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Doctoral Dissertation

Wood anatomical traits and dendroclimatic response of Arctic and high mountain plants to contemporary environmental changes

MSc. Mohit Phulara

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Wood anatomical traits and dendroclimatic response of Arctic and high mountain plants to contemporary environmental changes

Author: MSc. Mohit Phulara

Doctoral dissertation was carried out at International Environmental Doctoral School affiliated to Centre for Polar Studies affiliated to University of Silesia in Katowice, Poland

Supervisor: dr hab. Magdalena Opała-Owczarek, prof. UŚ

Co-supervisor: dr hab. Piotr Owczarek, prof. UWr

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Look deep into nature, and then you will understand everything better

— Albert Einstein

Abstract

Global warming is affecting ecosystem functioning worldwide at an unprecedented pace, with Arctic regions and high mountain areas experiencing these changes in a particularly pronounced manner. The Himalayas and the Arctic—both characterized by low temperatures and short growing seasons—are witnessing some of the most marked ecological shifts. Although plants in these regions have developed various adaptations, overlapping factors such as rising temperatures, glacier retreat, permafrost degradation, and physiological drought intensify environmental stress, posing a threat to both biodiversity and ecosystem functioning. Gaining a deeper understanding of how Arctic and high-mountain plants respond to climatic changes is crucial for predicting and mitigating their impacts.

This dissertation employs dendrochronological and wood anatomical analyses to examine how selected Arctic and high-mountain plant species adapt to changing environmental conditions and serve as indicators of these changes. By analyzing growth patterns, xylem structures, and correlations with climatic conditions, the presented findings provide insights into the effects of contemporary warming on plant communities in these extreme habitats. Incorporating dendroclimatological analyses, this work introduces new growth chronologies for various species and determines their dendroclimatic responses. Using dendroecological analyses, it assesses how the studied plant species respond to diverse environmental factors. The dissertation consists of a series of thematically linked articles, each focusing on a specific species or region and describing how annual growth rings in shrubs and dwarf shrubs record current climate change.

Article I concerns the dwarf willow (*Salix herbacea*) from subarctic Iceland, examining its capacity to capture environmental changes in two contrasting climatic regimes. Despite these climatic differences, the research demonstrates that *S. herbacea* is a valuable drought indicator, especially in the relatively dry region of northeastern Iceland. Building on this, **Article II** compares growth-ring chronologies of two species—*Salix herbacea* and *Salix arctica*—highlighting their different responses to variations in air temperature and precipitation. In addition, the variability in vessel size and fiber structures underscores the importance of wood anatomy in shaping each species' climatic adaptations. *S. arctica* responds positively to rising temperatures, whereas *S. herbacea* shows improved growth under higher precipitation. This contrasting response illustrates the diverse adaptive strategies within the genus to evolving environmental conditions.

Article III focuses on the polar willow (*Salix polaris*) from Central Spitsbergen in the High Arctic. The study found that summer temperature alone does not fully explain this species' growth. Instead, local factors—such as increased soil water infiltration, snowmelt timing, and winter "rain-on-snow" events—strongly influence dwarf shrub development. At lower elevations, *S. polaris* growth depends on soil moisture and early-summer precipitation, while at higher sites, late-season temperature exerts a more pronounced effect. These findings indicate that relying solely on air temperature as a determinant of plant growth may overlook critical microhabitat factors.

Turning to high mountain areas, **Article IV** presents a 66-year growth-ring chronology of the East Carpathian rhododendron (*Rhododendron myrtifolium*). A strong positive relationship was found between summer temperature and the width of annual growth rings in this species. This pattern contrasts with results for tree species (*Picea abies*, *Abies alba*) growing in the forest zone, where August air temperature showed a negative effect on annual growth-ring width. These results emphasize the resilience of *R. myrtifolium* to rising temperatures and its potential as a sensitive climate indicator.

Article V shifts attention to the Himalayas, where the wood anatomy of the shrub *Rhododendron campanulatum* was analyzed in detail. For the first time in the literature, anatomical evidence of wood development disturbances linked to aphid invasions in high-mountain habitats is presented—an issue largely associated with increasingly frequent drought events. Until now, this factor had not been considered in the context of threats to Himalayan high-mountain flora or in the interpretation of growth-ring chronologies. Such disturbances may have a significant impact on reliable reconstructions of climatic conditions in this part of Asia.

Overall, the results confirm that the response of the studied plant species to climatic changes is complex, depending on both the species and local habitat conditions. Dendrochronological and wood anatomical analyses form an essential foundation for investigating how Arctic and alpine plants respond to climate change. By integrating these methods with climate data and ecological observations, this approach deepens our understanding of how selected species adapt to rapidly changing climatic conditions across different regions. The findings highlight factors that may influence observed "greening" and "browning" trends in tundra ecosystems or trigger insect outbreaks (e.g., aphids).

Streszczenie

Globalne ocieplenie wpływa na funkcjonowanie ekosystemów na całym świecie w bezprecedensowym tempie, a regiony Arktyki i obszary wysokogórskie doświadczają tych zmian w sposób szczególny. Himalaje i Arktyka—charakteryzujące się niskimi temperaturami i krótkimi sezonami wegetacyjnymi —są świadkami jednych z najbardziej wyraźnych zmian ekologicznych. Chociaż rośliny w tych regionach wykształciły szereg przystosowań, nakładające się czynniki takie jak wzrost temperatury, regresja lodowców, degradacja wieloletniej zmarzliny i susza fizjologiczna zwiększają poziom stresu środowiskowego, zagrażając zarówno bioróżnorodności, jak i funkcjonowaniu ekosystemów. Lepsze zrozumienie jak rośliny arktyczne i wysokogórskie reagują na zmiany klimatyczne jest kluczowe dla przewidywania i łagodzenia ich skutków. Niniejsza rozprawa wykorzystuje analizy dendrochronologiczne i anatomiczne drewna do zbadania, jak wybrane gatunki roślin arktycznych i wysokogórskich adaptują się do zmieniających się warunków środowiskowych i pełnią rolę wskaźników tych zmian. Poprzez analizę wzorców wzrostu, struktur ksylemu i korelacji z warunkami klimatycznymi, przedstawione wyniki badań dostarczają informacji o wpływie współczesnego ocieplenia na zbiorowiska roślinne w tych ekstremalnych siedliskach. Wykorzystując analizy dendroklimatologiczne w pracy przedstawiono nowe chronologie przyrostowe dla różnych gatunków oraz określono ich reakcję dendroklimatyczną. Przy użyciu analiz dendroekologicznych oceniono jak analizowane gatunki roślin reagują na zróżnicowane czynniki środowiskowe. Rozprawa składa się z serii powiązanych merytorycznie artykułów, z których każdy koncentruje się na konkretnym gatunku lub regionie, opisując i analizując zapis współczesnych zmian klimatycznych w przyrostach rocznych krzewów i krzewinek.

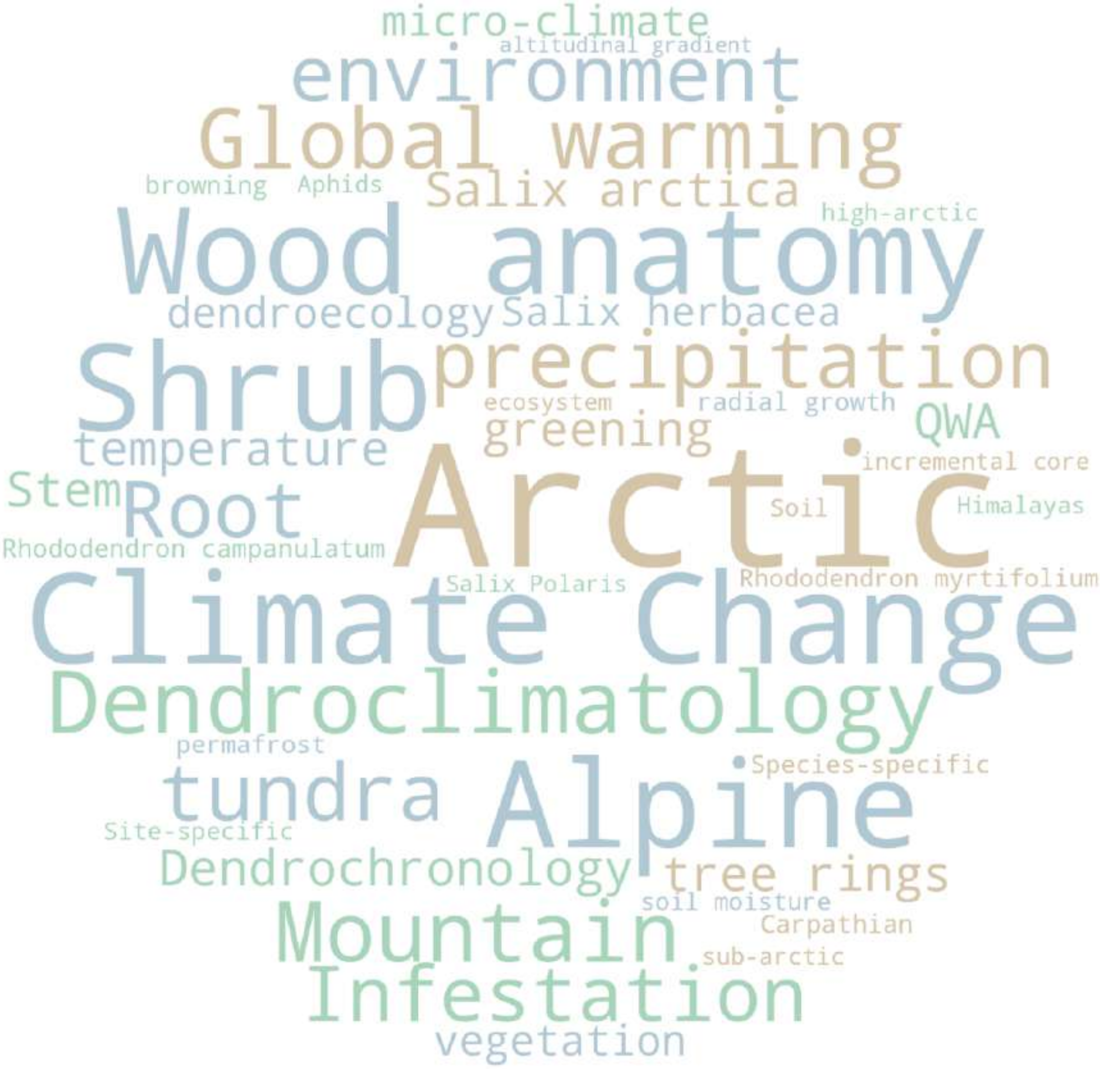
Artykuł I dotyczy wierzby zielnej (*Salix herbacea)* z subarktycznej Islandii, analizując jej zdolność do zapisu zmian środowiskowych w dwóch kontrastujących reżimach klimatycznych. Pomimo różnic klimatycznych badania pokazują, że *S. herbacea* jest cennym wskaźnikiem suszy, szczególnie w relatywnie suchym regionie północno-wschodniej Islandii. Rozwijając ten problem, **Artykuł II** porównuje chronologie przyrostowe dwóch gatunków: wierzby zielnej (*S. herbacea)* i wierzby arktycznej (*S. arctica)*, podkreślając ich różne reakcje na zmiany temperatury powietrza i opadów atmosferycznych. Ponadto, zmienność wielkości naczyń i struktur włókien podkreślają znaczenie anatomii drewna w kształtowaniu klimatycznych adaptacji każdego z tych gatunków. *S. arctica* reaguje pozytywnie na wzrost temperatury, podczas gdy *S. herbacea* rozwija się lepiej przy wyższych opadach. Ta

kontrastująca reakcja uwidacznia różnorodność strategii adaptacyjnych tego rodzaju do zmieniających się warunków środowiskowych.

Artykuł III koncentruje się na wierzbie polarnej (*Salix polaris)* z Centralnego Spitsbergenu w Wysokiej Arktyce. Stwierdzono, że sama temperatura lata nie wyjaśnia w pełni wzrostu tego gatunku. Zamiast tego, lokalne czynniki—takie jak wzmożona infiltracja wody w glebie, czas wytapiania pokrywy śnieżnej i epizody „*rain-on-snow*" w zimie—w zdecydowany sposób wpływają na wzrost krzewinek. Na niższych wysokościach n.p.m. wzrost *S. polaris* jest uzależniony od wilgotności gleby i opadów w okresie wczesnego lata, podczas gdy na wyżej położonych stanowiskach temperatura drugiej części sezonu wegetacyjnego ma zdecydowanie większy wpływ na wzrost tej krzewinki. Uzyskane wyniki wskazują, że zastosowanie jedynie wartości temperatury powietrza jako czynnika determinującego wzrost roślin jest niewystarczające i może pomijać wpływ kluczowych czynników mikrosiedliskowych.

Dotyczący obszarów wysokogórskich **Artykuł IV,** przedstawia 66-letnią chronologię przyrostów rocznych różanecznika wschodniokarpackiego (*Rhododendron myrtifolium)* z obszaru Karpat Wschodnich. Stwierdzono silną dodatnią zależność pomiędzy temperaturą lata a szerokością przyrostów rocznych tego gatunku. Prawidłowość ta kontrastuje z wynikami uzyskanymi dla gatunków drzew (*Picea abies, Abies alba*) rosnących w strefie lasu, gdzie stwierdzono negatywny wpływ sierpniowej temperatury powietrza na szerokość przyrostów rocznych. Uzyskane wyniki badań podkreślają odporność *R. myrtifolium* na wzrost temperatury i jego potencjał jako wrażliwego wskaźnika klimatycznego. **Artykuł V** przenosi uwagę na Himalaje, gdzie szczegółowo analizowano anatomię drewna krzewu różanecznika *Rhododendron campanulatum.* Po raz pierwszy w literaturze przedstawiono anatomiczne dowody zaburzeń rozwoju drewna związane z inwazją mszyc w stanowiskach wysokogórskich, co w znacznym stopniu jest związane z coraz częstszym występowaniem susz. Dotychczas ten czynnik nie był brany pod uwagę zarówno w kontekście zagrożenia dla flory wysokogórskiej Himalajów, jak i zaburzeń w przebiegu chronologii przyrostowych. Zaburzenia te mogą mieć istotny wpływ na wiarygodne rekonstrukcje warunków klimatycznych tej części Azji.

Uzyskane wyniki potwierdzają, że reakcja analizowanych gatunków roślin na zmiany klimatyczne jest złożona, zależna zarówno od gatunku jak i lokalnych warunków siedliskowych. Analizy dendrochronologiczne i anatomii drewna stanowią istotną podstawę do badania reakcji roślin arktycznych i alpejskich na zmiany klimatyczne. Integrując te metody z danymi klimatycznymi i obserwacjami ekologicznymi, podejście to pogłębia nasze zrozumienie, jak wybrane gatunki adaptują się do szybko zmieniających się warunków klimatycznych w różnych regionach. Uzyskane wyniki badań wskazują na czynniki, które mogą wpływać na obserwowane trendy „zielenienia” i „brązowienia” tundry lub spowodować gradację owadów (np. mszyc).


micro-climate
altitudinal gradient
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Global warming
browning
Aphids
Salix arctica
high-arctic
Wood anatomy
dendroecology
Salix herbacea
Shrub
precipitation
ecosystem
radial growth
QWA
temperature
greening
incremental core
Stem
Root
Arctic
Soil
Himalayas
Rhododendron campanulatum
Salix Polaris
Rhododendron myrtifolium
Climate Change
Dendroclimatology
permafrost
Species-specific
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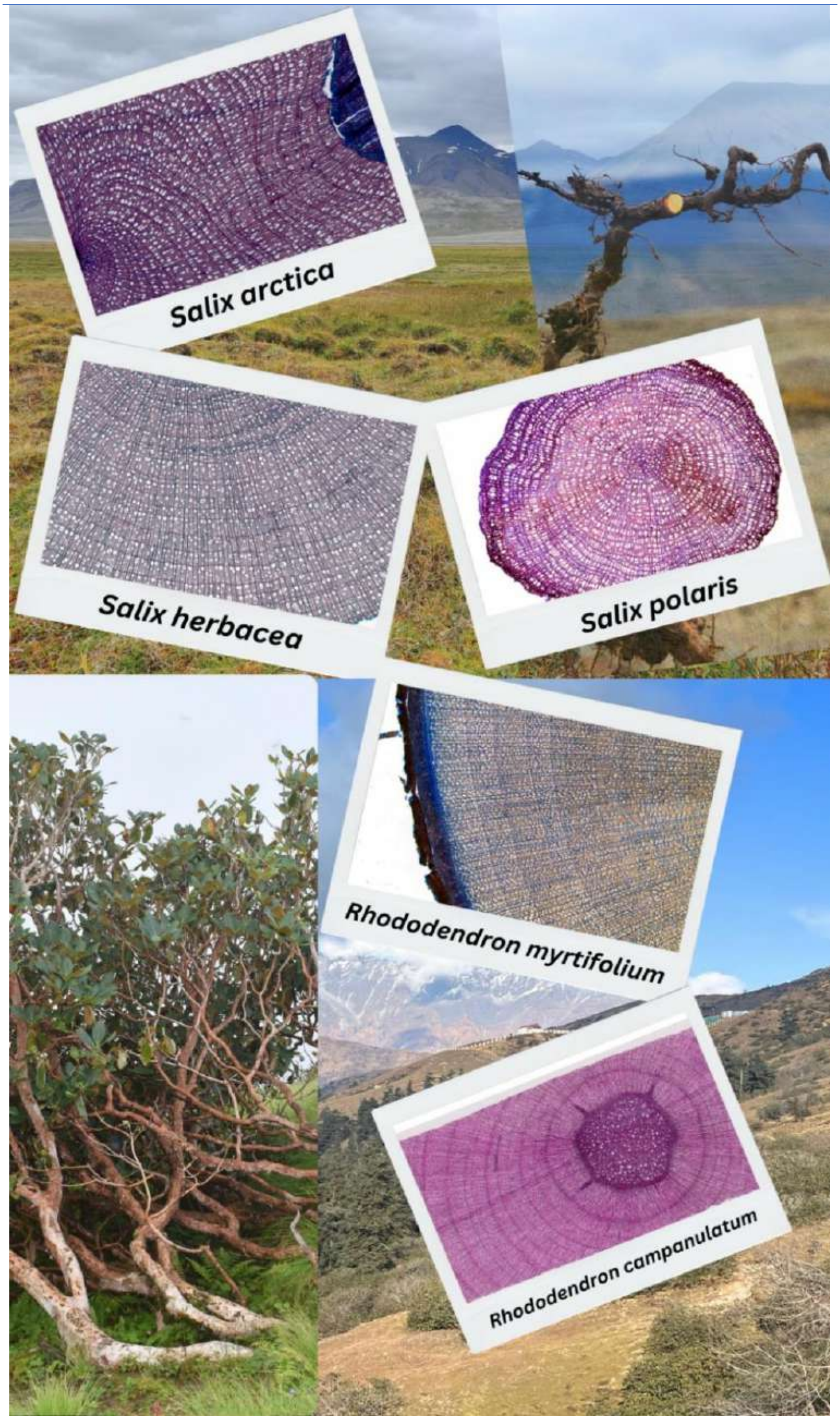

Note - This illustration provides an overview of this whole research, displaying cross-sections of all analyzed species along with corresponding photographs—from Arctic dwarf shrubs (*Salix* species) to High-Himalayan shrubs (*Rhododendron* species). The background visually represents the studied geographic gradient, transitioning from Arctic landscapes (top) to Himalayan regions (bottom).

1. Introduction

Climate change stands as one of the most pressing challenges of the 21st century, exerting profound effects on global ecosystems. Among the regions, most vulnerable to these shifts are the Arctic and high mountain areas, where environmental changes occur at an accelerated pace compared to the global average (Anisimov et al., 2007; AMAP, 2017; Post et al., 2019; IPCC, 2022). This phenomenon, known as Arctic amplification, results in a faster warming rate in the Arctic compared to the global average, intensifying climate impacts across the region (Overland et al., 2019; AMAP, 2021; Rantanen et al., 2022). In high mountain regions, rapid warming drives glacier and snowpack retreat, drastically affecting local biodiversity and downstream water availability (Körner, 2012; Pepin et al., 2015). Such warming triggers cascading ecological transformations—including shifts in vegetation patterns, permafrost thaw, and biodiversity decline—and establishes feedback loops, such as reduced albedo and increased greenhouse gas emissions, that further intensify climate dynamics (Myers-Smith et al., 2015a; Lu et al., 2022). These changes extend beyond regional boundaries, influencing global climate systems (Thomas et al., 2019; Herman-Mercer et al., 2020; Rosqvist et al., 2022).

Within these fragile environments, Arctic and high mountain plants have evolved specialized adaptations to extreme conditions such as low temperatures, limited nutrients, and short growing seasons (Billings and Mooney, 1968; Körner, 2021). Shrubs, in particular, play a pivotal role in stabilizing ecosystems by influencing soil dynamics, hydrology, and carbon sequestration (Sturm et al., 2001; Greenwood and Jump, 2014), and their rapid, variable responses provide critical insights into the broader ecological impacts of climate change (Blok et al., 2010; Jorgenson et al., 2010). Recent methodological advances have enhanced our ability to monitor vegetation dynamics. In addition to traditional dendrochronological techniques, tools such as high-resolution satellite imagery and NDVI analysis help capture broad-scale changes and subtle shifts in plant phenology (Epstein et al., 2012; Phoenix and Bjerke, 2016). These remote sensing methods complement ground-based observations by linking local measurements with landscape-level patterns, thereby refining our insights into how Arctic and high mountain ecosystems respond to ongoing climate change (Berner et al., 2020; Myers-Smith et al., 2020; Karlsen et al., 2024).

A notable trend in these regions is the surge in shrub growth and abundance. Increased shrub cover affects biodiversity, soil nutrient cycling, and water–energy exchanges (Wookey et al., 2009; Tape et al., 2012), and in high mountain areas, it can also alter snow accumulation and glacier dynamics, further impacting local hydrology (Greenwood and Jump, 2014; Wielgolaski et al., 2017). However, while many studies confirm widespread shrub expansion, the underlying processes vary considerably—reflecting a complex interplay of climatic, topographical, and biotic factors (Hollesen et al., 2015; Weijers et al., 2018; Francon et al., 2020b). Despite significant progress, shrub responses to climate change remain heterogeneous and only partially understood, particularly regarding how individual reactions scale to community-level dynamics (Myers-Smith et al., 2011; Martin et al., 2017). Steep altitudinal gradients and local microclimates further complicate these dynamics, creating knowledge gaps that hinder accurate predictions of future environmental shifts (Myers-Smith et al., 2011; Vowles and Björk, 2019; Kemppinen et al., 2021). Strengthening our predictive capabilities for global climate and ecosystem transformations requires an in-depth understanding of these complex interactions at multiple scales.

Identifying the most vulnerable Arctic-alpine plants is essential for developing targeted conservation strategies that preserve genetic resources and evolutionary potential (Stöckli et al., 2011). A multi-taxon approach along elevational gradients can help disentangle community-level diversity shaped by local variations in altitude and topography (McCain and Grytnes, 2010; Graae et al., 2018). Moreover, monitoring local populations may provide more sensitive indicators of future range shifts than broader presence–absence surveys (Bhatt et al., 2013; Myers-Smith et al., 2015a; Cotto et al., 2017; Gamm et al., 2018; Reichle et al., 2018).

1.1. Overview of the thesis

Arctic and high mountain ecosystems are recognized as climate change hotspots, experiencing faster warming and dramatic ecological shifts (AMAP, 2021; IPCC, 2022). Although the expansion of shrub communities is well documented, the cambium response mechanisms driving these changes remain partially understood (Bjorkman et al., 2018; Kemppinen et al., 2021). Wood anatomical traits—such as vessel size, cell-wall thickness, and density—offer unique insights into plant–climate interactions, capturing historical responses to temperature fluctuations, moisture variability, and extreme events (Liang and Eckstein, 2009; Babst et al., 2018). This thesis leverages dendrochronological methods and wood anatomy to elucidate growth patterns and stress signals in cold-adapted species. Focusing on Iceland, Central Spitsbergen, the Eastern Carpathians, and the Western Himalaya, the research bridges local-scale plant physiology with global climate trends.

My published work exemplifies this integrative approach through five studies. The PhD thesis consists of the following series of publications (3 published and 2 under review):

I. **Phulara, M.**, Opała-Owczarek, M. and Owczarek, P. (2022). Climatic signals on growth ring variation in *Salix herbacea*: comparing two contrasting sites in Iceland. – *Atmosphere* 13: 718.

II. **Phulara, M.**, Balzano, A., Opała-Owczarek, M., Owczarek, P., & Merela, M. (2024). Insights from roots to stems: Comparative wood anatomy and dendroclimatic investigation of two Salix species in Iceland. *Forests*, 15(10), 1707.

III. **Phulara, M.**, Opała-Owczarek, M., Szymański, W., Ślopek, J., Węgrzyn, M., Łupikasza, E., Korabiewski, B., & Owczarek, P. (2025). Multiple factors controlling polar willow growth in the High Arctic (Svalbard): Implications for future prediction of tundra productivity. Manuscript under review in *Global Ecology and Conservation.*

IV. Owczarek, P., **Phulara, M.**, Shuber, P., Korabiewski, B., Błaś, M., & Opała-Owczarek, M. (2024). Varied growth response of high alpine *Rhododendron myrtifolium* and forest zone tree species to climate warming in the Eastern Carpathians, Ukraine. *Dendrochronologia, 85*, 126198.

