeded taking advantage of any available sunlight (Freeland 1944). The exact timing of needle development can vary among different conifer species and can be influenced by local climate conditions and environmental factors (Jankowski et al. 2017).

Figure 3: Cross section of eastern white pine needle (adapted from Pallardy 2008).

3.2 Response of leaf biomass to drought

Drought can have significant effects on the needles of coniferous trees, including changes in their structure, physiology, and chlorophyll content (Moran et al. 2017). During a drought, the lack of soil moisture can lead to water stress in coniferous trees. As a result, the needles may become dehydrated, and lose turgidity, and therefore they may be wilted, curled, or even start leaf shedding (Brun et al. 2020). Drought conditions during spring with water potential of needles about -3 Mpa (Haberstroh et al. 2022, Wright et al. 2013) can inhibit the growth of new

needles or slow down their growth (Haberstroh et al. 2022). The formation of new needles may be delayed or limited due to water scarcity, which can lead to thinner foliage and reduced overall needle density (Wright et al. 2013).

Chlorophyll molecules are sensitive to environmental stressors, and prolonged drought can lead to the breakdown of chlorophyll pigments (Pukacki and Kamínska-Rozek 2015). This degradation reduces the chlorophyll content in the needles, resulting in a loss of their green color. They can appear lighter, yellowing, or even reddish-brown in severe cases (Anderegg et al. 2012). Drought-induced changes in needles, including dehydration and chlorophyll degradation, can impair photosynthetic activity. With reduced chlorophyll content, the ability of needles to capture sunlight and convert it into energy through photosynthesis is reduced. This can lead to a decrease in the tree's overall photosynthetic capacity and reduced growth. The physiological changes in the needles weaken the tree's resilience, making it more susceptible to attacks from pathogens and pests (Kolb et al. 2016). Coniferous species vary in their tolerance to drought, and the specific effects can differ depending on the severity and duration of the drought event (Castellaneta et al. 2022). Furthermore, some coniferous trees have adaptations that help them cope with drought, such as deep root systems or thick waxy coatings on the needles that reduce water loss (Pallardy 2008).

Reactions of conifers to droughts are also influenced by their (an)isohydricity, which describes their behavior in relation to their water status (Kannenberg et al. 2019b). This term has been applied to several phenomena, however, the most common one is changes in leaf water potential relative to soil water potential (Feng et al. 2019). In dry conditions, isohydric plants regulate the opening of their stomata so as not to lose so much water even if it means limiting their photosynthetic activity, so they maintain their leaf water potential relatively constant despite changes in soil water potential or vapor pressure deficit. On the other hand, anisohydric plants allow their stomata to remain open even in the face of decreasing water availability which can be beneficial for maintaining photosynthetic activity and growth, so they show higher fluctuations in leaf water potential (Ratzmann et al. 2019). However, even this (an)isohydricity behavior is influenced by the specific environmental conditions of a given place (Feng et al. 2019). Our species under study (*Picea abies* and *Pinus sylvestris*) are both categorized as rather isohidric trees and *Pinus sylvestris* even more than *Picea abies* (Martinez-Vilalta et al. 2014, Klein 2014).

Changes in structure and especially in color are imprinted in the leaf's reflectance (Fig. 4) because the stressed vegetation has less water and chlorophyll and consequently it has higher reflectance in the red part and lower in the near-infrared part of the spectrum. Based on various indices comparing the reflectance in the red edge region of the spectrum (approximately 700–800 nm) it is possible to estimate the health of vegetation, biomass increments, or chlorophyll content (see more in chapter 7.2).

Figure 4: Reflectance of healthy and stressed plants in visible and infrared part of electromagnetic spectrum. The vertical dashed line denotes the red-edge spectral region (Agrio 2023).
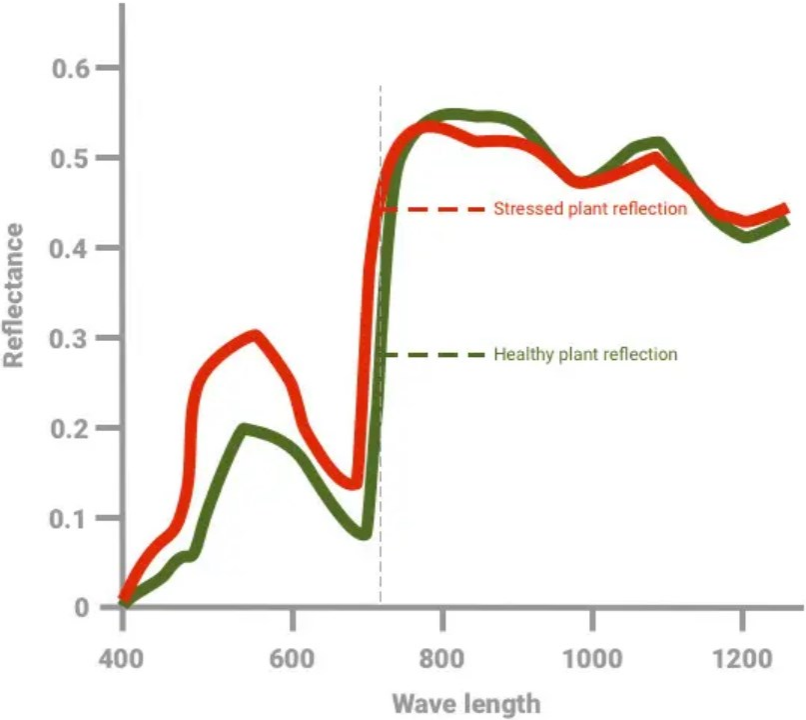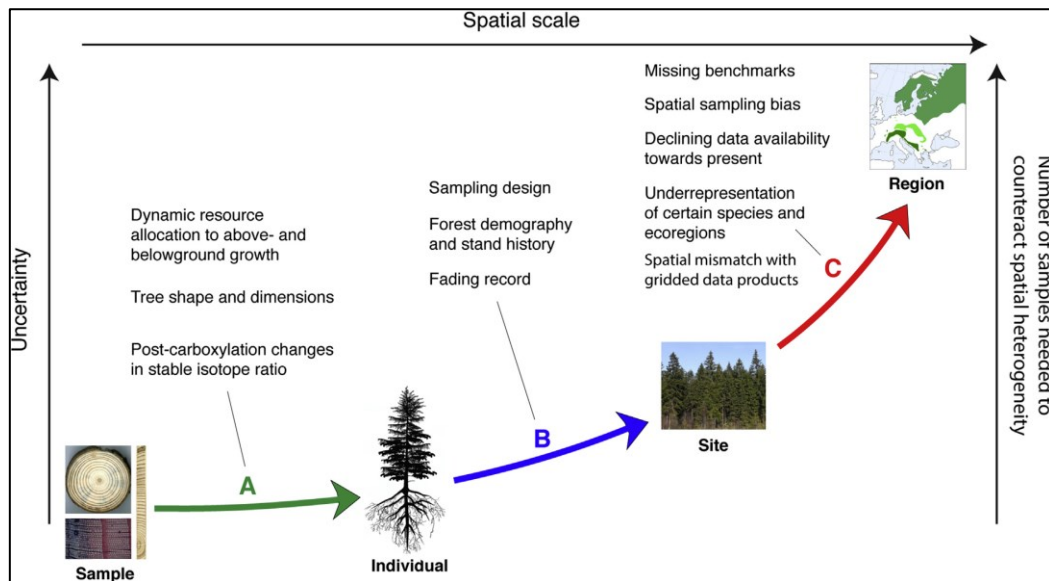
4. Relationship between stem and leaf biomass