V. **Phulara, M.**, Opała-Owczarek, M., Owczarek, P., Bast, A., Bhatt, I. D., & Gärtner, H. (2025). Tracing aphid infestations through wood anatomical markers: Insights from *Rhododendron campanulatum* D. Don of the Himalayan region. Manuscript under review in *Dendrochronologia.*

In **Article I**, a comparative analysis of *Salix herbacea* L. in sub-Arctic Iceland demonstrates its sensitivity to drought, suggesting its potential as an early indicator of environmental change. **Article II** reveals contrasting growth patterns between *S. herbacea* and *S. arctica* Pall., underscoring species-specific responses to moisture and temperature. In **Article III**, research on *Salix polaris* Wahlenb. in Central Spitsbergen emphasizes the role of site-specific drivers in shaping growth dynamics. **Article IV** presents a 66-year chronology of *Rhododendron myrtifolium* Schott & Kotschy in the Eastern Carpathians, highlighting its resilience to warming. Finally, **Article V** examines *Rhododendron campanulatum* D.Don in the Western Himalaya, where aphid infestations compound climatic effects, calling for updated conservation measures. Collectively, these findings underscore the value of integrating wood anatomical and dendrochronological approaches to predict the adaptive capacities of Arctic and alpine flora.

1.2. Outline of the state of research

While numerous studies have documented widespread shrub expansion and vegetation shifts in Arctic and high mountain regions, our understanding of the underlying anatomical and dendrochronological mechanisms remains incomplete. Traditional dendrochronological methods—developed primarily for trees—have provided valuable insights into past climate variability (Fritts, 1976), yet applying these techniques to shrubs has revealed methodological challenges such as cross-dating difficulties, missing rings, and herbivory effects (Bär et al., 2007; Hantemirov et al., 2011; Wilmking et al., 2012; Pellizzari et al., 2014). These issues underscore the need for standardized protocols and refined analytical approaches that reliably capture the complex growth signals of dwarf shrubs.

Recent advancements that integrate wood anatomical analyses with conventional dendrochronology have improved our ability to interpret growth responses. Measurements of vessel size, density and cell-wall thickness now help clarify how shrubs respond to temperature, drought, and precipitation variability at fine scales (Fonti et al., 2010; Weijers et al., 2010; Pellizzari et al., 2014). Arctic shrub growth and wood anatomical traits are strongly influenced by local environmental conditions, resulting in pronounced species- and site-specific responses. Variability in *Salix polaris* ring formation within a single site has been linked to summer temperatures and fine-scale microhabitat differences (Buchwal et al., 2013). While warm summers can synchronize growth patterns regionally, this effect is often disrupted by localized winter rain-on-snow events that suppress growth at specific sites (Le Moullec et al., 2019). More recently, Owczarek et al. (2021) demonstrated a shift in climate sensitivity, with moisture availability emerging as the dominant growth-limiting factor. Collectively, these studies highlight the strong interplay between broad climatic trends and local environmental conditions in shaping shrub anatomical and growth responses.

The integration of geospatial techniques with dendroecological analyses offers a more comprehensive understanding of how local microclimatic conditions and large-scale atmospheric patterns interact to drive vegetation change in Arctic and high mountain regions. Thus, NDVI has emerged as a critical tool for assessing vegetation dynamics across vast and heterogeneous environments (Blok et al., 2011; Berner et al., 2020; Prendin et al., 2020). Studies have shown that integrating NDVI data with plot-level observations helps capture subtle changes in shrub phenology and growth rates, and links these local responses to broader regional climate trends (Zhang et al., 2017; Manzanedo and Pederson, 2019).

Numerous reviews (Myers-Smith et al., 2015a; Phoenix and Bjerke, 2016) have highlighted that many previous studies were limited by short chronologies and localized sampling, underscoring the need for a more integrative, long-term, and spatially extensive approach to fully capture the complexity of shrub responses in the Arctic and high mountain regions. Emerging research also emphasizes that local climatic and geomorphological factors can generate contrasting growth outcomes. While large-scale atmospheric circulation patterns influence shrub expansion (Forbes et al., 2010; Schickhoff et al., 2015), microsite characteristics—such as early-spring snow cover melt (Vaganov et al., 1999; Körner, 2012) and soil drainage—can counteract or reverse these trends (Weijers et al., 2018; Francon et al., 2020a). Additionally, biotic interactions, including herbivory and competition (Le Moullec et al., 2019), introduce further complexities that obscure direct climate–growth relationships (Johnson et al., 2011; Bjorkman and Gallois, 2020).

Despite these advancements, uncertainties remain regarding how shrub populations adapt over time and across regions. Methodological inconsistencies hinder long-term reconstructions, highlighting the need for integrative approaches that combine dendrochronology, wood anatomical traits, and ecological data (Bär et al., 2008; Wilmking et al., 2012). Enhancing these methods is crucial for refining predictive models of vegetation change and for informing conservation strategies in rapidly evolving environments.

Arctic and high mountain ecosystems, being among the most responsive to modern climate shifts, offer a distinctive lens through which to study the interplay between vegetation growth and environmental variables. Shrubs in these regions are especially effective indicators of climate impacts due to their broad distribution and sensitivity. Against this backdrop, the following hypotheses have been proposed to frame the primary research objectives -

i. Tundra and high-mountain shrubs and dwarf shrubs are highly effective indicators of contemporary climate change.
ii. The growth reaction of different dwarf shrub species to varying environmental variables differs within the Arctic region, reflecting species-specific sensitivities.
iii. Contemporary increases in temperature can influence tundra communities positively (tundra greening) or negatively (tundra browning), thereby modifying growth-ring variability.
iv. High-altitude shrubs are highly sensitive to recent climate changes, with *Rhododendron* species serving as reliable bio-monitoring indicators for understanding these environmental shifts.

1.3. Research objectives

Building on the identified knowledge gaps and challenges highlighted in the outlines of the state of research, this study aims to:

i. Develop new growth-ring chronologies for selected Arctic and high-mountain shrub and dwarf shrub species, focusing on wood anatomical traits and their relationship with contemporary climate variables.
ii. Investigate the spatial variability in the climate sensitivity of dwarf shrub species, examining how different species and populations respond to temperature and precipitation changes.
iii. Investigate how a single species from a heterogeneous region and multiple species in a homogeneous region respond to climate change.

2. Study area

This study encompasses diverse field sites across cold regions, including the sub-Arctic (Iceland), High Arctic (Spitsbergen), and high-mountain areas in temperate (Eastern Carpathians) and subtropical (Western Himalayas) zones (Fig. 1). Samples from Iceland and the Eastern Carpathians were obtained from the University of Silesia and University of Wroclaw repositories, while new field collections were conducted in the Western Himalayas (India) and Central Spitsbergen.

The study targeted polar tundra, alpine, and subalpine biomes, spanning a wide range of temperature, precipitation, altitude, and coastal influences. By integrating these datasets, the thesis provides a comparative analysis of how climate, morphological settings and altitude influence wood anatomical traits and dendroclimatic responses in cold-sensitive environments. These varied conditions facilitate robust comparisons of shrub growth under diverse environmental pressures, yielding insights into adaptations to localized stressors (e.g., permafrost, erosion) and broader climate changes. Detailed site descriptions, including vegetation and soil conditions, are provided in the appended papers.

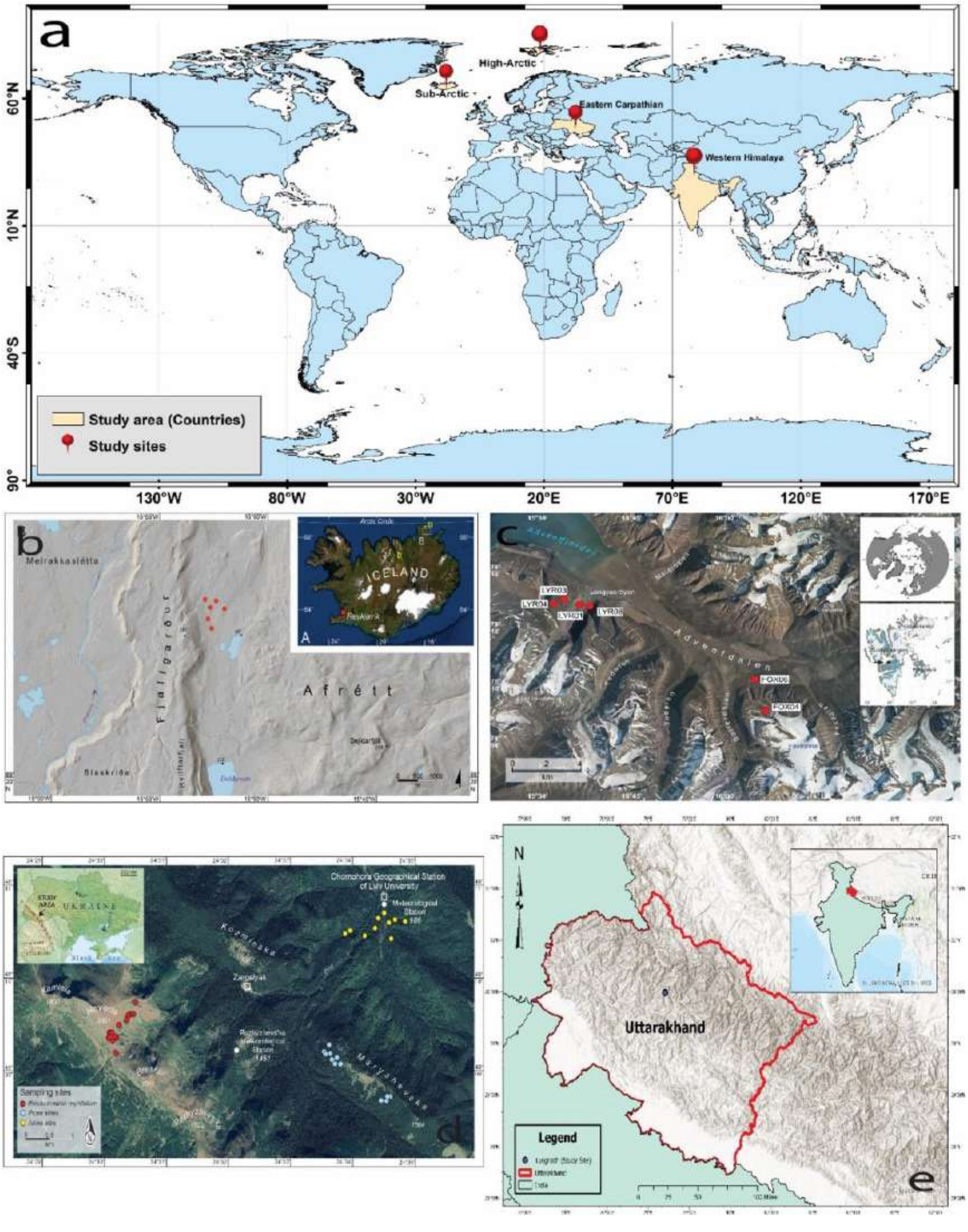

Figure 1. Overview of the study sites and sampling locations: (a) Distribution of studied areas in the world map; detailed maps showing sampling sites in (b) Sub-Arctic (Iceland); c) High-Arctic (Central Spitsbergen); d) Eastern Carpathians (Ukraine), and e) Western Himalaya (Uttarakhand, India).

2.1. Iceland

Iceland's distinctive landscape is shaped by intense volcanic and glacial activity along the Mid-Atlantic Ridge (Fig. 1b). More than 11% of the island remains ice-covered, notably Vatnajökull, Europe's largest glacier, beneath which active volcanoes such as Grímsvötn and Bárðarbunga are concealed. Extensive glacial outwash plains, basaltic bedrock, and prominent rift valleys (e.g., Þingvellir) illustrate the dynamic interplay of volcanic ("fire") and glacial ("ice") forces, making Iceland an optimal location for studying active tectonic processes and rapid geomorphic changes (Jóhannesson and Saemundsson, 1998.; Arnalds, 2015).

Iceland's climate exhibits pronounced regional contrasts due to varying maritime and continental influences. Coastal areas, warmed by the North Atlantic Current, receive substantial annual precipitation (1,500–4,000 mm/year), whereas the interior plateaus experience relatively arid conditions (<400 mm/year). Winters, particularly in northern regions, are characterized by strong winds and cold temperatures, and summers are generally short and cool across the island (Nakashima and Dagsson-Waldhauserová, 2019). Recent warming in Iceland, among the fastest observed globally, has intensified glacial retreat and altered fluvial dynamics, clearly demonstrating the region's high sensitivity to ongoing climate changes (Björnsson and Jónsson, 2004).

Within this context, Afrétt (66.351°N, 15.758°W), located in Northeast Iceland, is characterized by colder temperatures, moderate precipitation, and distinct seasonal climatic variations. According to CRU-based climate data (1993–2022), Afrétt has an annual mean temperature of 2.5 °C and annual precipitation totaling 844.1 mm. Classified under the ET (Tundra) climate type, Afrétt experiences cold winters with temperatures often below freezing (around -2 °C from December to February) and short, cool summers averaging approximately 9 °C during July and August. Precipitation is relatively consistent throughout the year, with higher values notably recorded during autumn months (particularly in October). These climatic features provide an ideal setting for investigating vegetation responses and shrub adaptation strategies to the ongoing climatic changes in subarctic environments.

To capture Iceland's broader climatic variability, two contrasting sites—Mýrdal and Afrétt—were selected for comparative analyses (**Article I**). Mýrdal, close to the Mýrdalsjökull ice cap, is characterized by volcanic ridges and plateaus under high-precipitation conditions, whereas Afrétt exemplifies colder, drier uplands influenced by a pronounced rain-shadow effect. These contrasting hydrothermal conditions at Afrétt provided a unique opportunity to closely examine how two sub-Arctic dwarf shrub species (*Salix herbacea* and *Salix arctica*) differ in their adaptation strategies and responses to climatic variability, offering valuable insights into species-specific resilience and sensitivity to environmental changes (**Article II**).

2.2. Central Spitsbergen

Central Spitsbergen, situated within the Svalbard archipelago (Fig. 1c), offers distinct advantages for climate research due to its well-defined High Arctic conditions. Within this region, the Adventdalen area (78.208°N, 15.795°E) encompasses two key sites: Longyearbyen and Foxfonna. This area was specifically selected for its representative High Arctic climatic and ecological features, including tundra ecosystems, continuous permafrost, and contrasting topographical characteristics between the two sites.

Based on climatological data from the CRU dataset (1993–2022), Longyearbyen exhibits a typical High Arctic climate (Climate Class: ET) with an annual mean temperature of -6°C and annual precipitation totaling approximately 298.3 mm. Winters are prolonged and cold, averaging around -14°C in January and February, while summers remain short and cool, peaking at approximately 5°C in July. Precipitation is consistently low throughout the year, a consequence of the area's pronounced rain-shadow position.

Central Spitsbergen has experienced rapid warming since the 1990s, with an average temperature increase of approximately 2°C, significantly reducing snow cover duration and accelerating glacier retreat. These warming trends directly influence local ecosystems, making Longyearbyen (Adventdalen) particularly sensitive and ideal for studying plant adaptations and resilience under intense environmental pressures. The location’s extreme seasonal and climatic variability provides a valuable natural setting to assess vegetation dynamics, shrub responses, and the ecological impacts of changing climatic conditions in the High Arctic (**Article III**).

2.3. Eastern Carpathians

Spanning parts of Ukraine, Romania, and Poland, the Eastern Carpathians exhibit complex topography (Fig. 1d) shaped by dynamic geological processes. Peaks exceeding 2000 m a.s.l.—such as Rodna, Maramureș, and Chornohora—form glacial cirques above steep valleys (Kłapyta et al., 2021; Karabiniuk et al., 2022). The region’s geology, characterized by flysch formations (interbedded sandstones and shales), increases susceptibility to landslides, while crystalline massifs at higher elevations support alpine meadows and distinctive cirque landforms.

Hoverla Massif, located in the Chornohora range of Ukraine (48.063°N, 24.617°E; Elevation: 1734 m), was specifically selected due to its clear and representative altitudinal vegetation zonation, making it particularly suitable for studying vegetation responses to climate changes in high-alpine environments. According to climatological data from the CRU dataset

(1993–2022), Hoverla has an annual mean temperature of 6.6 °C and annual precipitation totaling 796.3 mm, reflecting a temperate continental climate (Climate Class: Dfb). Winters are cold, averaging around -4 °C in January, and summers are mild to warm, peaking around 17 °C in July and August. Precipitation shows marked seasonal variability, peaking during the summer months and decreasing toward winter.

Significant warming observed since the 1980s (approximately +0.5 °C per decade in certain areas), combined with declining summer rainfall, presents notable risks to local ecosystems. These changes have the potential to alter forest structures, exacerbate erosion, and increase occurrences of droughts. Hoverla's clearly defined altitudinal vegetation belts, transitioning from beech and spruce–fir forests at lower elevations to subalpine dwarf-pine communities and alpine habitats at higher elevations, provide an ideal natural laboratory for assessing how alpine shrub species, such as *Rhododendron myrtifolium*, respond to shifting temperature and precipitation patterns. The region's transitional continental climate and high biodiversity further enhance its suitability for studying species adaptation to mountain-specific environmental stressors, including steep terrain, erosional processes, and increasingly frequent weather extremes (**Article IV**).

2.4. Western Himalaya

The Western Himalaya features diverse mountainous terrains with complex geology and ecological gradients. Major ranges, including the Pir Panjal, Greater Himalaya, and Karakoram, host prominent peaks and deep valleys formed by active tectonics and glacial erosion. Recent weakening of the summer monsoon has altered precipitation patterns significantly (Tewari et al., 2018). Concurrently, the observed warming of approximately +2 °C since the 1980s, particularly above 3000 m elevation, has accelerated glacial retreat, affecting alpine ecosystems.

Tungnath (30.555°N, 79.261°E; elevation 3512 m) was specifically selected for its exceptional elevation and clear representation of high-altitude treeline environments (Fig. 1e). According to CRU-based climatological data (1993–2022), Tungnath experiences an annual mean temperature of 1.3 °C and a total annual precipitation of approx. 531.9 mm. Its climate (Dwc; cold continental) is characterized by cold winters (approx. -7 to -8 °C from December to February) and short, cool summers (~10 °C in July–August), with approximately 60% of the annual precipitation concentrated in the summer.

These climatic conditions directly influence alpine vegetation at Tungnath, making it especially sensitive to environmental changes. Given its high elevation (3512 m) and position as one of the highest treeline sites globally, Tungnath was selected specifically to study how alpine shrubs and trees, notably *Rhododendron campanulatum*, respond to temperature and moisture shifts (**Article IV**).

2.5. Climate warming trends across study regions

Displaying the trend of each studied region, the plot (Fig. 2) reveals the influence of regional environmental factors on warming patterns from 1993 to 2022. Tungnath (Western Himalaya) experiences moderate warming at 0.28°C per decade, with a relatively low R^2 of 0.297, suggesting that other factors like monsoon variability and elevation contribute to temperature fluctuations. Iceland (Sub-Arctic) warms at 0.42°C per decade with a stronger R^2 of 0.423, influenced by oceanic patterns and greenhouse gas concentrations. The High-Arctic region of Spitsbergen shows the fastest warming at 1.01°C per decade, reflecting Arctic Amplification, driven by sea ice loss and climate feedbacks, with an R^2 of 0.633. Hoverla (Eastern Carpathians) shows significant warming at 0.63°C per decade, with an R^2 of 0.502, influenced by altitude and atmospheric patterns. Overall, all regions show warming trends, with the rate varying based on the environmental factors influencing each site. Some regions warm faster than others due to factors like feedback mechanisms, elevation, and regional climate influences.

```
Site                              | P-value        | Standard Error
-----------------------------------------------------------
Tungnath (Western Himalaya)       | 1.800000e-03 |   0.0081
Iceland (Sub-Arctic)              | 1.000000e-04 |   0.0091
Spitsbergen (High-Arctic)         | 1.450000e-07 |   0.0146
Hoverla (Eastern Carpathian)      | 1.190000e-05 |   0.0139
```

Figure 2. Climatodiagrams showing climatic characteristics for the four study sites during the period 1993–2022. Monthly mean temperatures (°C, red line) and monthly precipitation sums (mm, blue bars) are displayed for Afrett (Iceland), Central Spitsbergen (Svalbard), Eastern Carpathians (Ukraine), and Tungnath (Western Himalaya, India). The lower panel presents annual mean temperature trends (°C) at each site from 1993 to 2022, highlighting warming trends at each location. *(Source: Climatic data obtained from CRU TS v4.07; climatodiagrams prepared using ClimateCharts.net.)*

3. Types of vegetation

Cold-region vegetation (Fig. 3) spans both Arctic and alpine ecosystems, each shaped by low temperatures, short growing seasons, and nutrient-limited soils (Walker et al., 2001; Körner, 2003). In the Arctic, vegetation is predominantly constrained by latitude and permafrost, resulting in a treeless tundra of dwarf shrubs, mosses, and lichens (Billings and Mooney, 1968; Myers-Smith et al., 2011). In contrast, alpine vegetation develops at high elevations above the treeline, where steep temperature gradients and strong microclimatic variations drive distinctive plant communities (Körner and Paulsen, 2004; Pepin et al., 2015). Despite these environmental extremes, both Arctic and alpine ecosystems include plant species uniquely adapted to their habitats, many of which are now under pressure from rapid climate change (Sturm et al., 2001; Walther et al., 2005).

Figure 3. Studied plant species from selected regions: *A) Salix arctica* (Iceland), *B) Salix herbacea* (Iceland), *C) Salix polaris* (Central Spitsbergen, High-Arctic), *D) Rhododendron myrtifolium* (Eastern Carpathians, Ukraine), and *E) Rhododendron campanulatum* (Western Himalaya, India).

3.1. Arctic tundra

Arctic tundra is typically found where mean July temperatures remain below 10 °C, annual precipitation is relatively low, and soils are often underlain by permafrost (Walker et al., 2001). The region experiences short growing seasons of 1.5–4 months and low nutrient availability, supporting low-stature vegetation—shrubs, sedges, grasses, mosses, and lichens (Billings and Mooney, 1968). Soil moisture and microtopography strongly affect local vegetation patterns: water-saturated hollows favor sedges, while drier ridges support dwarf shrubs. Under contemporary warming, many parts of the Arctic are “greening” due to increased shrub cover (Myers-Smith et al., 2011). However, localized “browning” occurs where abrupt thaws or disturbances limit plant growth (Phoenix and Bjerke, 2016; Myers-Smith et al., 2020).

The Circumpolar Arctic vegetation map illustrates distinct plant zones (Fig. 4), with an expansion of shrub and tundra vegetation as rising temperatures and melting permafrost transform the landscape. It provides a detailed overview of the region’s vegetation composition, highlighting transitions from moss and lichen-dominated areas to shrubland, thereby indicating ongoing ecological changes. Hence, this research focuses on dwarf and prostrate shrubs as indicators of environmental change in the sub-Arctic (e.g., Iceland) and High Arctic (e.g., Spitsbergen).

Figure 4. Circumpolar Arctic Vegetation Map illustrating major plant communities distributed across the Arctic region—from polar deserts to shrub tundra. Each distinct vegetation zone, indicated by different colors, is shaped by regional climate and soil conditions. Side panels and charts provide additional regional context and representative photographic examples of vegetation types. *(Source: Circumpolar Arctic Vegetation Map [CAVM], https://geobotany.uaf.edu/cavm/index.shtml)*

- *Salix arctica* (Arctic willow): Remains under 20 cm tall, often rooting where branches contact the ground (Fig. 3A). Despite its tiny, compressed rings, it provides valuable dendroclimatic data (Schweingruber et al., 2013).

- *Salix herbacea* (dwarf willow): Found in Iceland's snowbeds, notable for its compact woody stems (Fig. 3B) and reliably distinguishable growth rings (Wheeler et al., 1989; Schweingruber et al., 2013).
- *Salix polaris* (polar willow): A prostrate shrub common in High Arctic Svalbard (Fig. 3 C) , forming mats on frost-affected soils. Its annual rings can reflect year-to-year climatic variations (Owczarek and Opała, 2016).

Among these taxa, *Salix polaris* exemplifies prostrate growth, producing low mats that survive under stable snow cover and cold soils. It has annual growth rings discernible through microscopic wood analysis, allowing reconstruction of past environmental conditions (Elvebakk, 1994; Owczarek and Opała, 2016). *Salix herbacea*, though similar in stature, occupies slightly milder sub-Arctic zones and displays relatively clear ring boundaries (Wheeler et al., 1989). Both species respond to temperature and moisture availability, with ring-width variability often reflecting summer warmth or snowmelt timing. By contrast, *Salix arctica* has extremely short stems with dense woody tissue, yet still produces growth increments that can be measured—albeit with more difficulty due to ring compression (Schweingruber et al., 2013). These shrubs collectively showcase the adaptations (e.g., prostrate habit, efficient resource use) that enable survival in Arctic conditions and provide dendroclimatic records essential for understanding changing tundra ecosystems.

3.2. Alpine vegetation

Alpine vegetation occupies elevations above the treeline, where seasonal snowpack, low temperatures, and wind exposure generate a patchwork of specialized plant communities (Körner, 2003; Körner and Paulsen, 2004). The growing season is typically short, with mean summer temperatures of about 6–7 °C; steep slopes and varied microtopography further shape plant distributions (Williams et al., 2009). Alpine vegetation is shaped by altitude, temperature, and soil conditions, transitioning from dense forests below the timberline to scattered, stunted trees (krummholz) near the treeline, as shown in Fig. 5. Above this zone, grasses and low-growing plants dominate the alpine grassland, eventually giving way to permanent snow cover. In many mountain ranges, warming climates have driven upward treeline shifts, potentially displacing cold-adapted alpine flora and altering community composition (Walther et al., 2005; Pepin et al., 2015).

In temperate-zone mountains, such as the Eastern Carpathians, beech (*Fagus sylvatica* L.), spruce (*Picea abies* (L.) H. Karst), and fir (*Abies alba* Mill.) forests eventually give way to subalpine dwarf pine stands and an alpine belt dominated by *Rhododendron myrtifolium* (Fig. 3D) at around 2000–2030 m (Boratyński et al., 2006; Voloshchuk and Shumik, 2012). In the Himalayas, treelines rise above 3500 m, and *Rhododendron campanulatum* (Fig. 3E) occupies subalpine shrublands and alpine meadows (Tiwari and Chauhan, 2006). Both species exhibit robust woody stems with distinctive ring structures, offering dendrochronological and wood anatomical insights into high-elevation climates (Singh et al., 2021).

Rhododendron myrtifolium typifies alpine belt shrubs in the Carpathians, forming dense mats on sunny slopes and displaying growth rings in its woody branches and roots (Boratyński et al., 2006). Its ring boundaries may reflect temperature-driven growth pulses and moisture availability during the short alpine growing season (Voloschuk and Prokopiv, 2011). Meanwhile, *Rhododendron campanulatum* in the Himalayas withstands even harsher conditions above 3280 m, sporting thick leaves and robust wood anatomy. Its rings can capture extreme frost events and shifts in monsoonal precipitation (Tiwari and Chauhan, 2006; Adhikari et al., 2012). Together, these Rhododendron species highlight how high-mountain shrubs respond to climate drivers—rising temperatures, altered snowfall patterns, and moisture changes—thus serving as bio-indicators of ecosystem transformations in some of the world’s tallest mountain ranges.

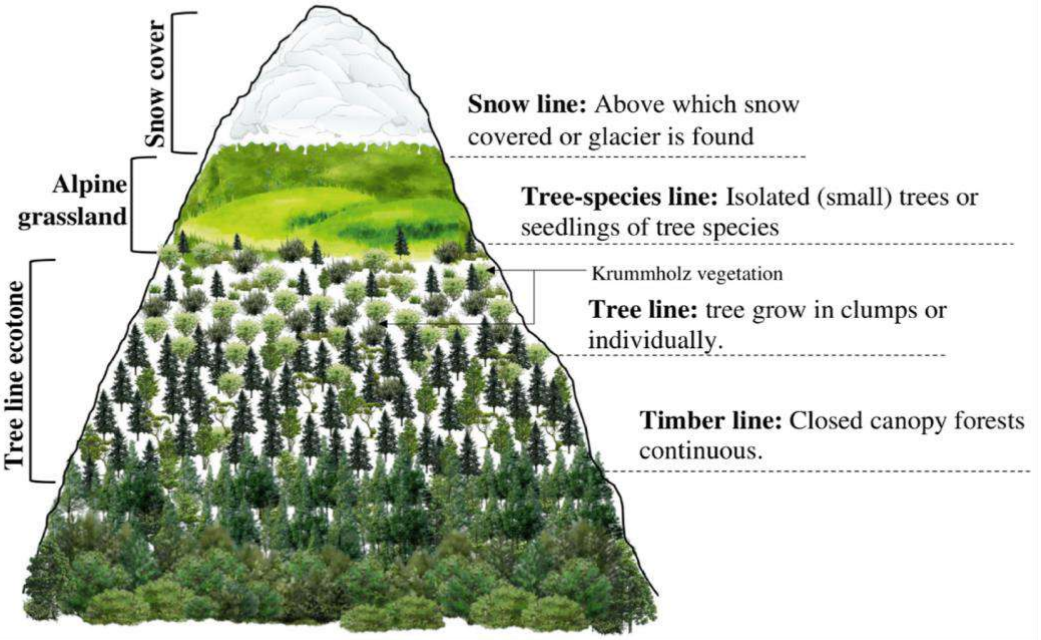

Figure 5. Schematic cross-section illustrating altitudinal vegetation zones in a mountainous region, transitioning upward from continuous closed-canopy forests below the timberline through the tree line ecotone (including isolated trees and krummholz vegetation), alpine grasslands, and finally reaching the snow-covered area above the snow line *(Source: adapted from Sharma et al., 2024; Heliyon,* *https://www.cell.com/heliyon/fulltext/S2405-8440%2824%2916828-4*).

4. Materials and methods

The methodological workflow adopted in this study is illustrated in Fig. 6. Samples were collected in the field according to species-specific growth patterns, including stems, roots, or a combination of both. Following collection, samples were transported to the laboratory, where thin sections were prepared using microtomes selected based on sample size and wood characteristics. For smaller *Salix* samples, cross-sections were prepared using a GSL-1 microtome, while radial and tangential sections were prepared using a Leica sliding microtome at the laboratory in Ljubljana. For larger *Rhododendron campanulatum* samples, sections were prepared using a laboratory microtome at the Swiss Federal Institute, WSL facility. After thin-section preparation, microscopic analyses were conducted to characterize wood anatomical traits. High-resolution images were captured using a microscope-mounted camera, and these individual images were subsequently stitched together using PTGui software. Following this, measurement of tree-ring parameters and development of growth chronologies, were performed. These analyses facilitated the evaluation of climate-growth relationships through response-function modeling, enabling detailed investigation of environmental influences on growth dynamics across different ecological regions.

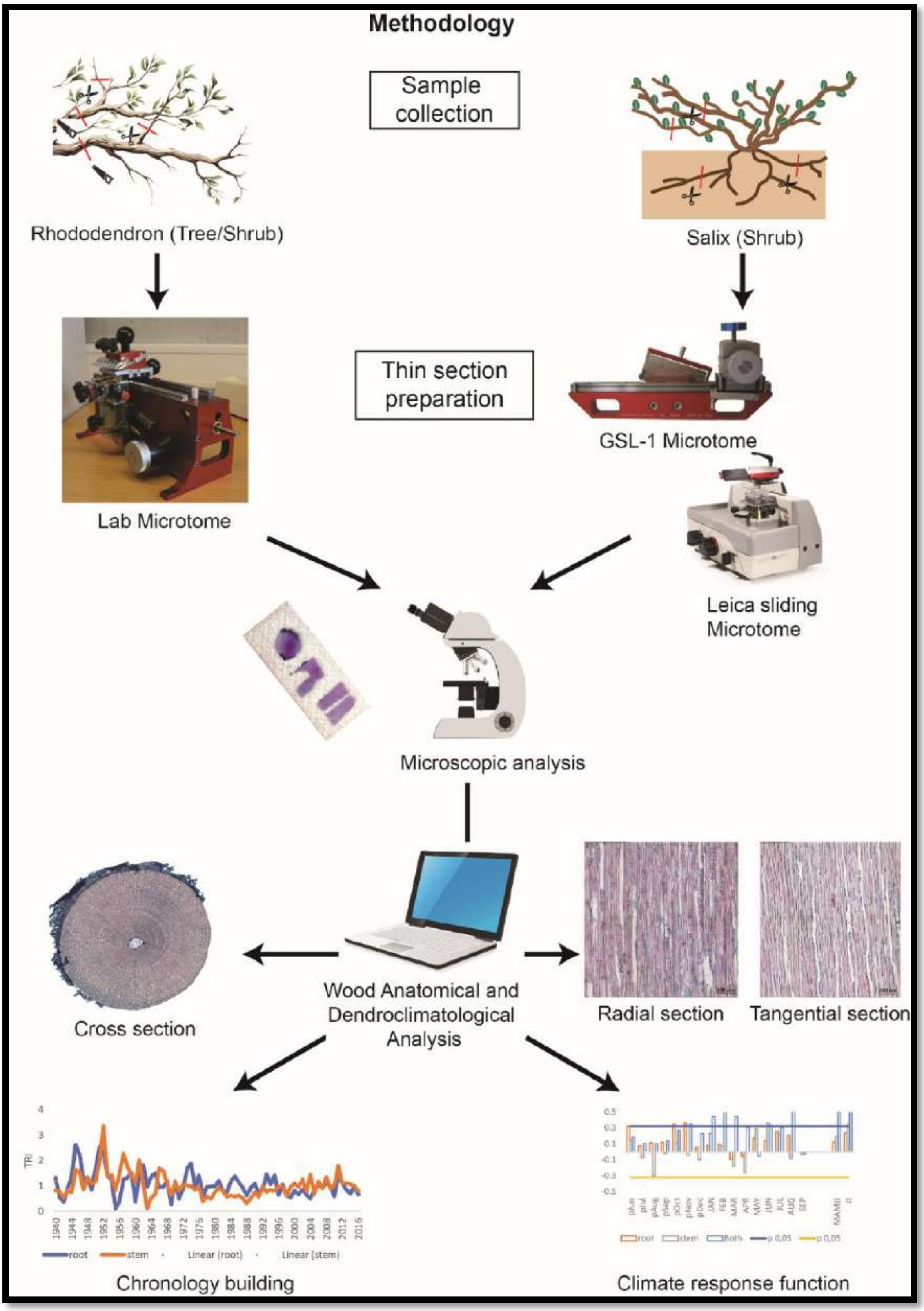

Figure 6. Schematic illustration outlining the step-by-step methodological workflow adopted in this study. The process includes sample collection from different plant species, thin-section preparation using various microtomes, microscopic analysis, and subsequent wood anatomical and dendroclimatological analyses. Final steps involve generating cross-sectional, radial, and tangential sections, chronology building, and establishing climate-growth response functions.

4.1. Field sampling

Sampling protocols were tailored to the regional and species-specific characteristics of the study areas. In High-Arctic region (Spitsbergen), entire dwarf shrub individuals of *Salix polaris* were collected—including exposed roots, root collars, and branches—to assess whole-plant growth responses. For Rhododendron shrubs in the Himalayas, stem discs were extracted from the largest branches at two to three positions above the soil to capture radial growth variability. Samples were preserved in paper bags containing 50–70% ethanol to prevent fungal growth and moisture damage, thereby ensuring anatomical integrity. This stratified approach enabled representative sampling across species, sites, and environmental conditions, facilitating robust comparisons of dendroclimatic signals and anatomical adaptations.

4.2. Laboratory and wood anatomical traits analysis

Laboratory methods were adapted to meet the diverse research objectives across different studies, ensuring the production of reliable data for both dendroclimatic and anatomical analyses. For preparing thin sections, the primary instrument was the GSL1 sliding microtome (Gärtner et al., 2015), which produced cross-sections of 15–20 μm at three to four locations along each specimen. Additional equipment, such as the Leica SM2010R sliding microtome and core-microtome, was employed for specific analyses of shrub and tree cores.

A serial sectioning procedure was applied to address challenges such as missing or wedging rings and variations in ring widths (Kolishchuk, 1990; Myers-Smith et al., 2015b). Cross-sections were stained using a solution of 1% safranin and astra blue, which enhanced the contrast between lignified and non-lignified tissues. For mounting, samples were either embedded in Canada balsam—with heating at 60 °C for 24 hours to ensure uniform distribution (Gärtner and Schweingruber, 2013)—or, in some cases, mounted using Euparal. Moreover, in some time utilizing cases, a UV-Kit was employed for rapid mounting.

Images were captured using various instruments: for most samples, a Leica FLEXACAM C1 camera connected to a Leica DM1000LED microscope was used, while for the *Rhododendron campanulatum*, a Zeiss AxioScan Z1 Slide Scanner was employed. Composite images were created by stitching individual microscope photographs using PTGui software (New House Internet Services B.V., Rotterdam, The Netherlands). Growth ring widths were measured using WinDENDRO (Regent Instruments, Inc., Québec, Canada) or WinCELL software, and quantitative wood anatomical traits (e.g., vessel frequency and tangential diameter) were analyzed using ImageJ. Each measurement was repeated at least three times to ensure accuracy and consistency.

4.3. Dendrochronological and dendroclimatological analysis

Chronologies for each site and species were developed using standardized dendrochronological techniques to accurately capture growth patterns and climate responses. A serial sectioning approach (Kolishchuk, 1990; Gärtner and Schweingruber, 2013) was applied to overcome issues related to missing and wedging rings. Growth-ring widths were measured using WinDENDRO and WinCELL, and cross-dating was performed visually and statistically with COFECHA to ensure temporal alignment (Grissino-Mayer, 2001).

Master chronologies were created by averaging the best-matched samples to provide representative growth trends. Shrubs generally do not exhibit distinct age trends in their growth patterns, which differentiates them from trees and influences the standardization methods used in dendrochronological analyses. As a result, individual series standardization methods, such as linear regression and horizontal means, are commonly applied for dwarf shrub detrending (Myers-Smith et al., 2015b; Young et al., 2016). In our analyses, the ring-width data for Arctic shrubs were standardized using a horizontal line through the mean, as no age trend was observed in the raw data. For other species, such as *Rhododendron* from the Carpathians, a double-detrending process was applied, involving negative exponential or linear regression, followed by fitting a cubic smoothing spline with a 50% frequency response at 32 years (Cook and Peters, 1981). This approach effectively eliminates age-related effects, ensuring an accurate representation of the growth patterns.

Dendroclimatological analysis employed correlation function analysis to examine relationships between tree-ring chronologies and meteorological data over a 16-month period, from June of the previous year to September of the current year. Meteorological data from several stations with long-term monthly temperature and precipitation records were obtained from the Veðurstofa Íslands (Icelandic Meteorological Office) and Rif Field Station (Icelandic Arctic Cooperation Network) for the study in Iceland, from Svalbard Airport (a coastal station) for Central Spitsbergen samples, and from Pozhyzhevsʹka Meteorological Station for the Carpathians. The data spans utilized vary based on the availability of records and the period up to the sample collection year. For the Icelandic stations, the data range from 1975 to 2016, while for the Pozhyzhevsʹka station, it spans from 1961 to 2020. For the Central Spitsbergen study, the data covers the period from 1971 to 2022, with monthly records of mean temperature (°C) and total precipitation (mm). For dendroclimatological analyses, common periods for each region were considered. Further details on this aspect are provided in the attached articles.

4.4. Statistical analysis

Various statistical methods were applied throughout the research articles to examine climate-growth relationships **(Articles I–IV)**, and evaluate anatomical differences in wood structures between species **(Article II)**. Seasonal and monthly climate-growth associations were analyzed using Pearson's correlation coefficients, with significance established at a 95% confidence level. Moving correlation analysis using 25-year windows assessed temporal variations in climate sensitivity, providing insights into the climatic drivers of growth variability in Arctic and high-mountain ecosystems.

In **Article V**, initial exploratory analysis indicated potential temporal variations in aphid infestation frequencies. Consequently, segmented (piecewise) regression was applied to statistically identify and model these temporal shifts, determining breakpoints associated with significant changes in infestation rates in **Article V**. Lowess smoothing informed the initial selection of breakpoint candidates. Analyses were conducted separately across distinct altitude categories (low, mid, high) to investigate altitude-dependent infestation patterns. The Davies test confirmed structural changes in regression slopes. Diagnostic analyses, including residual plots, temporal residual assessments, and quantile-quantile plots, validated model assumptions. All statistical analyses and visualizations were conducted using R software (R-Core-Team, 2023) within the RStudio environment (Posit-Team, 2023), utilizing the 'segmented' package for segmented regression and Davies test (Muggeo, 2008; Muggeo, 2024). Additionally, Welch's two-sample t-test was performed in **Article II** to confirm statistically significant differences in tangential vessel diameter and vessel frequency between species.

5. Results and interpretation

5.1. Climatic signals on growth ring variation in *Salix herbacea*: Comparing two contrasting sites in Iceland (Article I)

5.1.1. Contrasting site conditions and ecological background

Mýrdal and Afrétt represent two ecologically distinct sites that shape *Salix herbacea* growth. Mýrdal, in southern Iceland near the Mýrdalsjökull ice cap, averages 5.5 °C annually and receives 2363 mm of precipitation. The eroded volcanic ridges and plateaus create a wet environment supporting *S. herbacea* alongside *Dryas octopetala*. Excess moisture, however, can lead to soil erosion and instability. In contrast, Afrétt lies in northeastern Iceland, averaging 2.6 °C and just 658 mm of precipitation. Its hilly basaltic upland is prone to solifluction and supports sparse vegetation where *S. herbacea* grows with *S. arctica*. These contrasting climates—warm/wet vs. cold/dry—define the specific environmental constraints for *S. herbacea* in each site.

5.1.2. Divergent climate–growth relationships

Growth-ring analysis highlights strikingly different climatic sensitivities at the two sites (Fig. 7). In Mýrdal, stem increments correlate positively with March, May, and July temperatures (Fig. 7A), implying that early-season warmth and prolonged summer heat drive radial expansion. Meanwhile, June precipitation shows a negative relationship (Fig. 7B), suggesting that excessive rainfall can hamper growth through potential waterlogging or soil destabilization. By contrast, Afrétt's drier conditions make precipitation a pivotal growth factor (Fig. 7D). Winter (October–March) and summer (June, August) precipitation strongly boost growth, while higher June temperatures negatively affect ring widths (Fig. 7C), presumably due to increased evapotranspiration and moisture stress. Thus, temperature dominates in wet Mýrdal, whereas precipitation governs growth in dry Afrétt, reflecting *S. herbacea*'s ecological plasticity and its use as an environmental indicator.

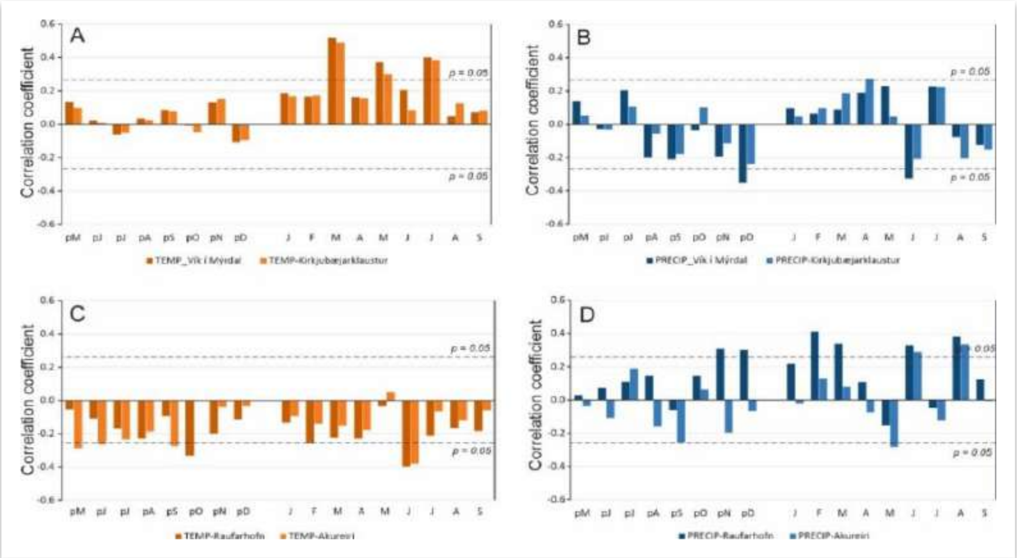

Figure 7. Correlation coefficients of ring-width data at two contrasting sites, Mýrdal (A,B) and Afrétt (C,D), with monthly temperature and precipitation from the nearest meteorological stations. Illustrating how different seasonal windows influence shrub growth responses.

5.2. Insights from roots to stems: Comparative wood anatomy and dendroclimatic investigation of two *Salix* species in Iceland (Article II)

5.2.1. Comparative wood anatomy of Icelandic *Salix* species

Microscopic analysis revealed distinct anatomical adaptations in response to Iceland's varied conditions. *Salix arctica* features larger vessels and fibers in both stems and roots (Fig. 8A, C), enhancing water transport efficiency—a critical advantage in environments with fluctuating moisture—but with a lower vessel frequency (approximately 232 vessels/mm² in stems and 130 vessels/mm² in roots). In contrast, *Salix herbacea* exhibits a higher vessel frequency (around 471 vessels/mm² in stems and approximately 359 vessels/mm² in roots) with smaller, thicker-walled vessels (Fig. 8B, D) that prioritize hydraulic safety over efficiency, thereby compensating for the reduced lumen size by increasing conductive pathways.

Additionally, *S. arctica* typically forms well-defined growth rings and produces reaction wood with gelatinous fibers, indicating adaptation to mechanical stress such as wind. Conversely, *S. herbacea* often shows pronounced tyloses and phenolic deposits—especially in root sections—suggesting enhanced defenses against drought and unstable substrates. These anatomical distinctions underscore the species-specific adaptive strategies within the genus *Salix*, with *S. arctica* adopting a rapid, water-efficient growth strategy and *S. herbacea* favoring a more stress-resilient approach in the harsh Arctic environment.

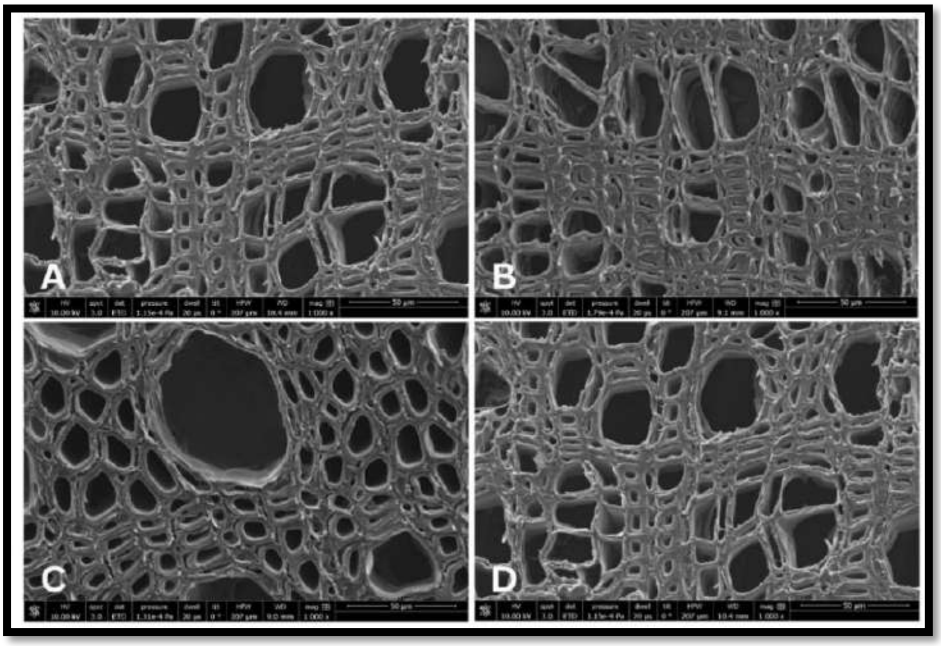

Figure 8. SEM photographs showing cross-sections of the root (A–C) and stem (B–D) of *Salix herbacea* (A,B) and *Salix arctica* (C,D), respectively, highlighting the conductive elements in normal wood

5.2.2. Stems vs. Roots: Differential Dendroclimatic Signals

The growth trends differ markedly between the two species: *Salix arctica* exhibits an overall increase, while *Salix herbacea* shows a consistent decline over time. These divergent trajectories are reflected in the distinct climate sensitivities of their stems and roots. For *S. herbacea*, both tissues display strong negative correlations with winter and summer temperatures, indicating that colder conditions and ensuing moisture deficits limit growth. In contrast, *S. arctica* stems respond robustly to warm conditions—with positive correlations for winter (rtJan = 0.41, rtFeb = 0.37, rtApr = 0.47) and summer temperatures (rtJAS = 0.55)—suggesting that warmth promotes aboveground expansion. However, its roots exhibit a negative response to the previous year's summer temperatures (rtpJAS = –0.32), implying that high temperatures may restrict belowground development due to increased evapotranspiration.

Regarding precipitation, *S. herbacea* stems are more responsive than its roots, showing significant positive correlations with both winter and summer precipitation, which highlights the species' dependence on moisture. In *S. arctica*, a positive correlation with the previous year's June precipitation (rpJ = 0.42) is observed, whereas current year's September precipitation has a negative effect (rpS = –0.48), indicating that its roots are particularly sensitive to critical moisture conditions. Analyses from two meteorological stations revealed that these correlations are more pronounced at Raufarhofn compared to Akureyri, underscoring the influence of local microclimatic conditions. Collectively, these findings suggest that while *S. arctica* growth is predominantly temperature-driven, *S. herbacea* is more responsive to precipitation, a divergence that has important implications for calibrating dendroclimatic models and understanding species-specific adaptive strategies in Arctic environments.

5.3. Multiple factors controlling polar willow growth in the High Arctic (Svalbard): implications for future prediction of tundra productivity (Article III)

5.3.1. Site-specific growth patterns and variation

Salix polaris in Spitsbergen displayed substantial growth variability across six sites reflecting altitudinal and topographic differences. Growth-ring series spanning 30–39 years showed consistently wider rings (103.9–115.3 µm) at valley bottoms and narrower rings (73.5–81.2 µm) at high-elevation plateaus with shorter, harsher growing seasons. Inter-sample correlation and sensitivity were higher at elevation, indicating stronger responses to annual climatic fluctuations and frequent missing or compressed rings due to extreme cold and limited moisture. Valley stands exhibited an overall positive growth trend, suggesting milder conditions support expansions, whereas plateau stands showed weaker or slightly negative trends. Shared negative indicator years (2006, 2014) matched anomalous climatic events, emphasizing how episodic extremes can modulate *S. polaris* growth in both valley and plateau habitats.

5.3.2. Seasonal temperature–moisture interactions driving growth

Salix polaris growth was governed by temperature–precipitation dynamics, shifting with site elevation (Fig. 9). In lower valleys, early-summer warmth (June) propelled faster snowmelt and earlier growth onset, but mid- to late-summer precipitation played a greater role as soil moisture became limiting. Spring precipitation (March–April) occasionally delayed growth by prolonging snow cover. At high-elevation plateaus, July–August temperatures were more influential, reflecting a later start to the growing season. Meanwhile, increased late-summer precipitation often correlated negatively with ring widths, potentially due to reduced solar radiation under overcast conditions. Winter warmth sometimes suppressed subsequent ring formation, as noted in 2014's mid-winter thaw. Overall, these patterns highlight how microclimatic variations shape *S. polaris*'s responses to Arctic warming.

5.3.3. Integrating remote sensing: Broader ecological and climatic implications

NDVI data corroborated the dendrochronological results, revealing higher vegetation productivity at valley sites and low, relatively static NDVI on exposed plateaus. Lower-elevation stands appear to benefit from lengthening growing seasons, whereas plateau vegetation remains severely constrained by cold, windy exposure, and limited snow protection. Merging satellite-based productivity metrics with ring-width data offers a multilayered perspective on tundra dynamics, indicating that warming fosters growth at favorable sites but leaves the harshest habitats minimally changed.