To describe the effect of drought on the productivity of woody plants it is possible to use a tree-ring analysis, which provides detailed information on trends in stem biomass at the tree or stand level (Girardin et al. 2016, Babst et al. 2017). An alternative method to determine biomass trends of forests is remote sensing, where satellite data provide information mainly on the canopy, hence leaf biomass and greenness as a proxy for chlorophyll content (Vicente-Serrano et al. 2016, Song 2012). Theoretically, information on stem biomass should be correlated with leaf biomass, and then the tree rings could be extrapolated to the landscape level using satellite data (Babst et al. 2018) (Fig. 5). It has been shown that the Normalized Difference Vegetation Index (NDVI) correlates with wood, seed, and foliage production (leaf area index) (Wang et al. 2004, Bhuyan et al. 2017, Bunn et al. 2013, Schröder and Körner 2018, Xu et al. 2019).

However, the majority of studies report certain spatiotemporal variability in this relationship (Vicente-Serrano et al. 2016, Lopatin et al. 2006). The spatial variability may be influenced by various factors, such as climatic conditions at different latitudes (Kaufmann et al. 2008), forest types (Bhuyan et al. 2017), topography and associated microclimatic conditions (Babst et al. 2018), or even the resolution of satellite imagery (Bhuyan et al. 2017) and the technical parameters of satellite imagery like spatial and temporal resolution, used vegetation index or the range of reflectance bands used by the given sensor may also play a role. So far, the majority of studies used low-resolution satellite data (max 250 m per pixel or more) since they cover large areas, e.g. et global to continental scales (Vicente-Serrano et al. 2012, Bhuyan et al. 2017), continents (Bunn et al. 2013, Kaufmann et al. 2008) or individual countries (DeRose et al. 2011, Xu et al. 2019). It has been shown that the correlation of tree rings and NDVI increases with the spatial resolution of satellite images (Bhuyan et al. 2017), however, there are almost no studies investigating the relationship at the landscape level using high-resolution Landsat satellite data (30 m per pixel), which is surprising since relatively long Landsat time-series allow direct comparison with tree-ring time series.

Figure 5: Uncertainties in the process of extrapolating tree rings to landscape (Babst et al. 2018).

The spatial variability in the relationship between tree rings and vegetation indices might result from climatic constraints of both biomass compartments (stem and leaves) which may vary across environmental gradients such as elevation and latitude (temperature gradients), longitude (in some cases moisture gradient), terrain topography, species composition and age of trees. While in warm areas the water availability is the main constraint for both biomass compartments (hence increasing their coherency) in cold environments the tree rings and NDVI may show different climatic signals. Whereas tree rings in high elevations respond positively to temperature (stem growth is driven by growing season temperature, Babst et al. 2013), NDVI (photosynthesis and hence canopy greenness) can be negatively affected due to direct radiation (Urban et al. 2012) and an increase in tropospheric ozone with elevation (Ainsworth et al. 2012). In moisture-limited areas both stem and leaf biomass show similar trends, however, the climatic signal of tree rings tends to be stronger which was observed by studies based on both the remote sensing data and eddy covariance data (Kannenberg et al. 2020, Moreno-Fernández et al. 2022, Gazol et al. 2018a, Kannenberg et al. 2019c, Schwalm et al. 2017). This is caused by low water potential, which limits the transport of assimilated carbon in the tree (Fatichi et al. 2014) and reduces the turgor in cells which is crucial for wood formation (Cabon et al. 2020). This leads to the accumulation of non-structural carbohydrates that might be used for the growth of roots (Teets et al. 2022) or stored for the next year. This means that in dry conditions the sink

processes (ability to invest assimilated carbon) are more important than the source processes (creation of assimilates; Cabon et al. 2022).

The temporal variability in the relationship between wood and leaf biomass may be caused by different biomass allocation strategies following drought events. It has been observed that the impact of extreme drought is imprinted in tree rings in a drought year (Gazol et al. 2018b) as well as more years later (Wu et al. 2017). Water stress damages the xylem or depletes reserves which suppresses stem growth even though the climatic conditions return to normal levels for up to four years (drought record inertia; Wu et al. 2017). On the other hand, carbon storage and investment into leaves may be little altered (Anderegg et al. 2015) or even show enhancement (Rita et al. 2019, Dong et al. 2022, Gazol et al. 2022). Trees invest more carbon in the canopy to gain more assimilates for the restoration of the whole body (Kannenberg et al. 2019c, Anderegg et al. 2013).

In general, the topo-climatic conditions and the nature of the vegetation cover cause spatial variability in the impact of drought, and thus in the potential inertia of its record. Therefore, the question is which factors influence varying responses of foliage and tree rings at the landscape level, where different topographic conditions and different stand characteristics play a role. Understanding this variability could explain the strategies of tree biomass generation in response to drought (investment in stem and leaf biomass) and help in developing models describing the relationship between leaf and stem biomass formation at the landscape level.

5. Topographic variability and its influence on growth

Geographic position and topography of relief is an important factor influencing tree growth since it represents various environmental gradients like prevailing climatic conditions and has an effect on site-specific factors like solar radiation, moisture availability, or soil properties.

One of the most important topographic factors is elevation because it represents a temperature gradient (Brinckmann et al. 2016). Woody plants in the lowlands of Central Europe are limited by available moisture, whereas in the mountains, low temperature is the main limiting factor (Hartl-Meier et al. 2014). The elevation where the overall climatic limitation is the smallest corresponds with climatically optimal conditions for given tree species. In terms of pointer years, the effect of drought events is strongly negative in lowland areas (Lebourgeois et al. 2010). On the other hand, in higher elevations, these events may be positive because they are connected with high temperatures reducing the temperature limitation (D'Orangeville et al. 2018). In the Czech Republic, *Picea abies* is increasingly limited by drought, with growth declines of up to 70% compared to normal in extreme drought events (Tumajer et al. 2017, Krejza et al. 2021). Drought-induced growth declines and low resilience to these events are evident across the entire elevation gradient, but most pronounced in mid-elevations (around 600 m above sea level; Krejza et al. 2021, Bose et al. 2020). The effect of elevation may be also indirect, for instance, in areas near the tree line where trees tend to be limited by available soil nutrients (mainly nitrogen), low temperatures also lead to reduced growth by slowing down the process of mineralization (Grace et al. 2002).

The geographic position is highly important because it determines the bioclimatic zone and hence prevailing conditions and physical processes on site. Similar effects as elevation are connected with latitude since it also represents temperature gradient and conditions in forest stands in high mountains are similar to boreal areas (Pfadenhauer and Klötzli 2020). Regarding responses to extreme climatic events, an increase in the resilience index and a decrease in the recovery index with latitude were observed (Gazol et al. 2017). On the other hand, Bose et al. (2020) did not find any significant effect. In some cases, the longitude also matters because it may represent the gradient of maritime/continental climate and thus also the gradient of moisture availability in the growing season (in the Czech Republic for instance; Mikolaskova 2009).

Local topographic aspects such as the orientation of slopes to solar radiation (represented for example by heat load index) may play a role since it determines surface temperature (Dearborn and Danby 2018). Also, variables like topographic wetness index or slope inclination can have

an effect because they represent terrain curvature and therefore stands with water accumulation or loss (Rabbel et al. 2018, Tumajer and Treml 2017). In mountainous areas, slope inclination has also an indirect effect because it can cause slope movements like avalanches, landslides, or debris flows, which can be manifested in the removal of trees or impacts on tree growth patterns (Stoffel 2006).

The importance of all these effects is however strongly dependent on the considered spatial scale. At the landscape level, the elevation or the geographical position has no effect and the local features matter a lot. On the other hand, at a continental scale, the local topography may be outperformed by variability represented by large geographical and environmental gradients.

6. Growth trends and climatic responses of study species in Central Europe

In Central Europe, the coniferous forests are dominated mainly by *Pinus sylvestris* (PISY) and *Picea abies* (PCAB). These species represent the main component of forest ecosystems with a large area and economic importance. On the territory of the Czech Republic, PCAB forms approximately 48 % of forest stands in the long term and PISY is the second most important species with 16 % representation (Forestry Report 2021).

6.1 Pinus sylvestris

Pinus sylvestris is a light-demanding, deep-rooting species with great plasticity tolerating a broad spectrum of site conditions. Due to the high ecological valence, it occurs in a large area from northern Spain and Scotland, across Scandinavia and central Europe to the Far East. Generally, it tends to be found in the lowlands in the northern parts of its range, while in the south it is found mainly at higher altitudes (reaching up to 2600 m above sea level in the Caucasus). Fire activity is important for this species. In some parts of Siberia, it is only found due to fires that remove more competitive species (typically spruce, Adámek et al. 2016). Given current global warming, the range of *Pinus sylvestris* can be expected to shift more northwards in the future and gradually disappear from southern areas (Durrant et al. 2016).

The climatic signal of *Pinus sylvestris* is strongly site dependent and it is therefore difficult to identify areas with a clear type of climatic signal, but at least some trends can be observed. In north-central Europe in North Germany and Poland, the climate in February and June is the main determinant of PISY growth. Mild, wet winters promote growth, while warm, dry summers tend to reduce ring width (Cedro 2006, Pérez et al. 2005, Bauwe et al. 2013). In Central Germany, strong correlations with the Palmer drought severity index (PDSI) can be observed, not only for PISY but also for beech and sessile oak (Friedrichs et al. 2009).