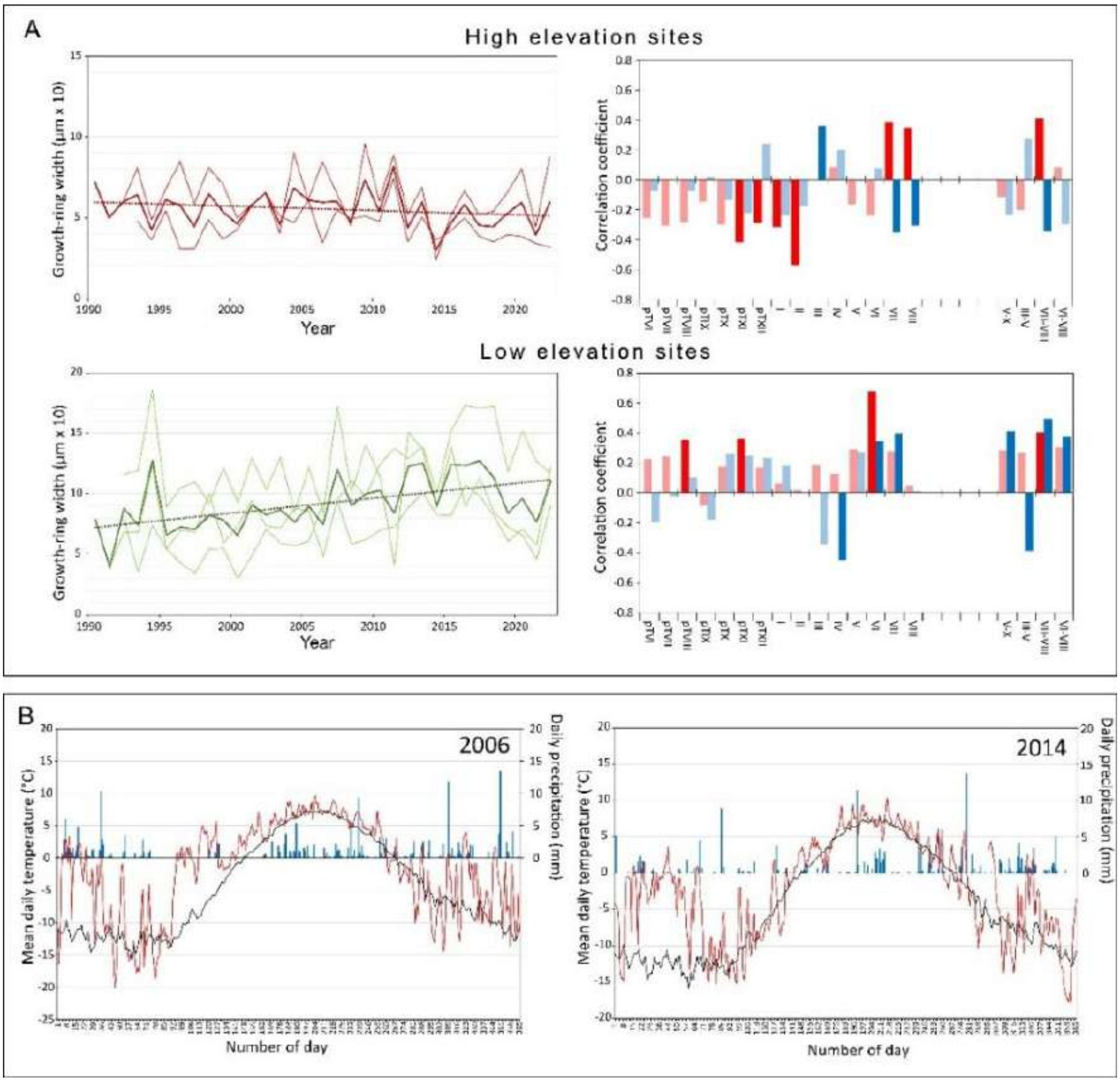

Figure 9. (A) Growth-ring chronologies of *Salix polaris* from high- and low-elevation sites, together with their correlation and response function analyses with climate data. (B) Air temperature and precipitation data for 2006 and 2014, illustrating years marked by notably reduced growth in *S. polaris*.

5.4. Varied growth response of High Alpine *Rhododendron myrtifolium* and forest zone tree species to climate warming in the eastern Carpathians, Ukraine (Article IV)

5.4.1. Comparing growth trends in High Alpine *R. myrtifolium* vs. forest-zone trees

In the Eastern Carpathians, ring-width chronologies constructed from 97 trees and shrubs reveal divergent long-term growth patterns between high-alpine *Rhododendron myrtifolium* and forest-zone conifers (*Picea abies* and *Abies alba*) (Fig. 10). The 66-year chronology for *R. myrtifolium* shows a strong positive response to warm-season temperatures (March–July), indicating that this high-alpine shrub benefits from rising temperatures above the treeline. In contrast, forest-zone conifers exhibit negative correlations with summer warmth—likely a consequence of drought stress—which is further evidenced by their high inter-sample synchronicity ($r = 0.90$) and convergent growth trends over time. Negative pointer years, associated with extreme frost or summer drought, were observed across all species; however, *R. myrtifolium* consistently demonstrates an upward trend under moderate warming, while the forest stands show gradual declines. Microscopic analyses of *R. myrtifolium* also reveal frequent wedging rings and growth eccentricities, reflecting the challenges of the subalpine environment.

5.4.2. Main climatic drivers of growth divergence and ecosystem shifts

Temperature and precipitation are the primary climatic drivers underlying the contrasting growth responses. *Rhododendron myrtifolium* shows a robust positive correlation with warm-season temperatures—its highest monthly correlation occurring in August—supporting the view that earlier snowmelt and moderate summer warmth are critical for its radial expansion.

In contrast, forest-zone conifers display weaker, even negative, temperature signals during hot August conditions, indicative of drought-induced stress. Moreover, while *R. myrtifolium* demonstrates only a slight positive association with early-spring precipitation, the conifers appear more sensitive to moisture availability during this period. Moving correlation analyses reveal that *R. myrtifolium*'s sensitivity to summer temperatures has increased over recent decades, whereas the conifers have become progressively more vulnerable to late-summer drought. These divergent responses suggest that continued warming may drive the upward migration of alpine shrubs at the expense of forest stands, with profound implications for regional biodiversity and carbon storage. Understanding these complex climate–growth interactions is essential for refining predictive models and guiding effective conservation strategies in the face of ongoing environmental change.

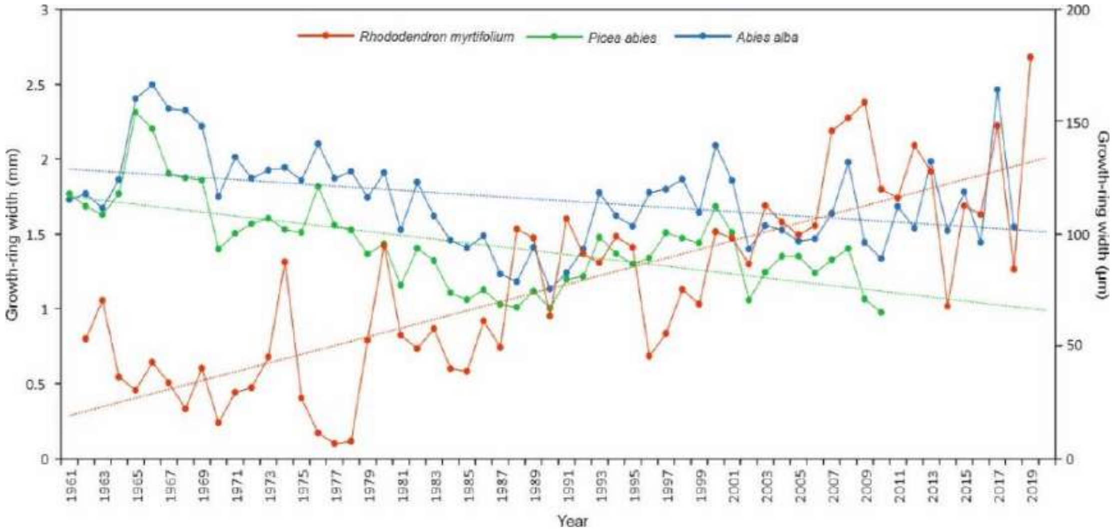

Figure 10. Growth trends (1961–2019) of the ring-width chronologies for the three analyzed species (*Rhododendron myrtifolium*, *Picea abies*, and *Abies alba*), illustrating their divergent trajectories over time.

5.5. Tracing aphid infestations through wood anatomical markers: Insights from *Rhododendron campanulatum* in the Himalayan region (Article V)

5.5.1. Wood anatomical traces of aphid infestation

Microscopic examinations of *R. campanulatum* revealed distinct anatomical signatures marking aphid activity (Fig. 11A,C), appearing as tangentially elongated, radially compressed callous zones within the annual rings. This cambial disturbance, located often near the latewood boundary, indicates peak feeding in late summer, although occasional earlywood findings point to some spring feeding events. Structurally, these traces differ from frost rings or hail wounds, as aphids partially preserve cambial cells. Frequent tyloses and phenolic deposits suggested a defensive response, especially in root sections. Variation in callous severity among samples may stem from differing infestation intensities or individual host resistance. Collectively, these markers enable long-term reconstructions of aphid infestations above 3100 m, providing an unprecedented look at high-altitude insect–plant dynamics.

5.5.2. Spatio-temporal patterns of aphid outbreaks

Our analysis reveals that aphid trace frequencies have fluctuated over time without a consistent link to seasonal temperatures. Notably, a uniform presence of aphids has been observed at high-altitude Himalayan sites since 1951, challenging previous assumptions about high-altitude limitations. When grouped by altitude (low, mid, and high), our data show that aphid infestations increase from early tree growth to the early 2000s—accompanied by an increase in sample depth—followed by a decline when sample depth remains constant (Fig. 11a). Although aphids occur throughout the 3100–3400 m a.s.l. range, fewer older tree samples at lower altitudes likely result from anthropogenic activities such as fuelwood harvesting. Segmented regression analysis indicates a common pattern across altitudinal zones: an initial rise in infestation levels peaking between 2000 and 2004, followed by a decline or stabilization.

5.5.3. Implications for climate reconstruction

Insect outbreaks can significantly alter tree physiology and growth through defoliation, cambium feeding, or root parasitism, thereby modifying the climatic signals preserved in tree rings. In addition, deciduous species often respond more rapidly to warming than evergreens, which can further affect climate reconstructions. Notably, our study is the first to trace aphid activity in Himalayan alpine plants, revealing that these biotic disturbances are randomly distributed and disrupt ring-width boundaries in many samples. Therefore, incorporating such biotic disturbances into climate reconstruction models is essential to avoid biases and misinterpretations of historical climatic conditions.

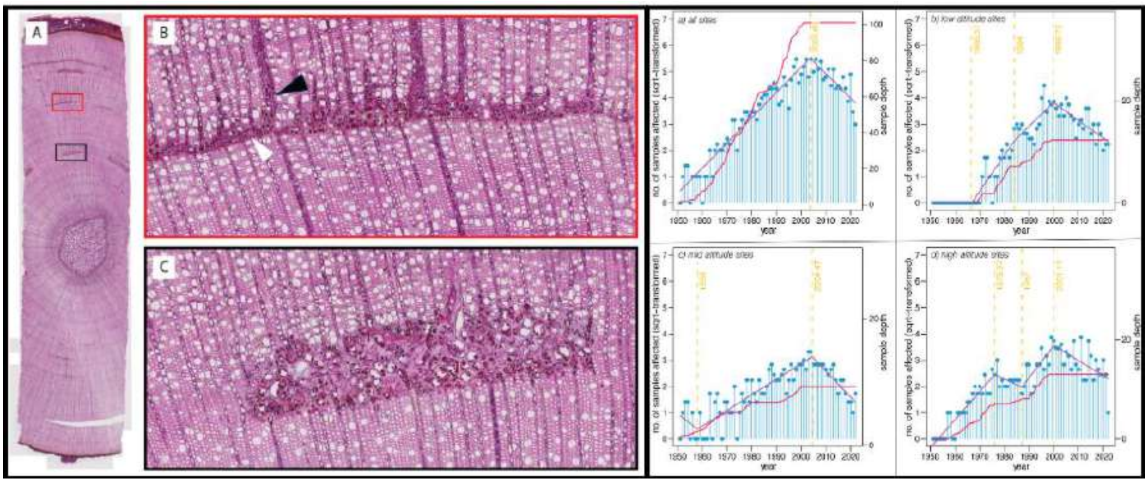

Figure 11. (A) Microsection of *Rhododendron campanulatum* highlighting an aphid trace (magnified in B and C). The red rectangle indicates a frost ring, and the black rectangle marks an aphid trace. (B) Magnified frost ring, showing bent rays (black arrow) and collapsed cells (white arrow) caused by a frost event. (C) Magnified aphid trace with locally restricted callous tissue transitioning back to normal cell structure. The bar charts (right side panel) depict infestation trends at a) all sites, b) low, c) mid, and d) high-altitude sites, with blue bars and dots representing the yearly count of infested samples, the red line indicating accumulated sample depth, and the purple line denoting the segmented regression model. Breakpoint years (yellow dotted lines) mark shifts in infestation patterns. The number of affected samples was square-root transformed for analysis.

6. Synthesis and Discussion

Among Earth's most vulnerable areas to climate change, Arctic and high mountain ecosystems contend with intensifying warming, shifting precipitation regimes, and severe weather extremes that collectively drive rapid transformations in vegetation dynamics. To understand how shrubs adapt to these changes, this research examined the dendroclimatic responses and wood anatomical traits of five key species—*Salix herbacea*, *Salix arctica*, *Salix polaris*, *Rhododendron myrtifolium*, and *Rhododendron campanulatum*—across diverse sites and climatic gradients. These comparative analyses reveal how different abiotic and biotic factors intersect to drive species-specific growth dynamics.

a) Growth variations and climatic sensitivities

While temperature remains a dominant driver of shrub expansion in cold-limited habitats, precipitation emerges as a critical factor in many sites. In Iceland, *Salix herbacea* exhibits strong correlations with both winter and summer precipitation, whereas *Salix arctica* is more responsive to summer temperatures, reflecting its higher sensitivity to thermal conditions. Similarly, in Svalbard, *Salix polaris* shows a clear temperature–growth relationship at higher elevations, but at lower elevations, early snowmelt and well-drained soils shift the growth limitation toward water availability. Comparative studies across the Arctic and in the Himalayas underscore that although warming remains a major driver (Buchwal et al., 2019; Le Moullec et al., 2020; Panthi et al., 2021), precipitation patterns can become decisive in water-limited settings (Opala-Owczarek et al., 2018; Owczarek et al., 2021; Dhyani et al., 2023). In the Eastern Carpathians, *Rhododendron myrtifolium* exhibits robust positive responses to summer temperatures—consistent with findings by (Sidor et al., 2015)—benefiting from conditions that challenge lower-elevation conifers. In contrast, the research from the Himalayas shows that *Rhododendron campanulatum* is influenced not only by temperature but also by persistent insect herbivory, highlighting how biotic stressors can override the dominant climatic effects (Walther et al., 2009; Roques, 2010).

b) Species- and site-specific responses

Wood anatomical traits play a pivotal role in shaping species resilience. In Iceland, *Salix arctica* exhibits larger xylem vessels that enhance water transport—a strategic advantage in warmer conditions—while *Salix herbacea* relies on smaller vessels that prioritize hydraulic safety under variable moisture. These anatomical differences illustrate species-specific adaptations that interact with local site factors. For instance, in Central Spitsbergen, site-specific investigations reveal that *Salix polaris* at higher-elevation stands benefit from permafrost moisture retention, whereas at lower-elevation areas, rapid snowmelt and well-drained soils induces seasonal drought stress.

Although some studies report weak or even negative correlations between summer temperature and *S. arctica* ring growth in certain regions (Schmidt et al., 2006), findings from Peary Land (82°N) by (Buchwal et al., 2019) and Qikiqtaruk–Herschel Island (Boyle et al., 2022) demonstrate a robust positive response to summer warmth. Moreover, research on *Salix polaris* also further highlights the influence of local hydrological conditions: (Owczarek et al., 2021) noted that water deficit in July renders precipitation the limiting factor for summer growth on Bear Island, while (Opala-Owczarek et al., 2018) showed that in coastal settings with greater rainfall, soil moisture and structure outweigh temperature in determining ring growth. In contrast to other studies showing only positive response to summer temperature (Buchwal et al., 2013; Le Moullec et al., 2020), these findings, combined with evidence that local factors—such as early-spring snow cover (Vaganov et al., 1999) and topographical variations (Ropars et al., 2015)—critically modulate shrub temperature sensitivity, underscore the need to consider both species and site-specific responses when interpreting the diverse growth responses observed across Arctic ecosystems.

c) Integrating findings across Arctic and Alpine regions

Initial studies (**Article I**) in sub-Arctic Iceland revealed that *Salix herbacea* serves as a sensitive indicator of moisture availability, especially under drought stress. Moreover, the contrasting anatomical and growth strategies underscore the heterogeneity within the two species of same genus: while *S. arctica* thrives under warming conditions, *S. herbacea* remains vulnerable to fluctuating precipitation regimes (**Article II**). In the High Arctic, Central Spitsbergen, research on *Salix polaris* (**Article III**) demonstrated how microsite conditions significantly alter climatic impacts. This site-specific variation echoes broader Arctic observations where rising temperatures initially support shrub expansion, but increasing temperature can constrain further growth.

Beyond the Arctic, *R. myrtifolium* in the Eastern Carpathians reinforced the idea that warm-season temperatures promote shrub growth in cold-limited alpine zones (**Article IV**). Unlike lower-elevation conifers that suffer drought-induced stress, *R. myrtifolium* capitalizes on enhanced snowmelt and summer warmth, highlighting species-specific resilience to changing climatic factors. Contrastingly, research in the Western Himalayas revealed how *R. campanulatum* not only responds to climatic conditions but also experiences long-term aphid infestations (**Article V**). Notably, these infestations persist above 3,200 m, challenging the assumption that extreme cold limits insect activity. Younger shrubs suffer higher infestation rates, whereas mature individuals maintain lower but chronic aphid presence, underscoring the rising influence of biotic stressors in alpine systems.

d) Regional comparisons and global implications

Across Iceland, Svalbard, the Carpathians, and the Himalayas, shrubs often respond favorably to initial warming, but secondary constraints (e.g., drought, biotic interactions) increasingly modulate those gains. *Salix* species in Arctic environments transition from temperature-limited to water-limited growth as snowmelt accelerates and soil drainage intensifies. In alpine systems like the Carpathians, *R. myrtifolium* capitalizes on moderate warming until lower-elevation drought stress emerges. *R. campanulatum* introduces the underexplored dimension of insect herbivory, underscoring the complexity of climate–growth interactions in high-altitude environments. These findings reflect a broader consensus in cold-region ecology: while global warming initially reduces thermal constraints, shifting precipitation regimes, winter disturbances (e.g., rain-on-snow events), and novel biotic stressors can alter or reverse the trajectory of shrub expansion. Consequently, ecosystem trajectories in Arctic and high mountain regions depend on a blend of abiotic drivers and biotic feedbacks, urging more nuanced modeling and management strategies.

e) Limitations and future directions

Several factors limit the scope of these studies. Many shrub chronologies span relatively short timeframes, restricting the detection of long-term climatic cycles. Non-climatic disturbances, such as soil erosion, volcanic activity, and permafrost thaw, can obscure climatic signals in ring-width and wood anatomical data. Additionally, variations in sampling protocols hamper cross-regional comparisons. Future research should integrate dendrochronological data with remote sensing (e.g., NDVI, high-resolution satellite imagery) to capture landscape-scale vegetation changes. In light of the Himalayan findings, biotic stressors (particularly herbivory) merit greater attention, as insects can thrive at unexpectedly high elevations. Long-term monitoring that unites multiple proxy records (e.g., soil moisture, daily temperature, insect surveys) will be critical for refining predictive models of how Arctic and alpine ecosystems evolve under continued warming.

These findings carry significant implications for dendroclimatic research and climate reconstruction. Several past dendro-entomological studies have shown that insect defoliation not only reduces growth but also alters the climatic signal in tree rings (Blais, 1958; Welsh, 2007). Moreover, deciduous species tend to respond more rapidly to warming than evergreens, further complicating climate reconstructions (Elmendorf et al., 2012; Gough et al., 2012). Insect activity can disrupt ring formation, leading to inaccuracies in estimating temperature and precipitation signals (Prendin et al., 2020). Therefore, integrating both abiotic drivers and biotic stressors into dendroclimatic models is essential for refining climate reconstructions and improving predictions of future ecosystem responses.

7. Conclusions

Arctic and high mountain ecosystems stand among the most climate-sensitive on Earth, where rising temperatures, shifting precipitation regimes, and extreme weather events are rapidly reshaping vegetation dynamics. As a result, this dissertation provides an extensive analysis of how *Salix herbacea*, *Salix arctica*, *Salix polaris*, *Rhododendron myrtifolium*, and *Rhododendron campanulatum* respond to these environmental pressures through a combination of dendrochronology, wood anatomical studies, and ecological observations. By focusing on multiple climatic regimes—from sub-Arctic Iceland and Svalbard to the Eastern Carpathians and the Himalayan Mountains—this research highlights the interplay between abiotic factors (temperature, precipitation, permafrost stability, snowmelt timing) and biotic influences (aphid herbivory) in shaping species-specific growth trajectories.

The findings reveal that **temperature** often serves as an initial driver of shrub expansion, particularly in cold-limited habitats, while **moisture availability** increasingly moderates or even overrides these thermal benefits. In Iceland, *S. herbacea* proved exceptionally sensitive to both summer and winter precipitation, illustrating how water stress can constrain potential warming advantages. Meanwhile, *S. arctica* displayed a stronger dependence on summer temperatures, echoing broader patterns of climate-driven radial growth in certain Arctic shrubs. In Svalbard, *S. polaris* underscored the role of **microsite conditions**: higher elevations with permafrost buffering showed enhanced growth under warming, whereas lower sites experienced seasonal drought stress linked to rapid snowmelt. Beyond the Arctic, *R. myrtifolium* in the Eastern Carpathians thrived under rising summer temperatures, showing greater resilience than drought-impacted lower-elevation conifers. In contrast, *R. campanulatum* in the Himalayas demonstrated that **biotic stressors**—notably aphid infestations—can persist at elevations above 3200 m, underscoring the growing influence of insect herbivory in high-altitude shrub ecology.

Collectively, these results emphasize the **species-specific** nature of climate responses and the **site-dependence** of growth outcomes. Warming alone does not uniformly benefit shrubs; factors such as permafrost degradation, soil moisture deficits, and winter disturbances (e.g., rain-on-snow events) introduce new growth constraints in cold regions. Likewise, long-term insect pressures in alpine habitats challenge assumptions that extreme cold inherently prevents herbivory at high elevations. As a result, future projections of shrub expansion and ecosystem restructuring require integrated models that account for temperature trends, precipitation patterns, winter disturbances, and biotic interactions.

Looking ahead, four key research priorities emerge to refine our understanding of vegetation changes in these vulnerable ecosystems:

1. **Extending Chronologies:** Expand site-specific and species-specific dendrochronological records across multidecadal to centennial timescales, enhancing our ability to capture local climatic variability and complex growth responses, and ultimately providing more robust reconstructions of past environmental changes.
2. **Remote Sensing Integration**: Combine ground-based ring-width dataset with high-resolution satellite imagery (e.g., NDVI, hyperspectral sensing) to assess how localized growth patterns scale up to landscape-wide vegetation changes.
3. **Biotic Factors in Modeling**: Incorporate insect herbivory and other biological stressors into climate impact models, recognizing their capacity to shape plant vitality, especially under sustained warming.
4. **Winter Disturbances**: Investigate the frequency and ecological impact of extreme winter events (like rain-on-snow), which can damage stems, hamper oxygen diffusion to roots, and ultimately shift growth constraints from temperature to water availability.

By synthesizing findings across Arctic and alpine regions, this dissertation provides a **comprehensive view** of shrub responses to contemporary environmental changes, underlining the importance of wood anatomical traits and dendroclimatic signals in understanding plant resilience. These insights will be crucial for future ecological research, guiding conservation priorities, and improving climate models in **cold-region** contexts, where evolving conditions demand both **long-term monitoring** and **multiscale approaches** to capture the full complexity of these sensitive ecosystem transformations.