The site dependence of the climate signal increases with elevation; factors such as slope and orientation, or soil type play a role. In the Czech Republic, this is strongly reflected, as shown, for example, by the work of Mácová (2008), who compared the influence of climate on trees in different locations. Samples were taken in three different areas of the Czech Republic (on sandstone cliffs, on dry warm sites, and cool wet sites). The results clearly show that the tree-ring widths respond positively to February and March temperatures at all sites, and the effect of rainfall was also significant. This signal was strong on dry and warm sites, but very weak on rocky sites (even weaker than at cool and wet sites). This is probably due to the ability of PISY to efficiently use the water deposited in weathered rock crevices. In the Carpathian region, the

signal of PISY also varies considerably between sites. At elevations around 800 m above sea level, trees respond mainly to PDSI and rainfall (Büntgen et al. 2010, 2012). In contrast, individuals growing at higher elevations above 1000 m a.s.l. show positive correlations with temperatures and do not respond to precipitation amounts (Büntgen et al. 2012).

In Central Europe, PISY generally shows positive correlations with February and often also January temperatures (Friedrichs et al. 2009). In the case of cold regions, March temperatures tend to be limiting (Feliksik & Wilczyński 2009, Koprowski et al. 2012). Positive effects of precipitation and, in general, the presence of soil moisture and negative effects of temperature are also frequent (Koprowski et al. 2012). Positive responses to temperature are also typical in humid and cold regions, possibly in mountain and foothill areas (Feliksik & Wilczyński 2009). Groundwater level also has a significant effect on the tree-ring widths. For example, pines growing on alluvial terraces are significantly limited by the amount of water in rivers and connected depth of the groundwater level. At high groundwater levels, pines have significantly smaller radial increments (Polacek 2006).

6.2 Picea abies

Picea abies is a typical tree of boreal and subalpine forests which naturally growths from mountaines and cold ares of central and northern Europe to Siberia. However, it was also introduced to Britain and lowlands of western and central Europe. The elevation span extends from the coast to about 2200 m above sea level in the Alps (Durrant et al. 2016). It is an undemanding tree species, and if it has sufficient moisture, it grows well on stony and acid soils, in cold areas, swamps, etc. However, acid rains, drought, and fires have a strong negative effect (Durrant et al. 2016). Its stands are concentrated mainly in southern Germany, Austria, and the Czech Republic, however, it is widespread also in the Carpathians and the Scandinavian Peninsula. In low and medium elevations of Central Europe, it shows high annual increments, making it widely planted and used in the timber industry (Durrant et al. 2016).

Many authors have studied the influence of climate on the *Picea abies* in its natural mountain environment in Central Europe. The results of these studies clearly show that the major climatic factor for growth is temperatures in the summer months (Babst et al. 2013) with correlations around 0.5 (Treml et al. 2015). Rydval and Wilson (2012) reported correlations even up to 0.67 with average temperatures from April to July in the Jizera Mountains. In mountain areas, the orientation of the slope and aspect should be taken into account, but its influence varies considerably between sites and may even be completely insignificant at the highest elevations

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(Treml et al. 2012). In general, while in high elevations temperatures during June-July are the main growth factor, around 900 m above sea level there is almost no climatic limit to spruce growth (Šagát et al. 2021), and at lower elevations and in the foothills, there is mainly the influence of precipitation and drought (Hartl-Meier et al. 2014, Čejková and Kolář 2009). A similar change of climatic signal is reported also along a latitudinal gradient (Mäkinen et al. 2002). PCAB as a shallow-rooting species is sensitive to drought which is most pronounced in lowlands (Tumajer et al. 2017). Spruce is supposed to be increasingly vulnerable to drought and heat waves with ongoing warming (Bošela et al. 2021).

Many PCAB tree-ring chronologies from the Czech Republic show a depression of growth in the 1970s and 1980s caused by acidification (mainly by sulfur and nitrogen; Kolář et al. 2015). However, since the 1990s the situation has improved, which can be observed in the tree rings (Treml et al. 2012). Similar trends are also evident in chronologies from the Ore Mountains (Kroupová 2002) or the Jizera Mountains (Rydval and Wilson 2012).

7. Material and Methods

7.1 Study areas and sampling strategy

7.1.1 Treml et al. 2021 (Global Change Biology)

To identify trends in extreme growth reductions, sites representing low elevations (200-600 m a.s.l.; 14 sites) and high elevations (900-1450 m a.s.l.; 14 sites) were selected for both study species sites in the Czech Republic and Slovakia (Fig. 6A, blue sites). The sampling was mainly carried out in the natural forests, but some sites were historically human-planted forests (typically low-elevation sites of PCAB), which are now part of protected areas without recent forestry management. At each site, about 40 dominant canopy-level trees without visible damage (1219 trees in total; Fig. 6C) were cored, and soil parameters such as soil depth, and soil particle size were determined to estimate soil water holding capacity.

7.1.2 Mašek et al. 2023 (Ecosystems) and Mašek et al. 2024 (International Journal of Biometeorology, in review)
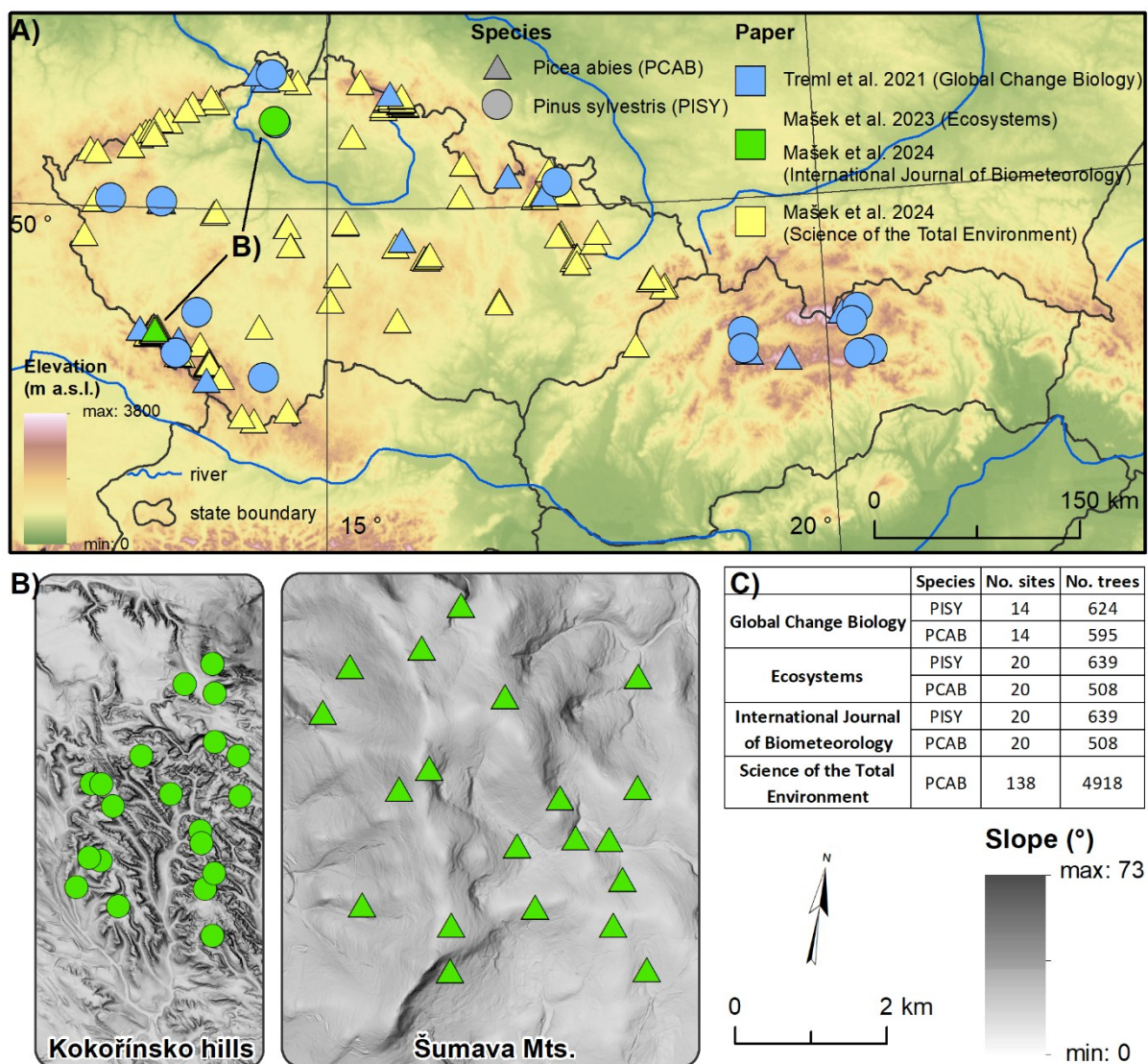
For purposes of linking the tree rings and satellite data at the landscape level, two areas with homogeneous monospecific forest canopies were selected: Kokořínsko hills (PISY) and Šumava mountains (PCAB; Fig 6A). In these areas, 20 representative sites were stratified and randomly selected based on landform (plateau, slope, valley bottom) and slope exposure (north, south; Fig. 6B). Each site was represented by a circle with a radius of 17 m, roughly corresponding to the pixel of a Landsat scene (30 m). In each plot, cores were taken from at least 26 dominant individuals and in four cases from all trees in the plot. For each tree, its diameter at breast height (DBH), height, and crown size were measured and we determined whether it reached stand level or whether it is below the main canopy level (thus its crown is not reflected in the remote-sensed canopy). All sites were located out of stands affected by recent disturbances.

7.1.3 Mašek et al. 2024 (Science of the Total Environment)

Tree-rig data for the last study focused on PCAB were obtained from the database TreeDataClim, which contains tree-ring measurements covering the main tree species in the Czech Republic (Fig. 6A).

In all cases the tree cores were processed by standard dendrochronological methods (Stokes and Smiley 1981): samples were dried, glued to wooden supports, and sanded to increase the visibility of tree rings. For measuring tree-ring widths, the program WinDendro was used (Regent Instrument 2011), and analysis was performed on high-resolution scans of sanded cores (1200 dpi). Tree rings were first automatically identified by the program, then visually checked and corrected if necessary. Cross-dating of the tree ring series was performed in PAST 4 (Knibbe 2004) by visual and statistical control using a t-test and Gleichläufigkeit coefficient. Further analyses were carried out in the R (R Core Team 2020).

Figure 6: Location of sampled sites for both study species (symbol) and each paper (color) at large-scale level (panel A). Sites sampled for landscape-level investigations in the second and third papers (panel B). Sampled species, amount of sites, and trees for each paper (panel C).