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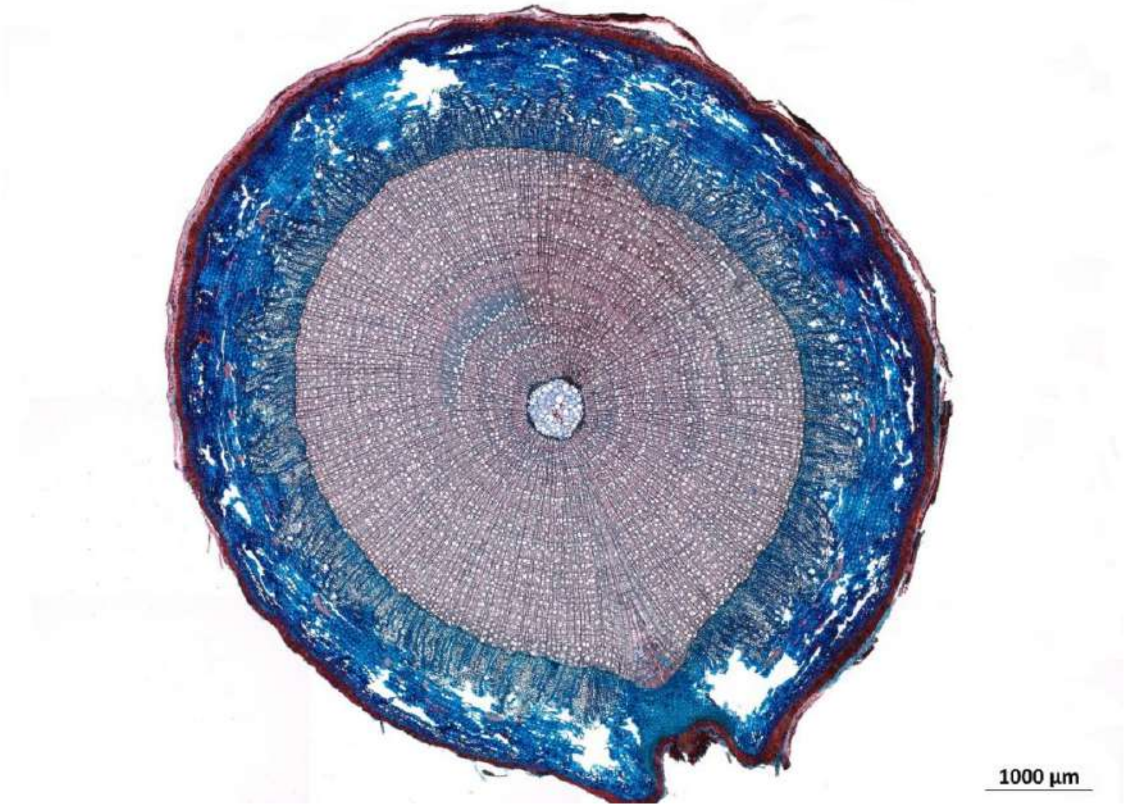
List of Publications

Article I

Climatic Signals on Growth Ring Variation in Salix herbacea: Comparing Two Contrasting Sites in Iceland



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Article

Climatic Signals on Growth Ring Variation in *Salix herbacea*: Comparing Two Contrasting Sites in Iceland

Mohit Phulara [1], **Magdalena Opała-Owczarek** [1,*] and **Piotr Owczarek** [2]

[1] Institute of Earth Sciences, Faculty of Natural Sciences, University of Silesia in Katowice, ul. Bedzinska 60, 41-200 Sosnowiec, Poland; mohit.phulara@us.edu.pl
[2] Institute of Geography and Regional Development, University of Wroclaw, Pl. Uniwersytecki 1, 50-137 Wroclaw, Poland; piotr.owczarek@uwr.edu.pl
* Correspondence: magdalena.opala@us.edu.pl

Abstract: *Salix herbacea*, being such an adaptive species, has never been studied for its climatic response. The main purpose of this study is to examine the dendrochronological potential of *S. herbacea*. Furthermore, it aims to identify the main environmental factors that are influencing its growth. We selected two sampling sites that are different in terms of morphology and climate. Overall, 40 samples of dwarf willow were collected from two research sites and were analyzed by following the standard dendrochronological methods. The ring width chronology of the dwarf willow from the Afrétt site spans 1953–2017, i.e., 64 years. The correlations between air temperature and the ring width of dwarf willow indicate that this species responds positively to spring and summer temperatures for the Myrdal site. For the Afrétt site, this species responds positively to winter and summer precipitation. These effects may be related to tundra browning, a process that has appeared since the beginning of the 21st century. Our work is the first attempt to create a growth ring chronology of *S. herbacea* and to investigate its climate sensitivity. Despite the differences in local climate in both sites, this species shows its potentiality and a direct imprint of recent environmental changes in its ring width growth pattern.

Keywords: Iceland; arctic; *Salix herbacea*; dendrochronology; climate; drought stress

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1. Introduction

Arctic terrestrial ecosystems are immensely sensitive to modern climate variations and they reflect the effects of changes in air temperature, precipitation, snow cover, permafrost, active geomorphic processes, and the intensity of wildfires. During recent decades, large-scale warming in the Arctic has accelerated and is now occurring at a two-fold rate of the global trend [1]. However, the climatic and inter-annual weather conditions in the Arctic vary dimensionally, as well as the dynamics of biological, biogeochemical, and geomorphic processes in terrestrial ecosystems [2–4]. Climate change has placed plants and animals at high risk, particularly in alpine and Arctic habitats [5–7]. Moreover, due to such radical environmental changes, plants cannot migrate to a new place as easily as animals. The alpine habitat is characterized by severe environments, such as high wind exposure and long winters, which lead to limited nutrient resources. The interactions between wind and topography also create irregularities in the winter snow distribution, resulting in microhabitats with different snow melting times. Global warming is expected to lead to longer growing seasons and lower snow cover in ridge microhabitats. Hence, the ring widths of trees/shrubs comprise the backbone of high-resolution, terrestrial paleoclimatology [8]. Information regarding the growth of trees/shrubs and their response to climatic and environmental factors would be potentially useful. They provide information on the present and past environment and for understanding the variability of climate and other environmental factors, particularly in areas where tree growth is sensitive to limiting climatic factors [9].

Shrub communities are expanding and their growth is also increasing as a response to climate change, and this is occurring at an unprecedented rate in many tundra ecosystems [10,11]. Moreover, they represent a major component of groundcover in the Arctic and alpine tundra; therefore, it becomes very important to understand the effects of climate change on dwarf shrubs and their capacity to respond to environmental changes. Tundra plants growing in Arctic environments are very sensitive to climatic conditions and thus specifically useful for dendroclimatic investigations [12–19]. However, researchers have observed, particularly in recent years, an increase in the environmental importance of Arctic dendrochronology research and studies on complex plant responses to changing environmental conditions [14,16,18,20–25]. Earlier dendroclimatological studies indicated that shrub growth rates were positively sensitive to summer temperatures for most species and at most of the sites [20,26]. However, recent studies of dendroclimatology show that shrub growth/climate relationships are not uniform across the tundra biome [17,21,27]. Thus, these studies conclude that there is still a need to analyze some other species and generate their relations with different climatic parameters in unexplored sites.

Dendrochronological research in Iceland has been limited, probably due to the lack of old trees and tree species that are considered suitable for ring width studies. However, recently, some studies have been carried out on the climate response of some tree species, such as Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and lodgepole pine (*Pinus contorta* Daugl. var. contorta). Both species have shown a good correlation with spring and summer temperatures [28]. Dendroclimatological studies have also been carried out on birch (*Betula pubescens* Ehrh.) in Baejarstadarskogur in Southern Iceland, which showed a strong correlation with the average summer (June–August) temperature [29]. Meanwhile, with the spatial distribution of *Salicaceae* shrubs in the northernmost regions of the Arctic, regional variability in climatic controls on this genus' growth can be assessed. This is further relevant for assessing Salix dwarf shrub's potential and role in future snow redistribution, geomorphic processes' activity, water balance, permafrost thaw, and nutrient availability [10,30], particularly in the most extreme and climatically diverse High Arctic ecosystems. However, up to the present date, no dendroclimatological studies have been implemented for *Salix herbacea* species.

Therefore, in this study, the dwarf shrub *Salix herbacea* L. (dwarf willow) was analyzed. *Salix herbacea* is well distributed in the Arctic areas, as in northern regions of Europe, Western Siberia, and North America, and also in the mountainous regions of Central Europe, e.g., the Alps [5–7,31]. *Salix herbacea* is regarded as an optimal species for studying the effect of climate change in the Arctic and alpine tundra due to its ecological characteristics and the Arctic–alpine distribution range [32–34]. *Salix herbacea* is commonly found in snow beds and also occurs on wind-exposed mountain ridges and screes, where snow cover disappears early in the spring [6]. *Salix herbacea* has been found at a maximum age of 43 years using dendrochronology [35]. However, the highest age reported for *S. herbacea* was determined by using some different methods. In a study done by [36], the clone age of *S. herbacea* was estimated to be at least 450 years by using some calculation of clones, while most other individuals were less than 100 years old. However, being such an adaptive species in such diverse environments and climatic conditions, its climatic response has never been generated. The main objective of this study was therefore to examine the dendrochronological potential of *Salix herbacea* at two climatologically contrasting sites in Iceland. Furthermore, we wanted to identify the main environmental factors that are influencing its growth. The research questions we examined were: (a) Is it possible to construct *Salix herbacea* chronology? and, if so, (b) How does this species respond to the climatic parameters? We hypothesized that specimens from sites with varying amounts of rainfall will potentially differ in dendroclimatic sensitivity. We here assess the potential influence of varying site conditions on growth rings by analyzing climate signals and growth trends of dwarf willow collected in northernmost and southernmost located sites, which is important to further estimate the potential of this species for studies of past climatic conditions.

2. Materials and Methods

2.1. Study Area

Two sampling sites were chosen for detailed research that are different in terms of morphology and climatic conditions (Figure 1A). The Mýrdal site (Figure 1B) is located in the southern part of Iceland, south of the Mýrdalsjökull ice cup. The landscape is dominated by ridges and plateaus built of Upper Pleistocene (younger than 0.8 Ma) hyaloclastite, pillow lava, and associated sediments and belongs to the Móberg Formation [37]. These subglacially and intraglacially created landforms are currently being intensively eroded, especially in its eastern part at the Mýrdalssandur edge. This part of Iceland receives a large amount of precipitation (2363 mm/year) and is relatively warm (avg. 5.5 °C) (Figure 1B).

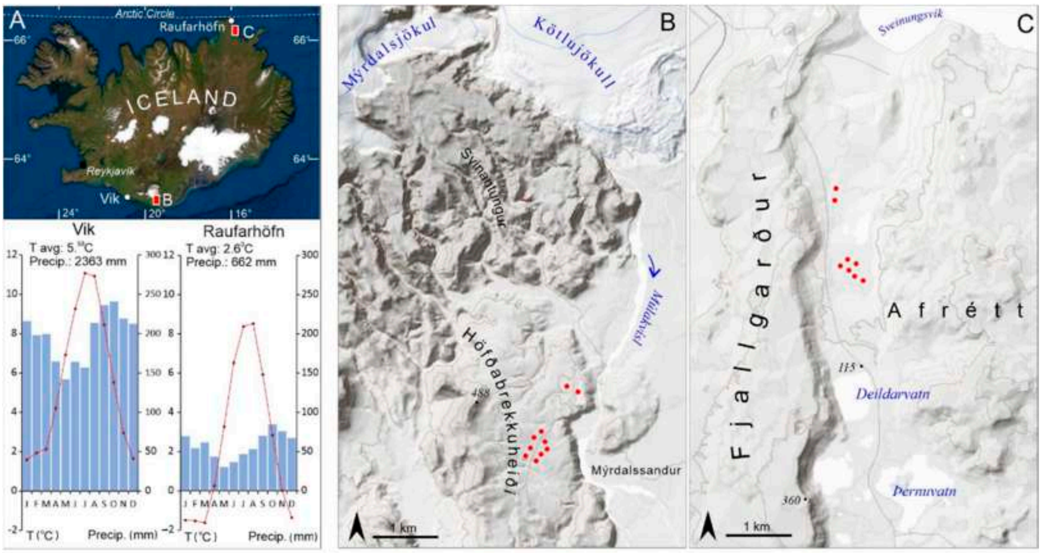

Figure 1. (**A**) Location of the study areas and meteorological stations with climatographs from Southern (Vik) and Northeastern (Raufarhöfn) Iceland; detailed locations (red points) of sampling sites at (**B**) the Mýrdal site and (**C**) the Afrétt site (source of background maps: National Land Survey of Iceland, https://www.lmi.is/, accessed on 15 November 2021).

The Afrétt site (Figure 1C) is located in the northeastern part of Iceland in a hilly volcanic upland, on the northeastern edge of the Þistilfjörður fjord. The landscape is dominated by dome-shaped eroded hills of a maximum height of 334 m a.s.l. (Selfjöll) cut by deep river valleys. The eastern and central part of the upland is built of Upper Pliocene and Lower Pleistocene (0.8–3.3 Ma) basaltic lavas [38]. The Afrétt Upland is widely varied—dry, hummocky terrain that is actively undergoing solifluction. Erosion forms associated with severe soil degradation are a typical feature of the landscape [39–41]. This area is one of the driest (658 mm/year) and coldest (avg. 2.6 °C) parts of the country (Figure 1C).

Based on the phytogeographical and ecological data, Iceland may be recognized as a region located in the Arctic and sub-Arctic zone [42–44]. Moreover, its climate is firmly controlled by different atmospheric circulation patterns and dynamics in oceanic current and sea ice extent [29,45,46]. Due to the influence of the warm North Atlantic Current, the climate in Iceland is not as cold as we would expect from the high latitude.

Vegetation cover in Iceland represents less than one fifth of its area; the rest of the country consists of barren mountains, deserts, and glaciers. Arctic–alpine tundra, dominated by dwarf shrubs, is the predominant vegetation in Iceland. Most of the land surface at the study sites is sparsely vegetated or un-vegetated. North Atlantic boreo-alpine heath and Icelandic lichen *Racomitrium* heath communities occur in lower-elevation areas, depressions, and valleys. Arctic dwarf shrubs, such as dwarf willow (*Salix herbacea* L.), mountain avens (*Dryas octopetala* L.), and crowberry (*Empetrum nigrum* L.), are common in these habitats.

All of these habitats are in various stages of degradation, from small openings to bare patches [47].

2.2. Field Sampling

Salix herbacea, commonly growing with other species such as *Salix arctica* (Afrétt site) and *Dryas octopetala* (Mýrdal site), were used in this study. Vegetation cover is not dense and ranges from 30 to 50%, and is characterized by patches of varying size, often forming isolated covers. The samples of *Salix herbacea* were collected from the elevation 90–105 m a.s.l. (Afrétt) (Figure 2A) and 250–270 m a.s.l. (Mýrdal). This plant is a deciduous, prostrate, creeping dwarf shrub, usually less than 15 cm tall. Branches of *S. herbacea* are dense, often forming mats or small pillows. Complete individuals of *S. herbacea*, including exposed roots, root collars, and branches (Figure 2B), were collected in 2017. Overall, 40 samples of dwarf willow were collected from the two research sites.

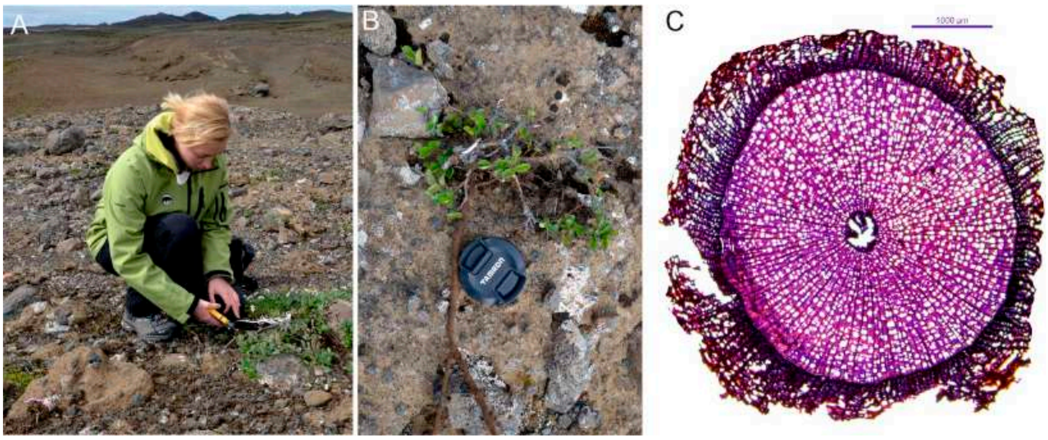

Figure 2. (**A**) Polar willow sampling in the Afrétt site, Northeastern Iceland; (**B**) dwarf willow specimen containing the root, root collar, and wooden branches collected for laboratory analysis; (**C**) example of a microscopic cross-section of dwarf willow.

2.3. Microscopic Preparation

We used microscopic techniques adapted to the specificity of dwarf shrubs [27,48–50]. In correspondence to the serial sectioning technique, sampling and measurement of cross-sections were performed at several locations below and above ground on the same individual, implementing the proper age determination and more accurate growth chronology construction [14,51]. This sectioning procedure consists of the extraction of 1-cm-long fragments from the main root and up to two main aboveground shoots at a mean distance of 2–3 cm from each other. In the field, the bent or injured shrub parts were not sectioned. In the further steps, microscopic slides were prepared by following the standard procedures used for dwarf shrub preparation [35,48].

Before cross-sectioning, the samples were soaked in water to rehydrate desiccated tissue. From each plant sample, a thin section of around 15–20 μm in thickness was cut with a sledge GSL1-microtome, and later on, it was stained by a mixture of Safranin and Astra Blue [52]. This was done to highlight lignified and un-lignified tissues, as well as to enable the identification of narrow and irregular ring boundaries. Hence, these staining solutions further enhance the contrast between cell walls and lumens. In total, 125 stained micro-slides were prepared from the samples of Iceland.

2.4. Growth Ring Measurements

For measuring the growth rings in the prepared micro cross-sections, digitalized photographs were taken (Figure 2C). The photographs of each sample were taken from each micro-slide under 10× magnification for regular cross-sections and under 20 × 20 magnification for irregular individuals. This enabled the detection and measurement of narrow growth rings either directly under a light microscope or from digital images taken from the sections. This all was performed using a Leica FLEXACAM C1 camera connected to a Leica DM1000LED microscope. Then, all the individual images for each micro-slide were stitched together in Adobe Photoshop (Adobe Systems Incorporated, San Jose, CA, USA) to form a single high-resolution image for the cross-section, required for accurate annual ring border recognition and ring width measurements.

Measurements were done along multiple radii extending from the center of the stem cross-section towards the cambium to account for growth irregularities. However, due to a large number of wedging and missing rings, at least two radii were measured for each micro-section under visual control, using the WinDENDRO tree-ring measuring system [53]. Therefore, in our analysis, based on the clear visibility of ring widths in the prepared micro-slides, we took a minimum of two and a maximum of 4 measurements from each slide. Then, all radii from one disc were cross-dated to assign the correct calendar year to each ring based on the matching patterns of ring development before being further analyzed [9,54].

2.5. Cross-Dating and Chronology Development

All the growth ring measurements were visually cross-dated and then they were tested statistically by using COFECHA software [55]. Moreover, all the poor-quality samples with a large number of missing rings, significant eccentricity, numerous wedging rings, scars, or visible reaction wood were excluded from further analyses. The cross-dating of the tree ring series was carried out in two parts: a visual comparison of the series in the form of line graphs in TSAPWin, and performing a statistical comparison in COFECHA to verify the accuracy of the visual cross-dating [56].

Cross-dating of raw ring width measurements of the *Salix herbacea* shrub species was performed. Firstly, the radial measurement series were cross-dated within cross-sections. This was augmented by a careful visual inspection of irregular and partially missing rings within a complete cross-section. Moreover, quality control was applied using the COFECHA program to check for measuring mistakes [57]. If necessary, some measurements were repeated and re-checked with COFECHA and removed from further processing if recognized as unusable.

2.6. Data Standardization

Raw growth ring width measurements after cross-dating were standardized to remove all noise from datasets, including the possible non-climatic age-related and/or biologically induced growth trends. To evaluate the climate–growth responses of shrubs completely, the chronology was standardized. As some samples did not present any apparent age-related growth trend, we, therefore, applied individual series standardization including linear regression and horizontal means, with the choice of function based on the best fit for each series, as an approach that is commonly used in dwarf shrub detrending [27,58]. Well correlated with each other ($r > 0.4$), individual radial growth curves were then transformed into the dimensionless ring width indices as ratios, averaged, and a pre-whitened overall site chronology was constructed for subsequent analyses.

2.7. Climate Data and Analysis of Climate–Growth Responses

Meteorological data from four stations with long-term monthly temperature and precipitation records were obtained from the Veðurstofa Íslands (Icelandic Meteorological Office) and Rif Field Station, Icelandic Arctic Cooperation Network (Table 1). The Kirkjubæjarklaustur and Vík í Mýrdal stations were located near the southern dendrochronological site, Mýrdal; stations Raufarhöfn and Akureyri were located near the Afrétt site in Northeastern Iceland (Figure 1A). For dendroclimatological analysis, the common period 1961–2013 was used. Pearson's correlation analyses were used to explore the climate–growth relationships. A 95% confidence level criterion was used to determine the statistical significance of the correlations. The ring width chronologies were compared with a 15-month window of climate data spanning the period from May of the previous year through July of the current growing season. Due to insignificant results, only the results for the current year are presented in the text.

Table 1. General information on selected long-term climatological data (mean monthly temperature and monthly precipitation totals) used in the studies.

No.	Station Name	Station Code	Location	Coordinates	Elevation	Distance to the Sampling Site	Timespan
1	Kirkjubæjarklaustur	722	S Iceland	63.79° N, 18.05° W	42 m a.s.l.	51.0 km	1930–2013
2	Vík í Mýrdal	798	S Iceland	63.42° N, 19.01° W	31 m a.s.l.	11.7 km	1961–2013
3	Raufarhöfn	505	NE Iceland	66.45° N, 15.95° W	4 m a.s.l.	12.5 km	1931–2021
4	Akureyri	422	NE Iceland	65.68° N, 18.09° W	23 m a.s.l.	122.5 km	1949–2021

3. Results

3.1. Chronology Development

Salix herbacea sampled in Iceland has well-defined and distinct visible growth rings whose average width ranges from 50 to 250 µm (Figure 3A). The borders between growth rings are highlighted by two to three rows of flattened cells and additionally by larger groups of vessels (Figure 3B). These anatomical features have allowed the construction of dendrochronological scales for this species.

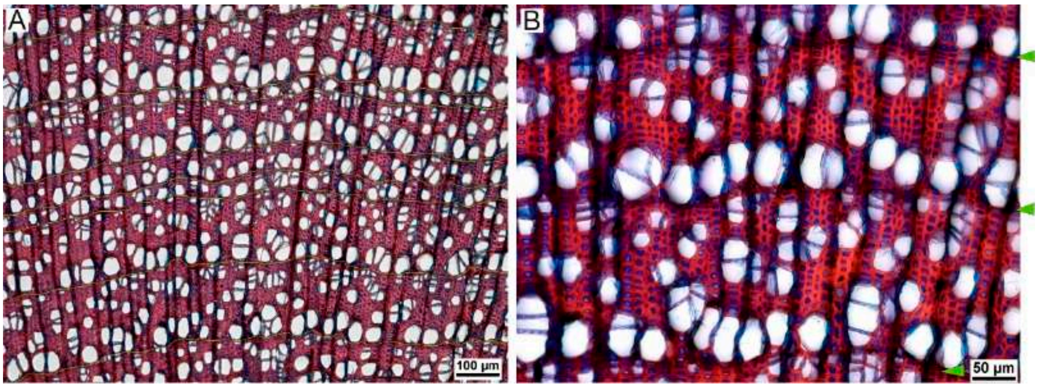

Figure 3. (**A**) Example of growth ring variations of *Salix herbacea* sampled; (**B**) detailed microscopic image showing distinct rings and semi-ring porous wood structure of *S. herbacea*.

From a total of 40 samples that were collected in July 2017 from the two sites with different climatic regimes in Iceland, 30 were included in the chronologies and used for further analysis (Table 2). The remaining sequences were removed due to a large number of missing rings and due to a very low correlation resulting from growth disturbances related to non-climatic factors, such as periglacial processes activity, erosion, and animal grazing. All the included cross-sections were subjected to a proper calendar dating of this woody material. This would not be possible without serial sectioning and cross-dating between the ring growth of different parts of the plant. Hence, this step validates the complete detection of growth rings and shrub dendrochronological dating.

Table 2. Dwarf willow sites sampled in Iceland and corresponding chronology information.

Parameter/Site	Mýrdal	Afrétt
Number of samples (sampled/cross-dated)	20/12	20/18
Correlation between samples	0.47	0.48
Mean measurement (mm)	32.59	32.72
Mean sensitivity	0.36	0.34
First year	1965	1953
Last year	2016	2016
Coefficient of variation: before/after 1990	26.77/13.90	24.02/19.36
Standard deviation: before/after 1990	0.26/0.13	0.27/0.17
Trend per decade: entire chronology/after 1990	−0.02/−0.02 *	−0.06/−0.18 **

* statistically insignificant, ** $p < 0.001$.

The oldest individuals of *S. herbacea* that were used in the chronology construction were 64 years old. The dwarf willow chronology from the Mýrdal research site spans 55 years, with the longest specimen having 61 years (Figure 4A). The ring width chronology of the dwarf willow from the Afrétt research site spans the period 1953–2017, i.e., 64 years (Figure 4B). A noticeable growth ring fluctuation is observed in the 1960s and 1970s. It is also confirmed by the calculated measures of dispersion. Standard deviation and coefficient of variation are significantly higher in the early part of the chronology (Table 2). After this period, systematically decreasing growth ring widths are visible, especially distinct after 2002 in the Afrétt chronology. At this site, a significant negative trend is observed in the dendrochronological data (Table 2). The high fluctuations in the very beginning are the reason for the smaller sample size, but the declining trend in the previous decade may be the imprint of recent environmental changes.

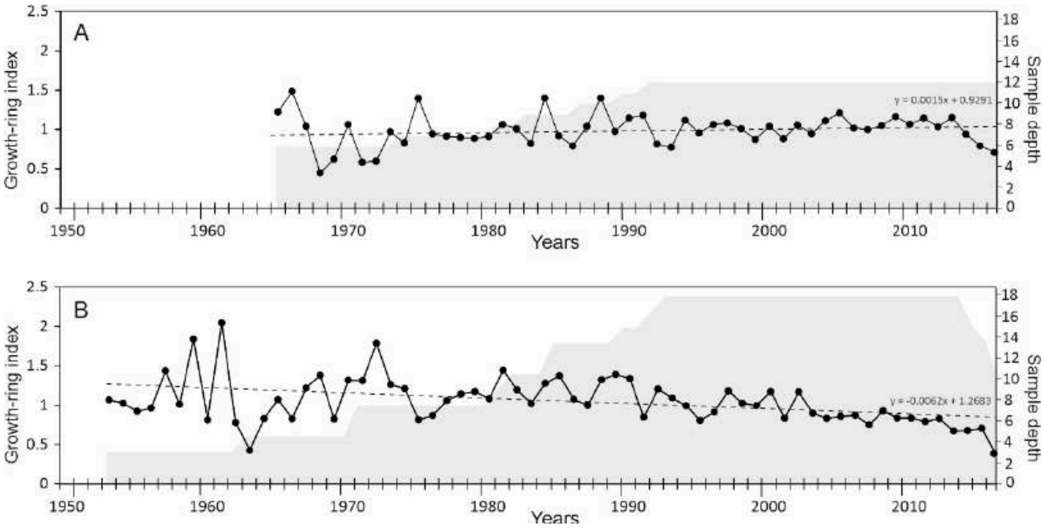

Figure 4. Indexed growth ring chronologies of dwarf willow from (**A**) the Mýrdal site and (**B**) the Afrétt site.