	Species	No. sites	No. trees
Global Change Biology	PISY	14	624
	PCAB	14	595
Ecosystems	PISY	20	639
	PCAB	20	508
International Journal of Biometeorology	PISY	20	639
	PCAB	20	508
Science of the Total Environment	PCAB	138	4918

7.2 Vegetation indices and remote sensing data

The NDVI (Normalized Difference Vegetation Index) is the most commonly used vegetation index based on the remotely sensed spectral properties of the canopy. NDVI is calculated from the basic spectral bands (red and near-infrared; NIR) so it is easily extractable from bands provided by almost any multispectral sensor. At the local scale, NDVI is used as a direct indicator of vegetation health and biomass. However, for large scales, it serves more as a dependent variable to predict a wide range of vegetation characteristics that are not directly detectable by remote sensing (Huang et al. 2020).

$$NDVI = \frac{(NIR - Red)}{(NIR + Red)}$$

NDVI is rather sensitive to "green understory" (Hais et al. 2019), so some studies use indices that account for this issue. The Normalized Difference Moisture Index (NDMI) is used to record drought in forest ecosystems based on satellite data (Hais et al. 2019, Wang and Qu 2007), or the Wetness Index to identify forest health (Crist and Cicone 1984, Skakun et al. 2003, Hais et al. 2019). These indices are based on NIR and Short-wave infrared (SWIR) bands making them more sensitive to defoliation (Hais et al. 2019).

$$NDMI = \frac{(SWIR - Red)}{(SWIR + Red)}$$

$Wetness =$ x1 * TM1 + x2 * TM2 + x3 * TM3 + x4 * TM4 + x5 * TM5 + x6 * TM6 + x7 * TM7

(where TM1-7 are spectral bands and x1-7 are coefficients for individual Landsat satellites)

A very common index is the Leaf area index (LAI), which is one of the most important parameters for modeling ecosystem processes such as carbon or water cycles (Gray and Song 2012). Several studies however report a high correlation between NDVI and LAI.

$$LAI = \frac{leaf\ area}{ground\ area}$$

For this dissertation, compiling the longest possible time series of multispectral satellite images with sufficient resolution was necessary. There are several satellites providing images of the Earth's surface in different spectral bands, but the vast majority of them were launched only in the late 1990s or early 21st century (Fig. 6; Zhu et al. 2018). In terms of temporal resolution, the MODIS would be a very good source of data since it has monthly information about NDVI. However, it has a spatial resolution of 250 m per pixel, which was not feasible for our purposes, because we were interested in landscape-level variability. The same problem applies to GIMMS

data (Global Inventory Modeling and Mapping Studies) which provide NDVI time series since 1981 but with a resolution of 8 km per pixel. Regarding quality, spatial resolution, and available bands, the Sentinel 2 would be perfect, unfortunately, the time series is too short (Fig. 7). Based on this, the only usable satellite was the Landsat satellite, which has been in operation since 1972. Unfortunately, as the spatial and spectral resolution of individual Landsat missions has varied over time, it is possible to construct a homogeneous set of satellite images from approximately 1985 onwards. At that time Landsat 5 was launched with a TM sensor and a resolution of 30 m per pixel, and the same parameters are still active today for Landsat 7 and 8. Therefore time series of vegetation indices were created for each site based on Landsat imagery (5,7,8) for the years 1985-2020 using Google Earth Engine. The aerial photographs (1982, 1992, 2004, 2015, 2018) were obtained to create a mask of undisturbed areas where acquired results are relevant.

Figure 7: Temporal range of available remote sensing datasets with high and medium resolution.
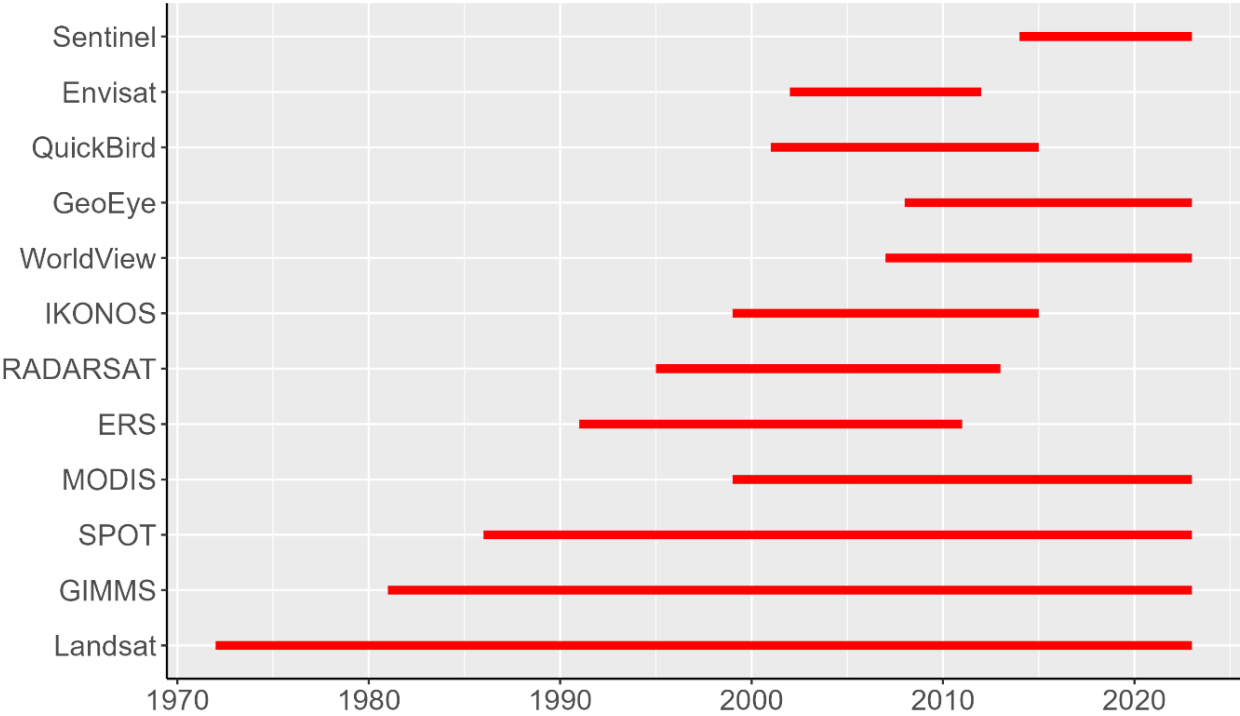
I calculated NDVI, NDMI, Wetness index, and some others like enhanced vegetation index (EVI), or soil-adjusted vegetation index (SAVI). The results for all those indices were heavily correlated (Fig. 8) so for easier comparison with other studies we carried out all the following analyses using NDVI only.