3.2. Correlation Analysis

The dendroclimatic correlations between air temperature and the ring width of dwarf willow indicate that this species positively responds to spring and summer temperatures (Figure 5A) for the Myrdal site. The radial growth of the dwarf willow from the investigated site of Myrdal responds strongly to March temperatures (r = 0.52 for Vík í Mýrdal station, r = 0.49 for the Kirkjubæjarklaustur station) and also shows a statistically significantly positive correlation with the mean temperatures of May (r = 0.37 and r = 0.30, respectively, $p < 0.05$) and July (r = 0.40 and r = 0.39, respectively, $p < 0.05$). Hence, there is a strong influence of spring–summer temperature on the variability of growth of this species

(r_{MAMJJ} = 0.49 for both meteorological stations). In general, no positive correlations with precipitation were found for the Myrdal site (Figure 5B). In fact, for June, even a negative correlation is noticeable (r = −0.33, $p < 0.05$ for Vík í Mýrdal station). The other months are not significant but, following the response function of June, August, and September, are also showing negative responses with precipitation. Hence, as this site is highly precipitated, thus, with an increase in precipitation, the growth does not respond well or it declines. No significant relationships with the climatic conditions of the previous year were found (Figure 5A,B).

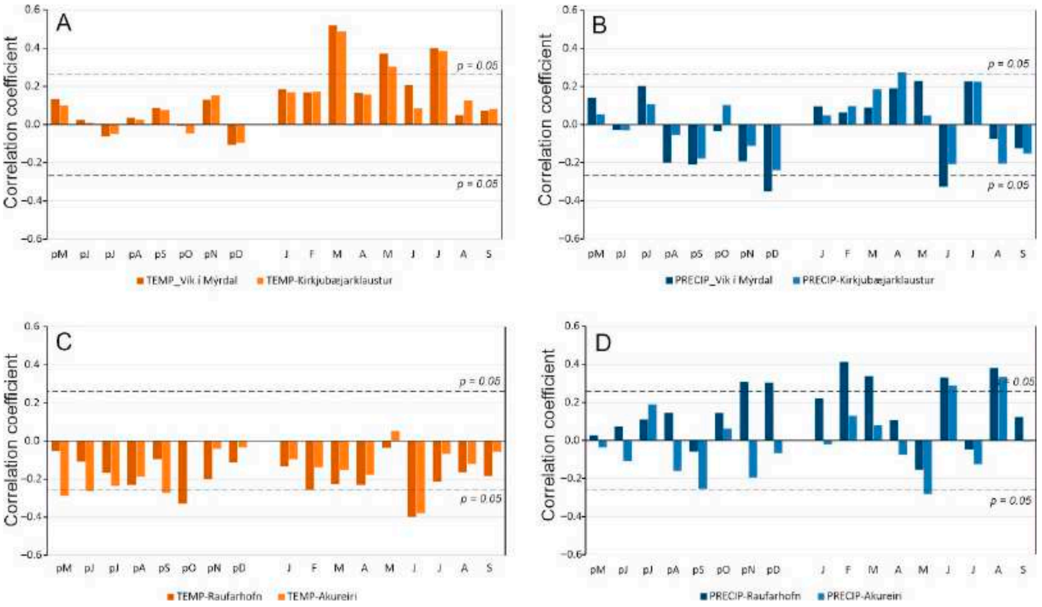

Figure 5. Correlation coefficients of growth ring data at two contrasting sites, Mýrdal (**A**,**B**) and Afrétt (**C**,**D**), to mean temperature and monthly precipitation totals from different meteorological stations.

For the Afrétt site, the climate–growth correlations between climate indices and ring width indicate that this species positively responds to winter (r_{JFM} = 0.46) and summer (r_{JJA} = 0.41) precipitation. High correlations were also calculated for seasonal sums of precipitation noted at the Raufarhöfn station from October of the previous year to March of the current year (r = 0.50). The highest positive correlation with a single month was obtained with February (r = 0.41 for the Raufarhöfn station), followed by March, June, and August precipitation (Figure 5D). Hence, the area is so dry annually that an increase in precipitation favors the growth of this species. Higher correlation values for the Raufarhöfn station result from its closer location to the Afrétt site (Table 1). The measurements from the Raufarhöfn station better reflect the local differentiation of rainfall conditions than Akureiri, which is located at a distance above 100 km. Meanwhile, no highly significant relation is found with the mean temperature apart from the negative correlation with the June temperature (r = −0.40 for Raufarhöfn station and r = −0.39 for Akureyri station), an indication of drought stress at this site (Figure 5C). A negative correlation was also shown for the period from August of the previous year to July of the current year (r = 0.36 for Raufarhöfn station). As this area is the driest, with an increase in warm conditions, the growth is affected inversely.

4. Discussion

The paper outlines the applicability of a new species in dendrochronology and its potential in the analysis of the Arctic environmental change. *Salix herbacea* has not yet been analyzed to date for its climatic response, while the shrubs of the Willow genus, such as *Salix arctica* [59–61], *Salix alaxensis* [62], *Salix polaris* [16,17,20,22,30], and *Salix uva-ursi* [15], have been widely used as a source of reliable climatic and environmental information for several years. *Salix herbacea* has visible growth ring boundaries that are measurable and correlated to a relatively high degree with climatic variables, allowing this species to be treated as a reliable source of environmental data. Even while growing in extreme site conditions, this studied species has centric and slight eccentric pith positions [63]. Hence, being the smallest woody plant, it attracts attention for several reasons.

Thus far, dendrochronological studies in Iceland have not been numerous, which is related to the extent of the forest cover [64]. Existing dendroclimatological results are limited to the native Iceland tree species, *Betula pubescens* and *Sorbus aucuparia*, from relatively isolated areas. Constructed tree ring chronologies show spring and summer temperature signals, with the maximum length of the records being approximately 130 years [28,29,65–67]. Other studies used dendrochronology for dating geomorphological processes [68], driftwood [69], and volcano eruption [70].

No studies, however, have targeted dwarf shrubs from Iceland as a paleoenvironmental archive. The results of our investigation fill this research gap. Our work is the first attempt to create a growth ring chronology of *Salix herbacea* and to investigate its climate sensitivity. Unlike the results of dendrochronological analyses of tree species from Iceland, *S. herbacea* reflects not only regional temperature signals, but also site-specific microclimatic conditions. This is particularly evident in the dry site in the northeastern part of Iceland. Similar observations, indicating the influence of microsite conditions on differences in the climate–growth response, were made for *Empetrum hermaphroditum*, *Salix glauca*, *Betula nana*, and *Betula pubescens* from the Low Arctic; however, the common growth pattern was reflected at all analyzed microsites [58,71,72]. The analysis of the isotopic composition and tree ring width data of pine from moist and dry microsites in Scandinavia revealed differences in climatic signal strength [73,74].

In the present study, we determined a positive correlation with precipitation during the growing season, which may indicate drought and water deficiency in the soil. This effect may be related to tundra browning, the process that appeared at the beginning of the 21st century, when narrow growth rings became dominant. Such a phenomenon was observed in the Afrétt chronology from 2004. A similar hypothesis was developed and confirmed in multidisciplinary work conducted in the area of Hornsund, SW Spitsbergen [22], and Bear Island [17]. The recent increased interest in Arctic dendrochronology is connected not only with a simple indication that shrub records can track recent temperature warming [20,26,75], but studies on the complex response of tundra plants to changing environmental conditions [14,16,22,25,49]. Direct dendrochronological research from sites with different microclimatic conditions is still needed, as for the correct assessment of climate change-induced shifts in hydrothermal conditions resulting in the transition from tundra greening to browning. Attention should also be paid to processes that can significantly disturb the climate signal recorded in annual rings of Icelandic dwarf shrubs. Volcanic soils and vegetation cover in Iceland are very sensitive to disturbance. Soil erosion and the destruction of vegetation and the root systems of dwarf shrubs are common in Iceland [39,40] and may affect the non-climatic variability of annual growth. Additionally, desertification of large parts of the island has contributed to increased dust storm activity [76,77], which may result in a reduction in annual growth due to dust-covered leaf blades.

5. Conclusions

This study presents the first comparison of the radial growth chronologies of dwarf willow shrubs from two different climate regime sites of the sub-Arctic region. Despite the differences in local climates in both studied sites, this species shows its potential with the recent environmental changes. The studied dwarf shrub *Salix herbacea* is a particularly valuable indicator of drought, which is the case for the dry site in Northeastern Iceland.

Through the application of shrub sampling across a relatively large area, supplemented by serial sectioning and careful detection of locally and completely missing rings, we were able to successfully cross-date species of Arctic shrubs with high environmental potential from two different and contrasting sites in the High Arctic. We suggest that the extension of the chronology lengths and the associated climatic signals is possible through more extensive fieldwork and by increasing the sample size of the species *Salix herbacea*, also from the northernmost polar areas. Moreover, this species shows a direct imprint of recent environmental changes in its ring width growth pattern. Thus, it will be a major tool to understand the recent changes in the environment and will also fill the gap in high-resolution in situ climate data. Thus far, the future research possibilities have increased in various aspects. As this study focused on the response to temperature and precipitation, it also indicates the potential to explore responses with other available environmental datasets. It also shows a need to highlight the main anatomical features that are observed, as these features will be a major representative of other species that are growing in such harsh environments.

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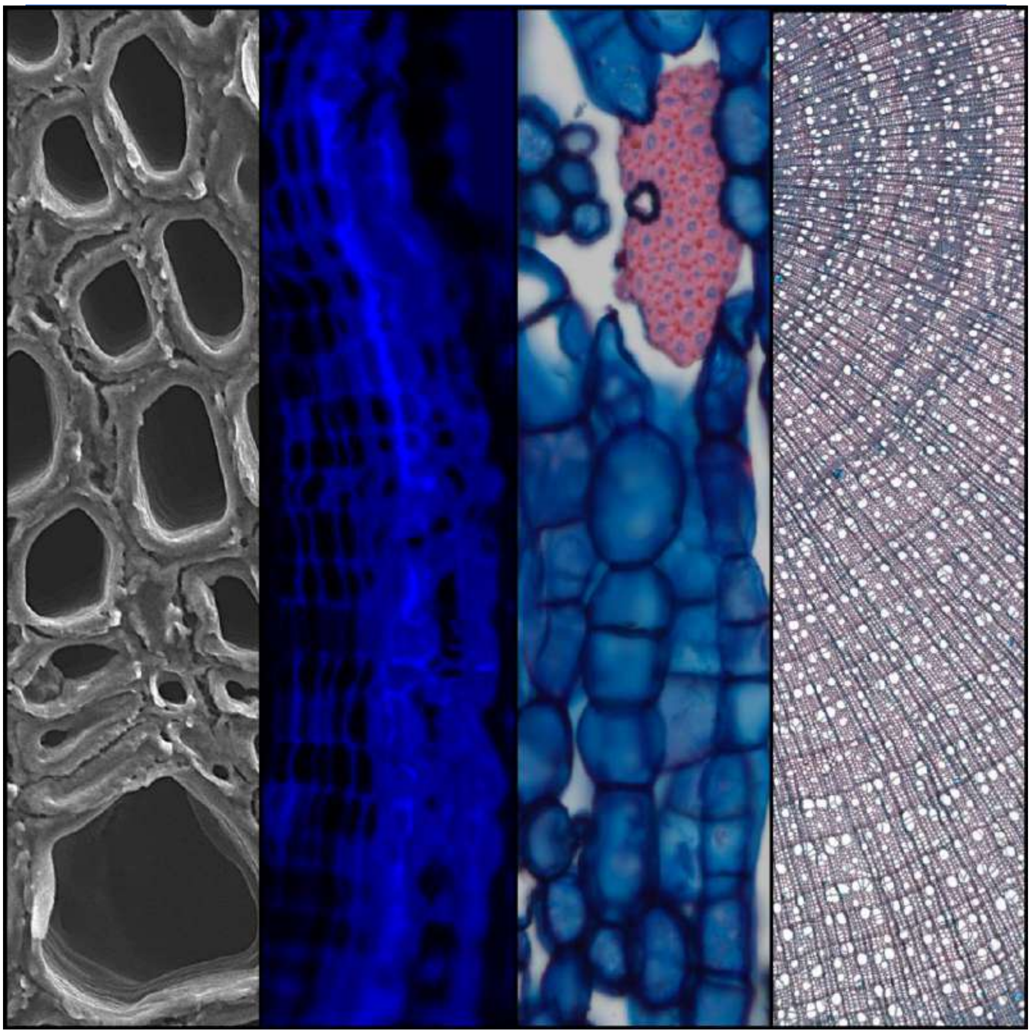
Article II

Insights from Roots to Stems: Comparative Wood Anatomy and Dendroclimatic Investigation of Two Salix Species in Iceland



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Article

Insights from Roots to Stems: Comparative Wood Anatomy and Dendroclimatic Investigation of Two *Salix* Species in Iceland

Mohit Phulara [1], Angela Balzano [2,*], Magdalena Opała-Owczarek [1], Piotr Owczarek [3] and Maks Merela [2]

[1] Institute of Earth Sciences, University of Silesia in Katowice, 40-007 Katowice, Poland; mohit.phulara@us.edu.pl (M.P.); magdalena.opala@us.edu.pl (M.O.-O.)
[2] Department of Wood Science and Technology, Biotechnical Faculty, University of Ljubljana, 1000 Ljubljana, Slovenia; maks.merela@bf.uni-lj.si
[3] Institute of Geography and Regional Development, University of Wroclaw, 50-137 Wrocław, Poland; piotr.owczarek@uwr.edu.pl
* Correspondence: angela.balzano@bf.uni-lj.si

Abstract: This study investigates the anatomical characteristics and growth patterns of *Salix arctica* and *Salix herbacea*, two prevalent dwarf shrub species in Iceland, to understand their responses to environmental changes. We employed optical and scanning electron microscopy methods and quantitative wood anatomy to analyze the stem and root structures of studied species. Additionally, we developed chronologies and assessed the climatic response of both the stem and root parts for both species. Our results reveal significant differences between the two species, with *S. arctica* exhibiting larger vessels and fibers compared to *S. herbacea*, both in stem and root. The growth trends differ between the species: *S. arctica* shows an overall increase, while *S. herbacea* exhibits a consistent decline. Both species' individual parts generally follow these trends, though a recent decline has been observed in the last few years. Climatic responses also differ, highlighting specific climatic parameters influencing each species. *S. arctica* responds positively to warmer temperatures, while *S. herbacea* reacts positively to increased precipitation but struggles with rising temperatures, highlighting its role as a drought indicator species. Soil erosion driven by volcanic materials and extreme climates significantly impacts shrub growth, causing rapid changes in growth ring widths and vessel sizes. Understanding these impacts is vital for improving sampling methods in polar environments. This study highlights the importance of integrated wood anatomical studies in comprehending the ecological consequences of climate change on Arctic shrubs, providing new insights into the complexity of shrub expansion both below and above ground.

Keywords: arctic shrubs; soil erosion; *Salix herbacea*; *Salix arctica*; wood anatomy; microscopy

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1. Introduction

The Arctic region is experiencing significant changes in vegetation patterns due to the impact of climate change. These changes involve variations in the abundance and distribution of arctic shrubs [1,2]. Consequently, polar regions' prevalent dwarf shrubs emerge as highly responsive to shifts in the natural surroundings, positioning them as crucial ecological indicators for climate conditions, geomorphic processes, and alterations in the active layer thickness or sea ice extent [3–6]. Thus, comprehending the individual growth patterns of dwarf shrubs and their varying responses to environmental factors emerges as a crucial component in comprehending the expansion patterns of these shrubs across the Arctic region [7–11] and for making accurate predictions about the future composition and functioning of northern ecosystems [12].

While significant research has been conducted on the aboveground components of plants in the context of climate change, less attention has been given to belowground traits, especially in the Arctic tundra [13]. However, in the context of plant survival and adaptation, roots play a crucial function by enabling water movement through the xylem and regulating essential physiological mechanisms [14,15]. Recent research on *Betula glandulosa* Michx., a frequently observed shrub species in the tundra ecosystem, has revealed that the root collars of those plants exhibit higher sensitivity to climate variations compared to their stems [16]. Limited research on belowground traits in tundra ecosystems [17,18], mostly due to the challenges posed by the complex sampling protocols, highlights the need for a comprehensive understanding of the wood anatomy of both roots and stems [15,19].

Dwarf shrubs growing in the harsh conditions of Iceland are susceptible to extreme climatic conditions and react quickly to changing environmental conditions [20–22]. As a result of extreme climatic and geomorphologic events, such as intensive erosion of volcanic soils, not only variations in the width of annual increment, but also huge changes in cell size, with maximum changes in individual plants exceeding 150–200%, have been observed in the wood anatomy of *Salix herbacea* [21]. Soil erosion and aeolian processes are the main factors influencing the degradation of the vegetation cover, which leads to the exposure of shrub roots and their periodic burial [21,23].

To address the variability in growth responses of tundra shrubs in the Arctic, it is essential to delve into site- and species-specific studies, as highlighted by recent research [24]. A recent study in Iceland from our research site [22] provided the first comparison of radial growth chronologies of *Salix herbacea* from two sites with different climatic regimes. Despite the contrasting local climates, *S. herbacea* exhibited climatic potential in terms of its growth chronology and response function. Building upon these findings, our study focuses on two different *Salix* species (family Salicaceae): *Salix herbacea* L. (dwarf willow) and *Salix arctica* Pall. (Arctic willow).

Despite the long-standing recognition of arctic willow as a potential source for dendroclimatological reconstruction [25–27], research on its anatomical aspects has remained limited, presenting a gap in our understanding. Recent advancements have shed light on its dendrochronological potential, despite challenges like cross-dating difficulties due to missing or incomplete growth rings [28,29]. However, utilizing *S. arctica* radial growth for proxy climate data generation is feasible, allowing for the reconstruction of past snow regimes in regions like the Zackenberg Valley for approximately a century [28]. Additionally, the population dynamics of *S. herbacea*, a prevalent species in the Arctic, remain relatively unknown, despite its ubiquity in regions characterized by solifluction or scree formation [26,30]. To date, there has been a lack of detailed wood anatomical studies focusing on Arctic shrub species, specifically comparing the anatomical characteristics of their stem and root parts. By collecting comprehensive data on whole shrubs, this study will facilitate further research on belowground traits, which play a crucial role in tundra ecosystems but have been relatively understudied [10,17,31].

Hence, we are going to investigate (a) the detailed wood anatomy of the stems and root parts for *S. herbacea* and *S. arctica* using different microscopic methods, including scanning electron microscopy (SEM), and (b) chronology development for the stem and root part of both species and to analyze their individual climatic responses. Thus, this research endeavors to fill existing gaps in our understanding regarding the anatomical features and climatic responses of two prevalent *Salix* species from the homogenous landform of Iceland and aims to improve the future sample collections for better investigations of studying Arctic shrub dynamics.

2. Materials and Methods

2.1. Study Area

The research site is located in the northeastern region of Iceland (Figure 1A), specifically within a volcanic upland known as Afrétt, which is bordered to the northeast by the Þistilfjörður fjord and to the west by a vast and marshy Melrakkaslétta plain (Figure 1B). The soil in this study area is relatively thin, measuring less than 1 m in depth. Developed on erodible volcanic ash, these soils are highly susceptible to erosion, predominantly due to modern aeolian processes [23,32,33]. The Afrétt uplands are particularly notable for their severe erosion [21].

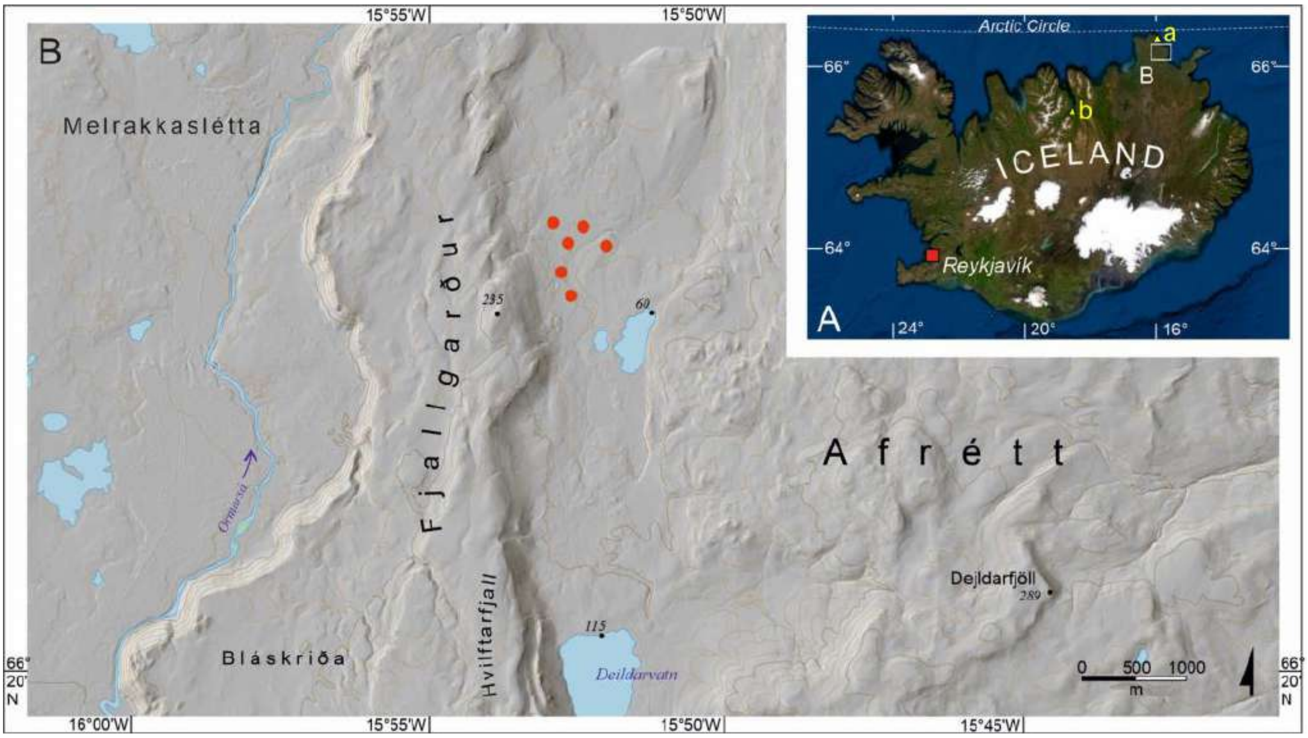

Figure 1. (**A**) Location of the study area (**B**) in Northeastern Iceland with an indication of meteorological stations (a) Raufarhöfn and (b) Akureyri, and (**B**) detailed study area map with locations of the sampling points marked with red color dots (background maps from the National Land Survey of Iceland. www.lmi.is, accessed on 5 August 2024).

Soil erosion in Iceland is influenced by various factors, making it hard to pinpoint individual causes [34]. Studies in Northeastern Iceland show erosion rates up to 8.6 cm per year, with dust storms moving up to one million tons of dust [35,36]. Recent research by [21] indicated that erosion rates, stable at 1.0 to 2.5 cm/year since the 1970s, increased to 4.4–5.4 cm/year in the 1990s, likely due to climate change and warmer summers. Erosion and dust storms cause rapid changes in the growth rings and cell sizes of shrub roots, indicating periods of erosion [21]. In Iceland, aeolian disturbances to the soil cover and geomorphic degradation are driven not only by abrasion and deflation but also by deposition, all of which are associated with dust storms [37–41]. Thus, here, shrubs are heavily affected by soil erosion.

To accurately determine growth patterns and identify the similarities variations in the individual parts of selected shrubs, samples of two *Salix* species were collected from a climatically homogeneous area in Northeastern Iceland, comprising lowlands and low plateaus composed of the same rock types. As elaborated in a recent publication by Opała-Owczarek et al. (2024), additional details can be found in it [20].

2.2. Study Species

The studied dwarf shrubs of *Salix*, specifically *Salix herbacea* and *Salix arctica*, are low-growing woody plants commonly found in Iceland. These species are challenging to distinguish in the field, but excavations have revealed that most rhizomes can be traced back to a thick taproot. Further details about this section are available in our recently published article [20].

2.3. Sampling Method

Samples of *S. herbacea* and *S. arctica* were collected from an elevation 70–80 m a.s.l. (Figure 2A,B). *S. arctica* stands out from other willow shrubs due to its hairy underside of leaves and leaf margins. Unlike *S. herbacea*, the growth habit of *S. arctica* on the ground appears to be more complex (Figure 2B). During field sampling, apart from collecting the possible availability of samples from the ground, an effort was made to extract a few complete plants of *S. herbacea* and *S. arctica*, taking long fragments from the roots and up to the main aboveground shoots. In this way, we collected only three individuals of each *S. herbacea* and *S. arctica*, including their roots and stems with prostrate branches (Figure 2A,B). Later, for transporting to the lab, they were sealed in plastic bags containing a mixture of 50% ethanol and 50% glycol (*v*/*v*) for preservation. Additionally, to build the growth ring chronologies, a minimum number of shrub samples were collected, i.e., about 10 per species. In order to not commit ecocide in such sensitive areas, only the corner edge of a large patch was targeted.