Figure 8: Correlation coefficients between time series (1985–2017) of vegetation indices: EVI, SAVI, Wetness, NDMI, and NDVI. Example for Pinus sylvestris site 20PL.
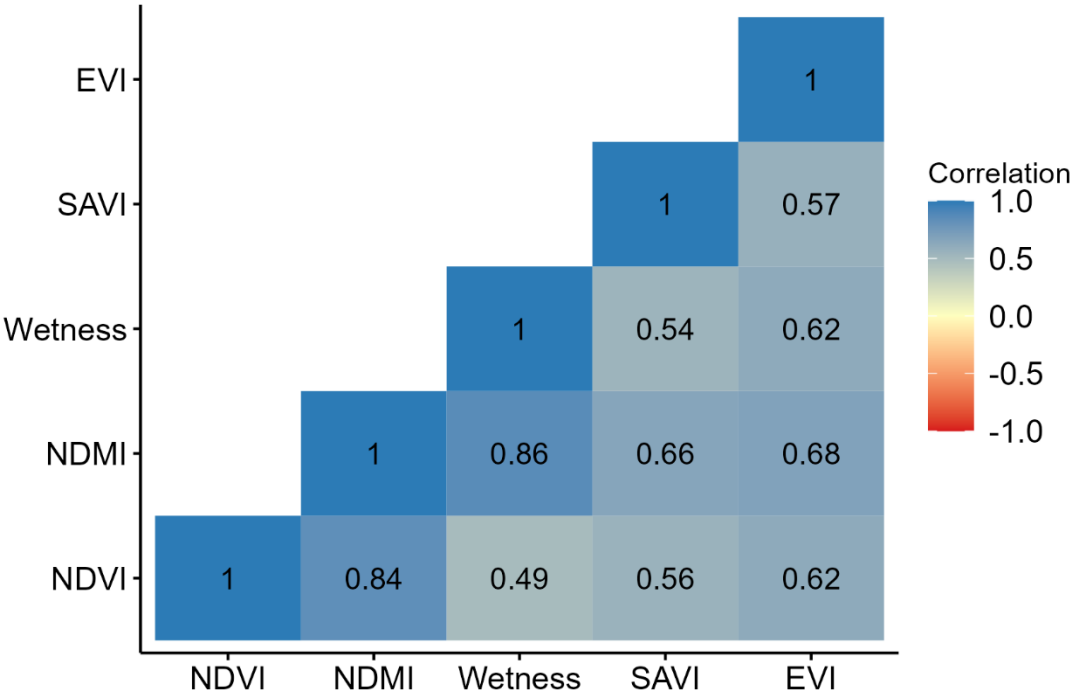
7.3 Statistical approach

The interaction between climatic conditions (mainly temperatures and Standardized Precipitation Evapotranspiration Index; SPEI) and growth variables (tree rings and NDVI) was analyzed by bootstrapped correlation analysis (Zang and Biondi 2015). To determine factors influencing climatic responses of both tree rings and NDVI, we used principal component gradient analysis (PCGA), analysis of variance (ANOVA) with post hoc test (Mašek et al. 2023), and spatial regression models (Mašek et al. 2024; Science of the Total Environment).

To inspect the influence of extreme climatic events such as droughts and heat waves on tree growth, there are two main approaches. The first is the determination of pointer-years (extreme growth changes) in the time series of tree growth (Schweingruber 1988) and explaining those

by climatic and other variables in linear mixed-effect models (Bates et al. 2015). To select pointer years, the relative growth change method (RGC) can be applied. In RGC, a given year's growth rate is compared to the average growth rate of several preceding years (Jetschke et al. 2019).

Another option is based on the forward selection of extreme climatic events in a time series of climatic variables and then calculating superposed epoch analysis (Chree 1913) or resilience indices (Lloret et al. 2011) to see if there is a significant growth response. Selection of extreme years may be done by taking for example 10 % of extreme values (highest or lowest depending on the variable), or a similar threshold (Sulikowska and Wypych 2020). In this case, it is important to be aware of long-term trends in time series of climate and if necessary to detrend them (Ols et al. 2023).

Both of these approaches were used in this study, the first in Treml et al. (2021) and the second in Mašek et al. (2024; International Journal of Biometeorology, in review).

8. Author's contribution statement

The presented thesis is composed of four publications related to the responses of tree rings and NDVI to drought. Their citation and contribution statement are provided in Table 1.

Table 1: List of publications included in this thesis

Nr.	Reference	Author's contribution (%)
1	Treml et al. (2021): Global Change Biology	40
2	Mašek et al. (2023): Ecosystems	80
3	Mašek et al. (2024): International Journal of Biometeorology (in review)	80
4	Mašek et al. (2024): Science of the Total Environment	70

I confirm the contribution of Jiří Mašek to the papers listed in Table 1.

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Doc. Mgr. Václav Treml, Ph.D.

9. Individual scientific papers

Chapter 9.1: Treml, V., Mašek, J., Tumajer, J., Rydval, M., Čada, V., Ledvinka, O., & Svoboda, M. (2021). Trends in climatically driven extreme growth reductions of Picea abies and Pinus sylvestris in Central Europe. Global Change Biology, March, 1–14. https://doi.org/10.1111/gcb.15922

Chapter 9.2: Mašek, J., Tumajer, J., Lange, J., Kaczka, R., Fišer, P., & Treml, V. (2023). Variability in Tree-ring Width and NDVI Responses to Climate at a Landscape Level. Ecosystems. https://doi.org/10.1007/s10021-023-00822-8

Chapter 9.3: Mašek J., Dorado-Liñán I., Treml V. (2024 in review). Responses of stem growth and canopy greenness of temperate conifers to dry spells. International Journal of Biometeorology.