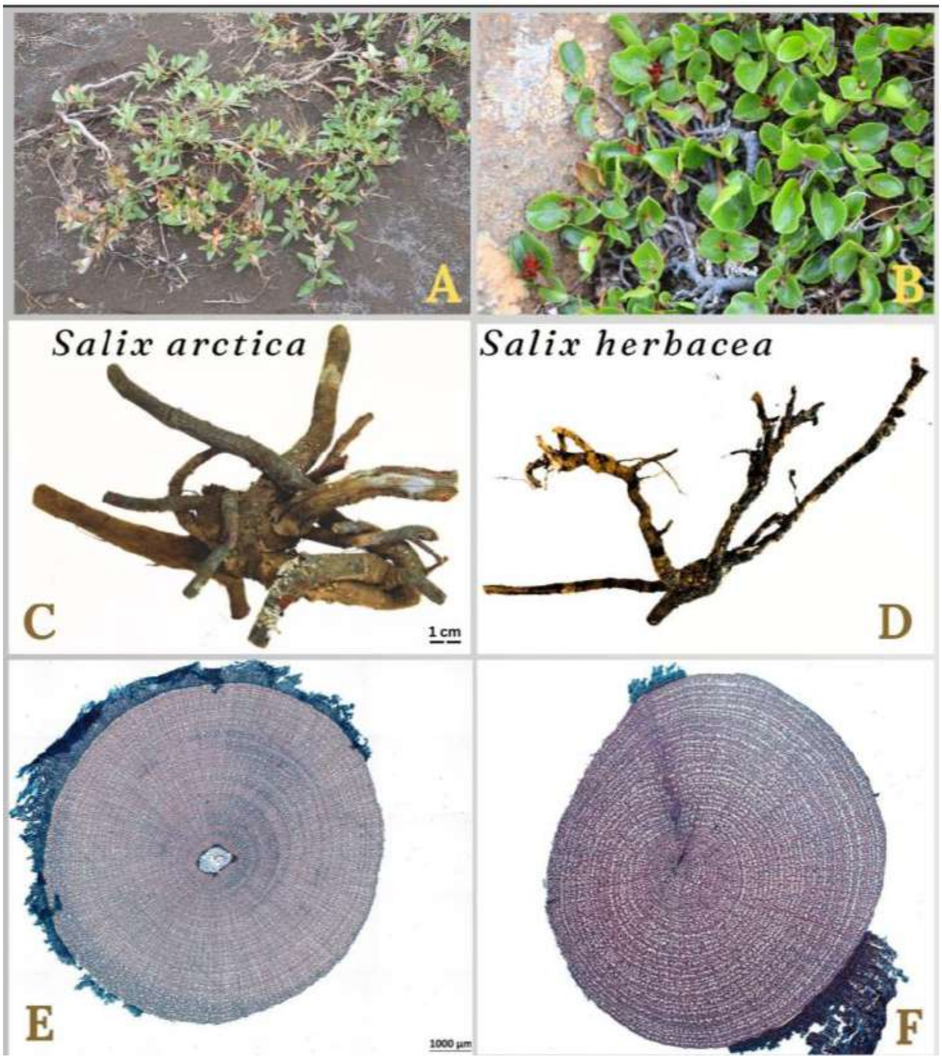

Figure 2. From the field collection to lab examination of the species, highlighting the prepared cross-sections. (**A**,**B**) *S. arctica* (SAAR) and *S. herbacea* (SAHE) at the field site, (**C**,**D**) collected specimens (whole individuals) for SAAR and SAHE, and (**E**,**F**) their prepared micro-sections (**E**) stem section of SAAR and (**F**) root section of SAHE.

2.4. Laboratory Method/Sample Preparation

Prior to the cross-sectioning process, the samples underwent a rehydration step by soaking them in water to restore moisture. Later, all samples were sectioned with a sliding microtome Leica SM2010R (Leica Biosystems Nussloch GmbH, Nußloch, Germany) into 15–20 µm cross-sections at 5–10 different points, depending on the length of individual samples and their multiple branches (Figure 2C,D).

To enhance the visibility and differentiation of lignified and un-lignified tissues, all prepared tissue sections were stained using a water solution of safranin (colors lignin red) and astra blue (colors cellulose blue). This staining technique not only emphasized the narrow and irregular ring boundaries but also improved the contrast between cell walls and lumens. Standard procedures for dwarf shrub preparation [42,43] were followed to prepare the stained microslides, including cross, radial, and tangential sections from both *Salix* species samples collected in Iceland. These stained sections were then permanently mounted on glass slides using Euparal mounting medium (Chroma 3C-239 Waldeck, Münster, Germany). In total, we prepared 15 slides for *S. herbacea* and 25 slides for *S. arctica*, covering both stem and root parts for performing the detailed anatomical analysis (Table 1).

Table 1. The number of plants and sections used for studying the wood anatomy.

Pant Species	No. of Plants	Stem	Root	Slides/Sections
S. herbacea	3	05	10	15
S. arctica	3	19	06	25

2.5. Microscopic Analysis

To address the unique characteristics of dwarf shrubs, we employed specific microscopic techniques adapted [6,42,44,45] for all prepared oriented anatomical planes (cross, radial, and tangential) from the roots and stems parts of both *Salix* species. The prepared microslides were examined using a Zeiss Axio Imager A.2 light microscope (Carl Zeiss Microscopy, White Plains, NY, USA), and the images were captured using a Zeiss Axiocam 712 color camera (Carl Zeiss Microscopy GmbH, Jena, Germany). Then, these digitalized photographs were taken in consideration for studying the wood anatomical features and to perform qualitative and quantitative wood anatomy with ImageJ 1.53k software.

In addition, to ensure accurate visualization and differentiating lignin, suberin, and non-structural phenolics, the fluorescence microscopy feature of our optical microscope was employed utilizing ultraviolet (UV) excitation and long-pass (LP) 420 emission, coupled with standard band-pass (BP) filter sets for DAPI, FITC, and Texas Red.

Additionally, some of the replicates of a few thin sections were used in a scanning electron microscope FEI Quanta 250 SEM (Hillsboro, OR, USA) to reveal the intricate 3D structure and fine details of cell walls and tiny structures. Prior to observation, the wood sections (15–20 µm) were cut with a sliding microtome, flattened on specimen mounts pretreated with glycerin albumen (Agar Scientific Ltd., Essex, UK), and oven-dried at 70 °C for 15 min to activate the adhesive properties of albumin [46]. The sections were subsequently coated with gold (Q150R ES Coating System Quorum Technologies, Laughton, UK) and, finally, observed.

2.6. Quantitative Wood Anatomy

To conduct a wood anatomical analysis (QWA), we utilized ImageJ (version: 1.53k) software, enabling us to evaluate the parameters under investigation [47]. On cross-sections of root and stem sections for both species (Figure 2E,F), we performed QWA analysis to measure the two most important parameters to understand their xylem cell arrangement and to differentiate them in order of, i.e., vessel frequency and tangential diameter of the vessel lumina. For the tangential diameter of the lumina, we measured the tangential length of vessels within the last five tree rings, randomly selecting up to 50 vessels, considering both earlywood and latewood.

This process was repeated at least three times for each part of the species, i.e., stem and root, respectively. For vessel frequency, we counted the number of vessels solitary and in groups as an individual within an area of one square millimeters [48]. While conducting automated measurements of the vessel lumen area (VLA), a filter was employed to disregard cells with an area smaller than the smallest vessel observed in the image. These smaller cells were identified as fiber cells, belonging to the ground tissue of the rings. Hence, while measuring it, we changed this filtering value depending on the section and species.

Then, to check our measured values in terms of statistical significance, we applied the *t*-test. The two-sampled *t*-test (Welch's *t*-test) was performed to verify the significant variations in our calculated values of the tangential diameter and vessel frequency for both species.

2.7. Dendrochronological and Dendroclimatological Analyses

We developed the mean growth ring chronologies based on the ring width series, combining individual measurements from the stems and roots of each Salix species separately. Three to eight cross-sections per individual shrub were cut, and the so-called serial sectioning approach was applied. This approach applied to shrub dendrochronology [49], consisting of multiple ring width measurements and cross-dating at the intra-plant level. For both species, dwarf shrub ring widths were measured using the Windendro program (Regent Instruments 2014). After visually comparing the different radii measured within each individual, the mean growth curves of all shrubs were then compared and statistically tested using COFECHA software (Version 6.02) [50]. From approximately 10–12 plants collected per species, 7–9 best correlated samples were chosen for development of the mean ring width chronology. Measurements influenced by non-climatic factors, often geomorphological, were excluded. These rejected samples exhibited significant eccentricity and disrupted growth patterns. Hence, only those samples were taken that were best fit for the development of their individual parts chronologies. Several descriptive statistics—commonly used in dendrochronology (e.g., standard deviation (SD), which estimates the variability of measurements for the whole series, and mean sensitivity (MS), which is an indicator of the mean relative change between consecutive ring widths)—were calculated for all chronologies. The ring width data from both species were standardized using the 1st horizontal line through the mean, as no age trend was observed in the raw data. Dimensionless indices were obtained by dividing the observed ring width value by the predicted value, and the growth indices were averaged by year using a bi-weight robust mean, which reduces the influence of outliers [51]. This process allowed the development of mean standardized chronologies for each species that represented the common high-frequency variation of the individual series, which were used for dendroclimatological analyses.

The exploration of climate–growth relationships between climatic variables and *S. arctica* and *S. herbacea* chronologies was conducted using the correlation function. In the text, we analyzed the results significant at the 0.05 level. We considered a 16-month time window, from June of the previous growth year (2015) to September of the following growth year (2016) over the common period 1975–2016. For the climatic response analysis, we used meteorological measurements (mean monthly temperature and monthly precipitation totals) from the Raufarhöfn (station code 04502; 66°27.360′, 15°57.162′; 4 m a.s.l.; located a distance of 15 km from the sampling site), as it was closer to the study site. In comparison, the correlations with data from the Akureyri (station code 04422; 65°41.767′, 18°06.679′; 31 m a.s.l.; 125 km from the sampling site) were not as significant.

3. Results

After thoroughly examining entire specimens, we successfully distinguished between these complex plants by analyzing their stems and roots. Given their subterranean growth habit, identifying these species in Arctic environments is particularly challenging. Notably, the structures classified as roots lack a central pith, distinguishing them in our analysis (Figure 2). In *S. herbacea*, the growth pattern is much more eccentric as compared to other species of *Salix*., e.g., *S. arctica* (Figure 2). However, its ring boundaries are less distinct as compared to *S. arctica*. In *S. herbacea*, the root sections do not show a much bigger difference as compared to the stem sections in terms of vessel sizes. Most sections of *S. herbacea* show the presence of gums and tyloses in terms of phenolic compounds in a considerable part of the xylem of stems and roots (Figure 3C,D). The performed analysis for the sections of *S. arctica* shows that its growth pattern is less eccentric than *S. herbacea*. In *S. arctica*, the root sections show a bigger vessel size than the vessels of the stem sections.

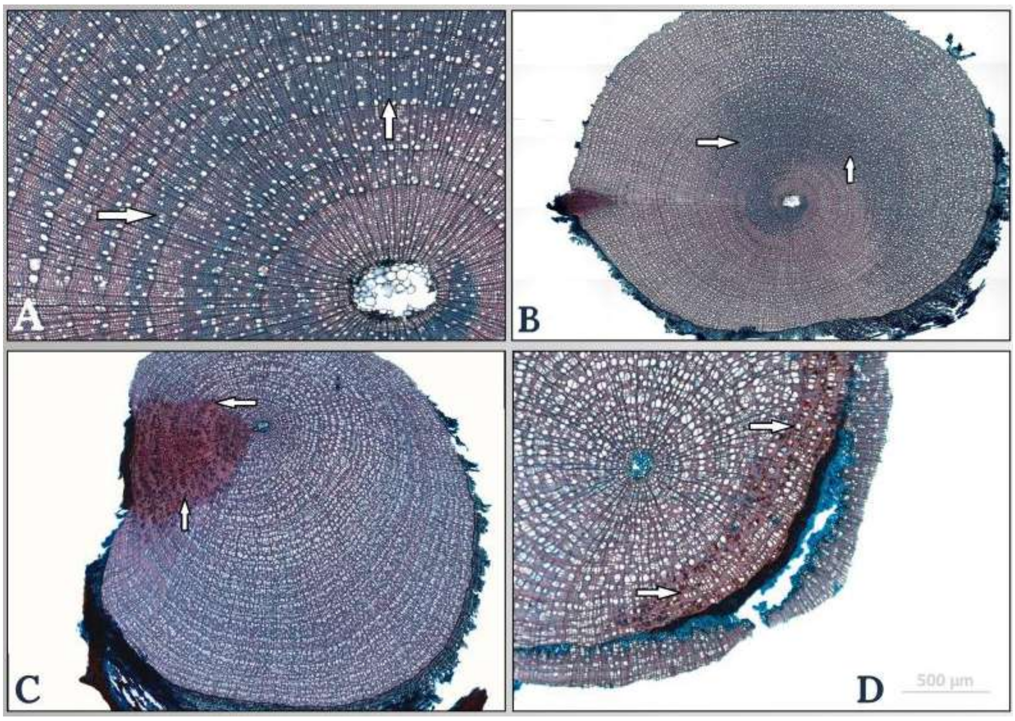

Figure 3. Cross-sections of the stem part of (**A**,**B**) *S. arctica* more often show tension wood, (**C**,**D**) *S. herbacea* more often shows the presence of gums and phenolic compounds (white arrows) in the reaction zone after an injury (scale—500 µm).

The occurrence of tension wood, a common phenomenon in dwarf shrubs, is evident in Figure 3A,B. Tension wood fibers can be observed to possess irregularly shaped secondary cell walls, referred to as gelatinous fibers [52], which are stained blue due to the lesser content of lignin than in normal wood (stained in red). In *S. herbacea*, wound wood with the formation of gums and tyloses was frequently found (Figure 3C,D).

Additionally, as revealed by SEM micrographs (Figure 4), wood fibers, both in the stem and root, are significantly larger in *S. arctica* than those in *S. herbacea*, which, instead, have thicker cell walls and narrower lumens (Figure 4A,B). Conversely, in *S. arctica* (Figure 4C,D), the fibers feature thinner cell walls and wider lumens, underscoring the distinct anatomical cells size variance between the two species.

3.1. Anatomical Characteristics in the Stem and Root of *Salix herbacea*

The anatomical study of the wood in the stem and root of *S. herbacea* from the Arctic region has not yet been sufficiently investigated, mainly due to the demanding sampling preparation. Furthermore, the differentiation between root and stem sections under field conditions, especially without foliage, is associated with considerable difficulties, as shown in Figure 2. Despite these difficulties, it is assumed that the wood anatomy of *S. herbacea* is comparable to that of other species of the genus *Salix*. A comprehensive description of the anatomical features, based on the IAWA list of microscopic features for the identification of hardwoods (IAWA Committee, 1989), is given in Table 2.

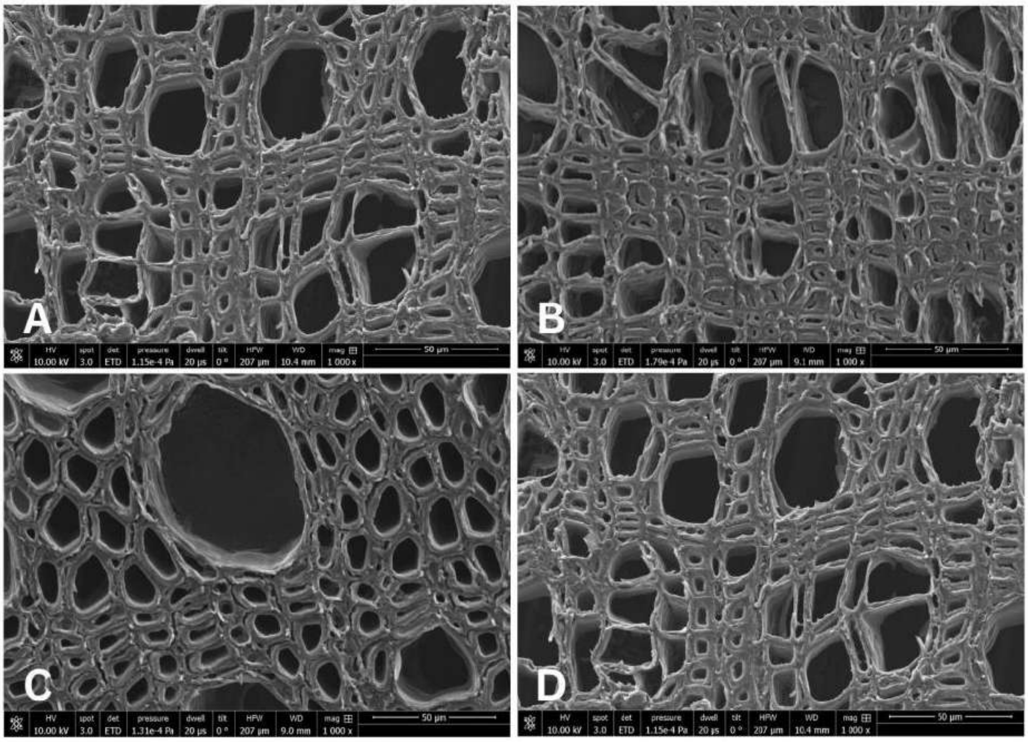

Figure 4. SEM photographs showing cross-sections of the root (**A**–**C**) and stem (**B**–**D**) of *S. herbacea* (**A**,**B**) and *S. arctica* (**C**,**D**), respectively. In the photographs, the conductive elements in normal wood are shown.

The growth patterns of Arctic shrubs, including *S. herbacea*, contribute to a distinct anatomical differentiation between stem and root. In *S. herbacea*, our detailed analysis shows that stems examined in cross, radial, and tangential sections (Figure 5A–C) have less distinct growth ring boundaries and a semi-ring porous structure (Figure 5A). The arrangement of vessels is mainly in tangential bands, with radial groupings of two to four and a fluctuating occurrence of single vessels with an angular outline (IAWA features 9 to 11 are absent). Here, we found the presence of apotracheal axial parenchyma, which is diffuse, and a little presence of banded parenchyma can also be seen in the form of axial parenchyma in marginal or in seemingly marginal bands. The rays are exclusively uniseriate and heterogenous. There is a common presence of gums and deposits in vessels. Vascular tracheids are present, and ground tissue fibers are simple in minutely bordered pits. The fiber wall thickness is thick-walled.

As seen through the radial sections, *S. herbacea* has simple perforation plates. While the inter-vessel pits arrangement is alternated with size from medium to large. The vessel ray pits are, with much-reduced borders, too apparently simple: pits rounded or angular. The tangential diameter of the vessel lumina is 25.20 μm, which varies in the average range of between 22.63 and 27.40 μm, so, overall, <50 μm, whereas the vessel's frequency per square millimeter is 471/mm^2.

Roots (cross, radial, and tangential) (Figure 5D–F). It is important to note that the wood anatomy of the roots of *S. herbacea* from arctic regions may be influenced by the harsh growing conditions of the studied region, such as low temperatures and soil nutrient levels, which may result in differences in the structure and anatomy of the root wood compared to that of other willow species. Here, the tangential diameter of the vessel lumina is 28.24 μm, which lies in the average range of between 21.70 and 34.72 μm, so, overall, <50 μm, whereas the vessels per square millimeter are 359/mm^2. In roots, the gums and deposits are rarely seen as compared to the stem sections. The rest of the features same as defined for the stem sections.

Table 2. Anatomical features of both *Salix* species and their stems and roots following numbered characters from the IAWA list; characters not listed are either absent or do not apply.

Anatomical Characters	***Salix herbacea* (SAHE)**				***Salix arctica* (SAAR)**			
	Stems		**Roots**		**Stems**		**Roots**	
	No.	**Features**	**No.**	**Features**	**No.**	**Features**	**No.**	**Features**
Growth rings	1–2	Less distinct			1	Distinct		
Porosity	4	Semi ring porous						
Vessel Arrangement	6	Vessels in tangential bands						
Vessel Grouping	0	Radial multiples of 2 to 4 with a variable proportion of solitary vessels					10	Radial multiples of 4 or more
Solitary vessel outline	12	Solitary vessel elements outline Angular						
Perforation plates	13	Simple perforation plates						
Inter-vessel pits: arrangement and size	22, 23	Inter-vessels pits alternate; Shapes of alternate pits polygonal			23,29	Shapes of alternate pits polygonal; Vestured inter-vessel pits		
	26, 27	Medium to large (7–10 um; >10 um)			27,29	Vestured pits		
Vessel ray pitting	31	Vessel ray pits with much-reduced borders to apparently simple: pits rounded or angular						
Tangential dia. of vessel l.	40	25.20 μm		28.24 μm	40	26.24 μm		46.97 μm
Vessels per square mm	50	$471/\text{mm}^2$		$359/\text{mm}^2$	50	$232/\text{mm}^2$		$130/\text{mm}^2$
Tyloses and deposits	58	Gums and other deposits in heartwood vessels are common			0	No tyloses		
Tracheids and fibers	60	Vascular tracheids						
Ground tissue fibers	61	Fibers with simple to minutely bordered pits						
Fiber wall thickness	70	Fibers very thick-walled	69	thin- to thick-walled	69	thin- to thick-walled	68	Fibers very thin-walled
Axial parenchyma absent or extremely rare	75–76	Axial parenchyma absent or extremely rare Axial parenchyma diffuse			76, 78	Axial parenchyma scanty diffuse and scanty paratracheal		
Banded parenchyma	89	Axial parenchyma in marginal or in seemingly marginal bands						
Ray width	96	Rays exclusively uniseriate						
Rays: cellular compos'n	104	All ray cells procumbent						
Mineral Inclusions: Prismatic crystals	136	More frequent				Present		

Table 2. *Cont.*

Anatomical Characters	***Salix herbacea* (SAHE)**				***Salix arctica* (SAAR)**			
	Stems		**Roots**		**Stems**		**Roots**	
	No.	**Features**	**No.**	**Features**	**No.**	**Features**	**No.**	**Features**
Druses	144		More frequent				Present	
Geo. distribution					164, 165, 182			
Habit	190				Shrubs (Arctic)			
Family, genus, species, authority			Family-Salicaceae Genus-Salix Species-herbacea				Family-Salicaceae Genus-Salix Species-arctica	

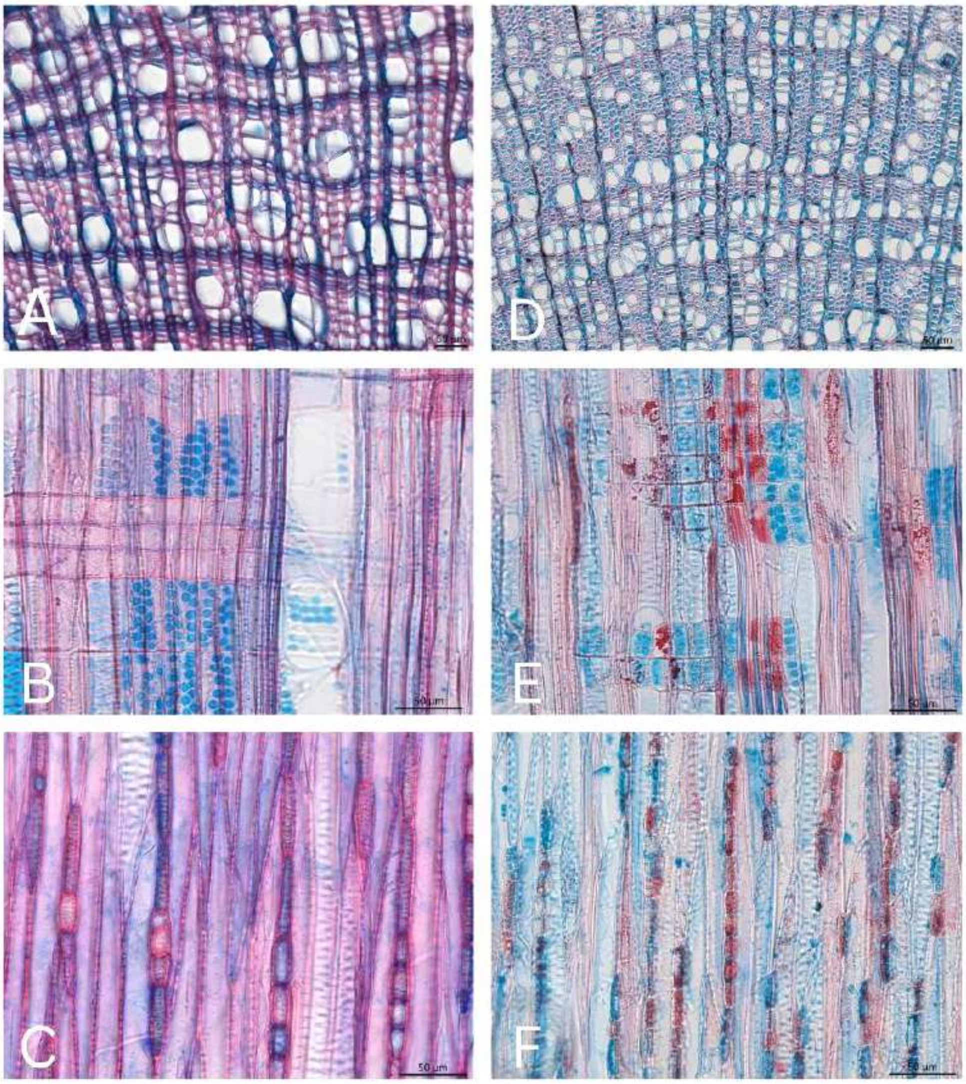

Figure 5. Photomicrographs showing three sections: cross (**A**,**D**), radial (**B**,**E**), and tangential (**C**,**F**) for roots (**A**–**C**) and stems (**D**–**F**) of *Salix herbacea* (cross—20× and radial and tangential—40×, scale: 50 µm).

The bark anatomy in *S. herbacea* shows a few irregular tangential layers of parenchyma, sieve tubes, and fibers. Sieve tubes are irregularly shaped, and companion cells are small. Parenchyma cells are angular. Fibers are in tangential layers. Sclereid groups are in older parts of the phloem. Prismatic crystals and crystal druses occur along fiber bands. The periderm consists of one layer of rectangular, large, thin-walled cells and small, thick-walled cells.