Chapter 9.4: Mašek, J., Tumajer, Jan, Lange, J., Vejpustková, M., Kašpar, J., Šamonil, P., Chuman, T., Kolář, T., Rybníček, M., Jeníček, M., Vašíčková, I., Čada, V., Kaczka, R., Rydval, M., Svoboda, M., Nedělčev, O., Hais, M., & Treml, V. (2024). Shifting climatic responses of tree rings and NDVI along environmental gradients. Science of the Total Environment, 908(October 2023). https://doi.org/10.1016/j.scitotenv.2023.168275

10. Conclusions

This doctoral thesis exemplified that a combination of tree rings and remote sensing analyses is a powerful tool for the description of the climate-growth response of the whole above-ground segment of trees. Tree rings responded to climate and landscape topographical variables more sensitively compared to canopy greenness, perhaps because of prioritizing of function of leaves over the investment of carbon into tree stems and because of the higher proportion of noise in the signal of NDVI data.

The climatic signal of tree rings was slightly stronger compared to NDVI for both *Pinus sylv*estris and *Picea abies*. At a large-scale level, the climate-growth responses of tree rings were influenced by aridity gradient attributed to changing temperature along elevation and latitude. The correlations with summer climate conditions (June–August) changed from positive to negative for temperature and oppositely for moisture along the temperature gradient. Besides changing temperatures, a gradient of site fertility was also important, whereas the effects of the local topography (insolation, slope, and water availability) were relatively marginal. On the other hand, at the landscape level, there was an influence of terrain curvature in the case of *Pinus sylvestris*. While sites on plateaus were strongly moisture-limited in summer, sites in valleys revealed a positive influence of temperature in spring.

The climate-growth response of NDVI was influenced by surface position and terrain morphology factors (elevation, slope, terrain curvature) at a large scale level. The correlation of NDVI with temperature/moisture of *Picea abies* was generally negative/positive through the entire aridity gradient and over the dendrochronological year (the period between the previous June and the current September). The negative correlation of NDVI with growing season temperature results from the negative effect of drought (high temperatures) at a warmer margin of the climatic niche and the positive effect of cloudy conditions (lower temperature and higher diffuse radiation) at the colder range margin of *Picea abies*. On cloudy days, diffuse radiation can easily penetrate the crowns of trees and photosynthesis is more efficient (hence increase in vegetation greenness). Moreover, during sunny days, there is an increase in tropospheric ozone, which has a negative effect on chlorophyll content, thus reducing the canopy's greenness.

Different climate-growth relationships of tree rings and NDVI along environmental gradients led to the coherency of both proxies in the warm and dry-limited areas. Oppositely in cold and moist areas, the coherency decreased or even changed to a negative correlation of both proxies. This decrease in coherency was detectable at both landscape and large-scale levels.

The most warm and dry years negatively affecting growth of trees in Central Europe were 1917-1918, 1923-1924, 1942-1943, 1948, 1964, 1986, 1976, 1996, and 2003 for *Picea* and 1904-1905, 1917-1918, 1934-1935, 1942, 1948, 1964, 1976, 1984, and 2000 for *Pinus*.

Extreme growth reductions of *Pinus sylvestris* tree rings were mainly connected with summer drought through the entire elevation gradient of its distribution range. While *Picea abies* in lowlands also revealed the drought limitation, in higher elevations there was mainly the influence of low temperature. Nevertheless, the importance of cold temperature as a trigger of extreme growth reductions is decreasing for both species towards the present and there is an increase in the effect of drought in all elevations.

The responses of the tree rings and NDVI to drought events substantially differ. Both proxies dropped in a year of drought, however, while the tree-ring width continued to be suppressed for up to four years with slow recovery, the NDVI values enhanced in the two years following the drought. This is probably because trees prioritize restoration of the canopy damage first since it is an important organ for assimilation. These differences were more pronounced for *Picea abies* which is a shallow-rooting species. The higher sensitivity of *Picea abies* to drought was also corroborated by an increasing number of growth depressions connected with drought events during the last century. Although *Pinus sylvestris* often grows at unfavorable drought-prone sites, thanks to its deep root system and higher isohydricity it was less affected by drought events compared to *Picea abies*. However, even for *Pinus,* drought events tend to be more important for growth depressions towards the present.

At the large-scale level, there was a change of extreme growth reduction triggers with elevation, however, it is disappearing toward presence, and the extreme growth reductions tend to be triggered by summer drought for both species. In responses to dry events at the landscape level, there was no significant influence of topography for any species although *Pinus sylvestris* which grows in a topographically complex area revealed a much more variable stem growth response.

To conclude, this doctoral thesis reported that climate-growth responses of Central European conifers (*Pinus sylvestris* and *Picea abies*) and the impact of drought events are different between stem biomass (chronologies of tree-ring width) and canopy greenness (chronologies of NDVI from Landsat data). In addition, the responses of tree rings and NDVI are affected by topographical gradients which are changing with considered spatial scale. Such information is useful for studies attempting to extrapolate tree rings into space using vegetation indices from satellite imagery or to estimate biomass responses to climate forcing in terrestrial biosphere models.

11. References (related to chapters 1-7)

Adámek, M., Hadincová, V., & Wild, J. (2016). Long-term effect of wildfires on temperate Pinus sylvestris forests : Vegetation dynamics and ecosystem resilience. Forest Ecology and Management, 380, 285–295. https://doi.org/10.1016/j.foreco.2016.08.051

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