3.2. Anatomical Characteristics of Salix arctica

Similar to *S. herbacea*, the anatomy of *S. arctica* is also assumed to be similar to other species of the genus *Salix*. Overall, the growth form of *S. arctica* in Iceland allows it to be well adapted to the challenging environmental conditions and thrive in the region. In most of the descriptions available, its anatomy is described quite similarly to *S. herbacea*. According to the IAWA List of Microscopic Features for Hardwood Identification (IAWA Committee 1989), its anatomical features are also well described (Table 2). In our study, however, we observed stems (cross, radial, and tangential) (Figure 6A–C) growth ring boundaries here are well distinct, and other IAWA features (4, 6, absence of 9–11, 12, 13, 22, 26, and 31) are similar to those mentioned for *S. herbacea*. The tangential diameter of the vessel lumina is 26.24 µm, which lies in the range of 17.83–36.52 µm, smaller than *S. herbacea*, so, overall, <50 µm, whereas the vessel's frequency per square millimeter is 232/mm^2, which is smaller than *S. herbacea*, a rare presence of gums and deposits in heartwood vessels. The fiber wall thickness is thin- to thick-walled. Here, the axial parenchyma is scanty diffuse but also scanty paratracheal. With clearly visible banded parenchyma in the form of axial parenchyma in marginal or in seemingly marginal bands. Rays are exclusively uniseriate and much more clearly visible than *S. herbacea* and heterogenous.

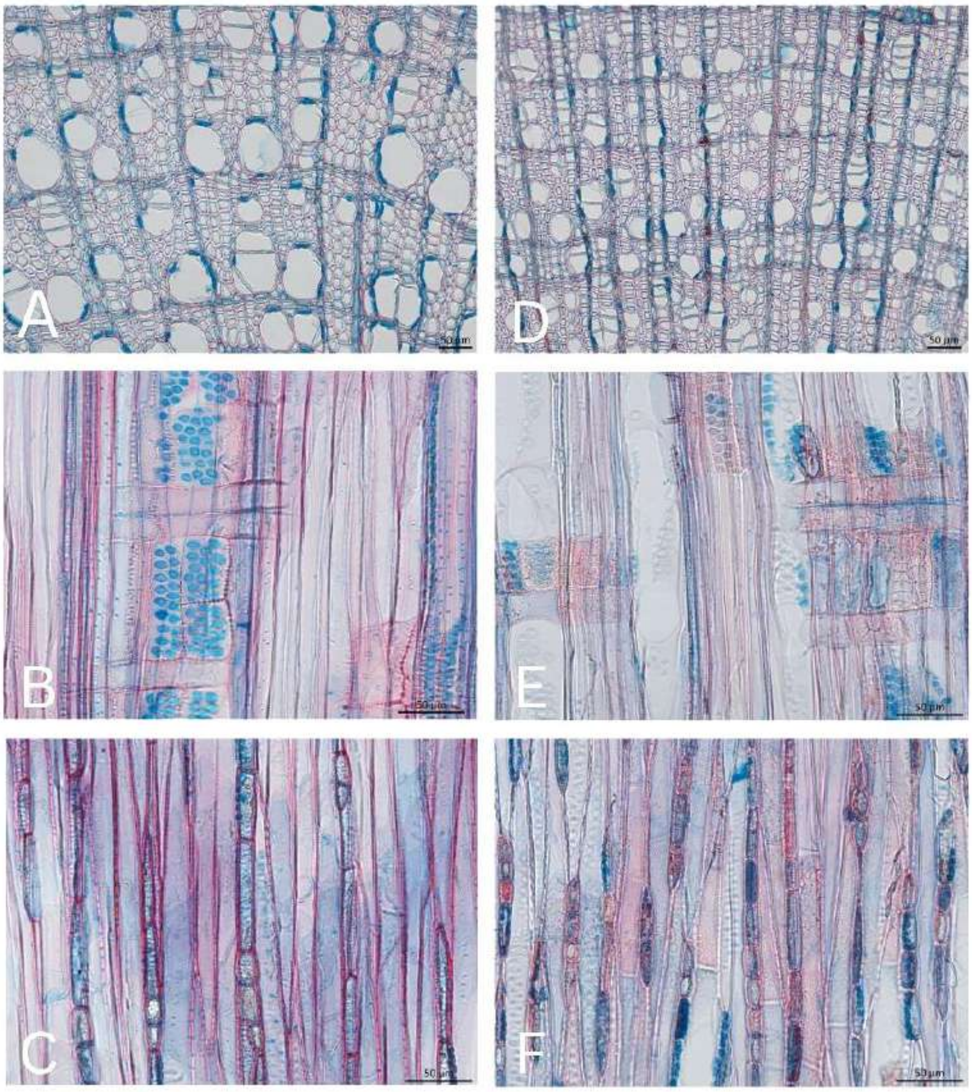

Figure 6. Photomicrographs showing three sections: cross (**A**,**D**), radial (**B**,**E**), and tangential (**C**,**F**), for roots (**A**–**C**) and stems (**D**–**F**) of *Salix arctica* (cross—20× and radial and tangential—40×, scale: 50 µm).

Roots (cross, radial, and tangential) (Figure 6D–F). Most of the features are similar as mentioned above for the stem part. As seen through the radial sections, it also has simple perforation plates. While the inter-vessel pits arrangement is also alternated here with sizes from medium to large, for some of the sections, we found the shape of alternate pits polygonal. The vessel ray pits have much-reduced borders that are apparently simple: pits rounded or angular (Figure 6B,E). Moreover, for some sections, vessel ray pits with distinct borders are similar to inter-vessel pits in size and shape throughout the ray cell. The tangential diameter of the vessel lumina is 46.97 µm, which lies in the range of 45.45–50.59 µm, so, overall, <50 µm, whereas the vessels per square millimeter are 130/mm^2. Tyloses are hardly present, with the rare presence of gums and deposits in heartwood vessels. Here, we found the presence of paratracheal axial parenchyma, which is scanty paratracheal.

In contrast, the bark of *S. arctica* exhibits consistent tangential arrangements of parenchyma, sieve tubes, and fibers. The parenchyma cells in this species appear more rounded and larger in size. Additionally, the periderm comprises multiple layers of rectangular, large, thin-walled cells along with small, thick-walled cells. Other anatomical characteristics are relatively similar between the two species. Notably, the presence of prismatic crystals and crystal druses is not as abundant in *S. arctica* compared to *S. herbacea*. The bark of *S. arctica* is thicker and probably acts as a more protective barrier than the one of *S. herbacea*, while the latter presents much more crystal abundance (prismatic and druses).

3.3. Statistical Variabilities in the Anatomical Parameters

Using Welch's *t*-test, we found no significant difference in the average tangential diameters of stems between *S. herbacea* and *S. arctica* (p = 0.730), because *S. arctica* exhibits greater variability (std. error of 2.747 mm) compared to *S. herbacea* (std. error of 0.811 mm), suggesting high variability in the measurements. However, significant differences were found in the tangential diameters of the roots (p = 0.0000051), with *S. arctica* roots having a larger mean diameter. Moreover, in the vessel frequency of both stems (p = 0.001837) and roots (p = 0.0000069), *S. herbacea* showed higher frequencies in both cases, as shown in Table 3.

Table 3. Statistical parameters for comparing the tangential diameter and vessel frequency between the stem and roots of *S. arctica* and *S. herbacea*, respectively.

Statistical Parameter	Tan. Diameter (SAAR Stems)	Tan. Diameter (SAHE-Stems)	Tan. Diameter (SAAR-Roots)	Tan. Diameter (SAHE-Roots)	Vessel Frequency (SAAR-Stems)	Vessel Frequency (SAHE-Stems)	Vessel Frequency (SAAR-Roots)	Vessel Frequency (SAHE-Roots)
Mean	26.24 mm	25.203 mm	46.969 mm	28.243 mm	232.667	471.667	130.333	359.375
Std. dev.	6.729	1.988	1.926	5.244	66.521	111.044	19.242	63.817
Std. error	2.747	0.811	0.786	1.854	27.157	45.333	7.856	22.563
t-statistic	0.362		9.299		−4.523		−9.587	
p-value	0.730		0.0000051		0.001837		0.0000069	

3.4. Stem and Root Growth Ring Chronologies

The chronological analysis of both species reveals a varying trend in 1975–2016. *S. herbacea* displayed a clear declining trend over the entire time span (Table 4, Figure 7A). In contrast, *S. arctica* showed divergent trends with a higher variability over the entire span: an increasing trend in stem growth and a bit of a decreasing trend in root growth (Figure 7B). However, both the stem and root parts of both studied species have exhibited a declining trend in the last few years, starting from 2014 onwards.

Table 4. Chronology statistics for *Salix* ring width chronologies from NE Iceland.

Species	Chronology Length (Years)	Number of Samples Collected/Included in Chronology	Mean Correlation between Samples	Mean Ring Width	Standard Deviation	Mean Sensitivity
SAAR stem	1939–2016 (77)	10/8	0.468	72.3	45.7	0.454
SAAR root	1940–2016 (76)	12/7	0.552	98.5	54.0	0.532
SAHE stem	1969–2016 (47)	10/9	0.437	95.3	11.7	0.335
SAHE root	1975–2016 (41)	10/7	0.429	81.4	19.5	0.382

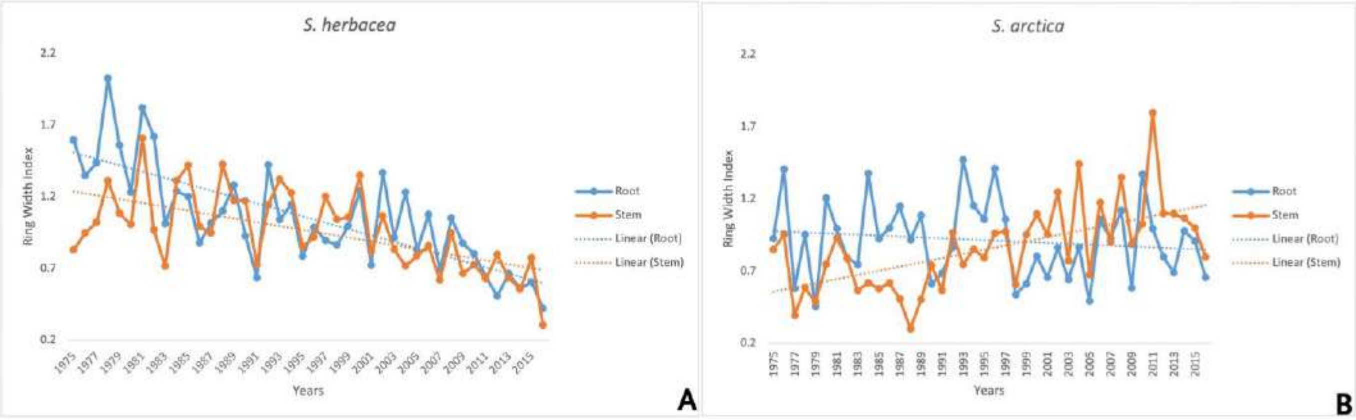

Figure 7. Standardized chronologies of stem and root parts for the Salix species in a time span of 1975–2016. (**A**) *Salix herbacea* and (**B**) *Salix arctica*.

Here, the maximum calculated ages for the stem and root parts of *S. arctica* were determined to be 77 and 76 years, respectively. For *S. herbacea*, the maximum ages were 54 years for the roots and 47 years for the stems, but for the chronology development, the most highly correlated samples and the most consistent period of high correlation were taken specifically from 1975 to 2016.

3.5. Climate Sensitivity of Root and Stem Parts

To further investigate the potential drivers of shrub growth, we conducted a dendroclimatological analysis, revealing significant variability between the two selected Salix species. Over a 16-month period, from the previous year's June to the current year's September, *S. herbacea* roots exhibited a more pronounced response to temperature, whereas *S. arctica* stems were more temperature-responsive. However, with respect to precipitation, *S. herbacea* showed an inverse relationship, demonstrating a significant negative response.

For *S. herbacea*, both roots and stems show a highly negative significant correlation with winter season temperatures (r_tJFM = −0.45 and −0.49, respectively) and also with summer (July, August, and September) temperatures (r_tJAS = −0.38). In contrast, *Salix arctica* stems exhibited a positive significant correlation with winter (r_tJan = 0.41, r_tFeb = 0.37, and r_tApr = 0.47) and summer temperatures (r_tJAS = 0.55). However, within the same species, its roots displayed a negative response to the previous year's summer temperatures (r_tpJAS = −0.32).

Regarding precipitation, the stems of *S. herbacea* were more responsive than the roots, showing a positive correlation with both winter (r_pFM = 0.38, 0.26) and summer precipitation (r_pJA = 0.41, 0.29). For *S. arctica*, a significant positive response was observed with the previous year's June precipitation (r_pJ = 0.42), while a negative response was seen with the current year's September precipitation (r_pS = −0.48), and so the root part is responsive rather than the stem. Analysis of the data from two meteorological stations indicated that the temperature and precipitation correlations were more significant for the Raufarhofn Station compared to the Akureyri Station.

4. Discussion

Our study provides a comprehensive analysis of the anatomical and dendroclimatic characteristics of *Salix arctica* (dwarf willow) and *Salix herbacea* (Arctic willow) in response to environmental changes in Iceland. The findings highlight significant differences between the two species in terms of vessel size, growth trends, and climatic responses. Comparing these results with past studies [5,53–57], it enhances our understanding of the adaptive strategies of these Arctic shrubs. However, these common Arctic species remain underexplored in terms of their root and stem's anatomical description and their individual climatic responses, requiring further investigation. Hence, comparative analyses of shrub growth sensitivity provide valuable insights into regional vegetation responses [58].

Here, we employed various microscopy techniques to gain deeper insights into the growth behavior of these species in sensitive regions. The results revealed significant complexity within a small region of interest, emphasizing the importance of a detailed analysis. While many anatomical features were similar between the two species, notable differences included larger vessel and fiber lumina in *S. arctica*, contributing to a higher vessel frequency in *S. herbacea* due to its smaller-sized vessels and fibers. *S. arctica*'s structure and growth pattern support its widespread distribution throughout the Arctic, whereas *S. herbacea* displays variability in structure and function, with its xylem placing a greater emphasis on safety compared to *S. arctica*. The larger vessel sizes observed in *S. arctica* compared to *S. herbacea* could suggest a greater adaptation to cope with extreme cold climates and enable more efficient water transport during the short growing seasons [43]. However, *S. herbacea* is a promising species for studying climate change impacts in Arctic and alpine environments, but the recent studies in Iceland have examined its growth response and the effects of erosion on vessel size [21,22], enhancing our understanding of Salix species under Arctic climate change [59,60].

Since the distinct wood anatomical characteristics enable the differentiation of various plant organs. Stems and adaptive stems are identified by the presence of a pith, whereas roots typically lack a pith (Figure 3B). The analyzed *Salicaceae* species commonly exhibit characteristic eccentric growth, including locally absent rings, and a lobate growth form. This growth pattern is often observed in response to extreme growth site conditions, resulting in prostrate stems with reduced growth on the upper side and enhanced growth on the lower side, consequently leading to eccentric pith positions [61], as seen in Figure 3B–D. It can be caused by pressure, e.g., by stones in the active layer [43]. While the sections we made justified that, in our studied site, the stem part is also affected by such environmental causes, the root part is still untouched or unaffected.

Typically, stems react to burial with reduced growth, whereas exposed roots exhibit increased growth [62–64]. Diffuse-porous species significantly increase in vessel size after stem burial [62,65], while ring-porous species show decreases in earlywood vessel size [62,66,67]. Additionally, ring-porous species tend to appear diffuse-porous or root-like after burial and revert to ring-porous after exposure [66,68–70].

Generally, root vessels are consistently larger than stem vessels in both species. Moreover, there is significant variation in vessel size between *S. herbacea* and *S. arctica* roots, whereas stem vessels show no prominent variation between the two species. The wood anatomy of shrubs shows differences in growth ring widths and vessel sizes before and after exposure, indicating varied responses to environmental stress [68,71]. This discrepancy might indicate that the stem section we chose has undergone periodical fluctuations in its growth habitat with time. As in the selected sections of both species, reaction wood signatures were absent in the roots but present in the stems. This phenomenon may be attributed to aeolian processes, which cause both erosion and deposition [37–40,72]. Diffuse-porous species, like *Salix*, significantly increase vessel size after stem burial [62,65,69,73], while ring-porous species show decreases in earlywood vessel sizes [62,66–68]. The study area is indeed particularly affected by soil deflation and aeolian accumulation. These processes can cause both, which can expose plants or cover them with soil mineral deposits, which could affect their growth patterns. The slow drainage of water-saturated sediments can temporarily bury plants and affect their access to light and nutrients; conversely, wind erosion can expose root systems, making them more susceptible to temperature fluctuations and desiccation. This dynamic environment likely contributes to the observed differences in anatomical and growth responses between the two species. It should also be noted that the activity of other geomorphological processes in the Arctic that cause erosion and deposition, such as debris flows, may also contribute to the occurrence of this differentiation [6].

When erosion exposes plant roots, this can lead to increased vulnerability to extreme temperatures and desiccation, potentially stressing the plants and inhibiting their growth. This exposure can lead to physiological stress and affect the plant's ability to transport water and nutrients efficiently. Conversely, the slow drainage of water-saturated sediments that bury plants under the soil can reduce their access to sunlight and disrupt photosynthesis, resulting in reduced growth. These alternating exposed and buried conditions create a challenging environment that affects the growth patterns and anatomical characteristics of *S. arctica* and *S. herbacea*.

The constrained growth conditions in Arctic research sites reveal varying ring counts at different radii on cross-sections, especially in aboveground stem segments. Using a serial sectioning approach [49], we noticed age differences between the stem and root parts of *S. herbacea*, potentially influenced by environmental changes over the past decade. The presence of gums and tyloses in *S. herbacea* sections may affect its growth dynamics. The increased presence of tyloses in *S. herbacea* suggests an adaptive strategy to protect against water stress and cavitation. This highlights a defense mechanism that helps to maintain the functionality of the vascular system under harsh environmental conditions, likely due to the plant's greater exposure to erosion and thermal stress. The different responses of *S. herbacea* and *S. arctica* illustrate the diversity of adaptive strategies developed by plants to survive in arctic environments. While *S. arctica* showed an overall increase in growth, some variations are influenced by the specific microhabitat conditions. However, *S. herbacea* exhibited a consistent decline, with recent years indicating a decline in both species. *S. arctica*'s growth was positively correlated with the temperature, aligning with findings from Greenland [74], whereas *S. herbacea* responded positively to winter and summer precipitation but struggled with the rising temperatures, as shown for the complete plant individuals of *S. herbacea* [22].

Our results performed for the stem and root parts align with a recent study from the studied site in Iceland [20], showing the climatic response for complete individuals of *S. arctica*'s positive response to the summer temperature of August and September and *S. herbacea*'s negative climate–growth correlation with May, April, and July. Similarly, in our analysis, *S. arctica* demonstrated significant positive relations with summer season (July, August, and September) temperatures (rtJAS = 0.55) and winter season temperatures (rtJan = 0.41, rtFeb = 0.37, and rtApr = 0.47), correlating higher summer temperatures with increased radial growth [75]. Conversely, *S. herbacea* had a significant negative response to winter temperatures for roots and stem parts, respectively (rtJFM = -0.45 and -0.49) and a positive response to winter (Jan, Feb, and March) and summer (July and August) precipitation (rpFM = 0.38 and 0.26; rpJA = 0.41 and 0.29). This clearly indicates that the growth of *S. arctica* is temperature-dependent, with its stems being more responsive, whereas *S. herbacea* shows a stronger response to precipitation, particularly in its roots. Hence, these findings underscore the importance of species-specific responses and the complexity of interpreting growth based solely on temperature, given environmental challenges such as missing rings and extreme conditions [27,76].

Distinct anatomical differences between *S. herbacea* and *S. arctica*, such as the presence of tension wood in *S. arctica* and the absence of gums and tyloses, suggest adaptive traits to withstand harsh conditions. Wide-field fluorescence microscopy and LP emission filters revealed suberin and lignin in the bark, with suberin acting as a selective barrier against water and solute transportation. In Iceland, *S. arctica*'s larger stem diameters and thicker bark support its high tolerance to environmental stress. Our findings highlight the intricate relationship between climatic factors and growth patterns of *Salix* species, emphasizing the need for comprehensive investigations into the environmental drivers shaping anatomical features in Arctic vegetation.

This study offers a detailed anatomical analysis of two common Arctic willow species: *Salix herbacea* (dwarf willow) and *Salix arctica* (Arctic willow). Variations within and between these species highlight the Arctic ecosystem's complexity. We recommend systematic sampling of complete individuals and well documentation of whether parts are exposed or unexposed during their collection. This study emphasizes the variability among different parts of Arctic shrubs and the need for standardized sampling for reliable dendrochronological analysis. Hence, understanding local growth and variability is crucial before making global inferences in Arctic ecosystems.

5. Conclusions

Our research provides a detailed anatomical and dendroclimatic analysis of two common Arctic willow species: *Salix herbacea* (dwarf willow) and *Salix arctica* (Arctic willow). Our results point out notable differences included in larger vessel and fiber lumina in *S. arctica*, contributing to a higher vessel frequency in *S. herbacea* due to its smaller-sized vessels and fibers. *S. arctica*'s structure and growth pattern support its widespread distribution throughout the Arctic, whereas *S. herbacea* displays variability in structure and function, with its xylem placing a greater emphasis on safety compared to *S. arctica*.

The growth trends also differ between the species: *S. arctica* shows an overall increase, while *S. herbacea* exhibits a consistent decline. Both species' individual parts generally follow these trends, though a recent decline has been observed in the last few years. While the dendroclimatic responses were not highly significant, they varied between the two species. *S. arctica* showed positive responses to winter and summer temperatures, whereas *S. herbacea* behaves quite the opposite as it struggled with the rising temperatures. Thus, being a drought indicator species, *S. herbacea* responded positively to summer and winter precipitation.

Our findings underscore the need for standardized sampling protocols in shrub anatomy and dendrochronological analysis to ensure reliable comparisons. Future studies should systematically sample complete individuals and document whether collected parts are exposed or unexposed, given the complex growth patterns of these species. This approach will improve our understanding of Arctic tundra dynamics amid environmental changes. Our study reveals the interaction between climate, anatomical traits, and shrub growth. Understanding local growth and variability is essential before making global inferences, particularly in the intricate Arctic ecosystems.

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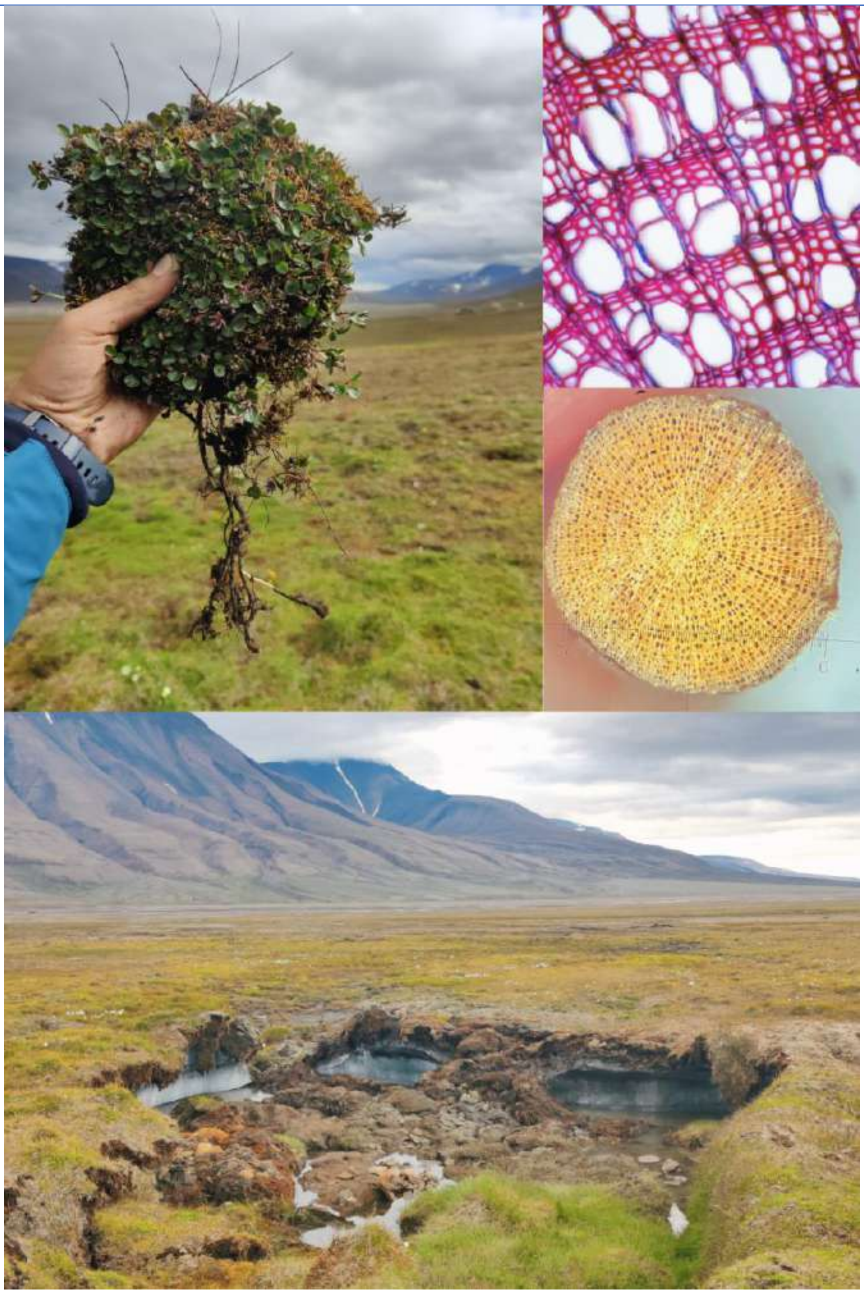
Article III

Multiple factors Controlling Polar Willow Growth in the High Arctic (Svalbard): Implications for Future Prediction of Tundra Productivity



Global Ecology and Conservation

Multiple factors controlling polar willow growth in the high Arctic (Svalbard): implications for future prediction of tundra productivity

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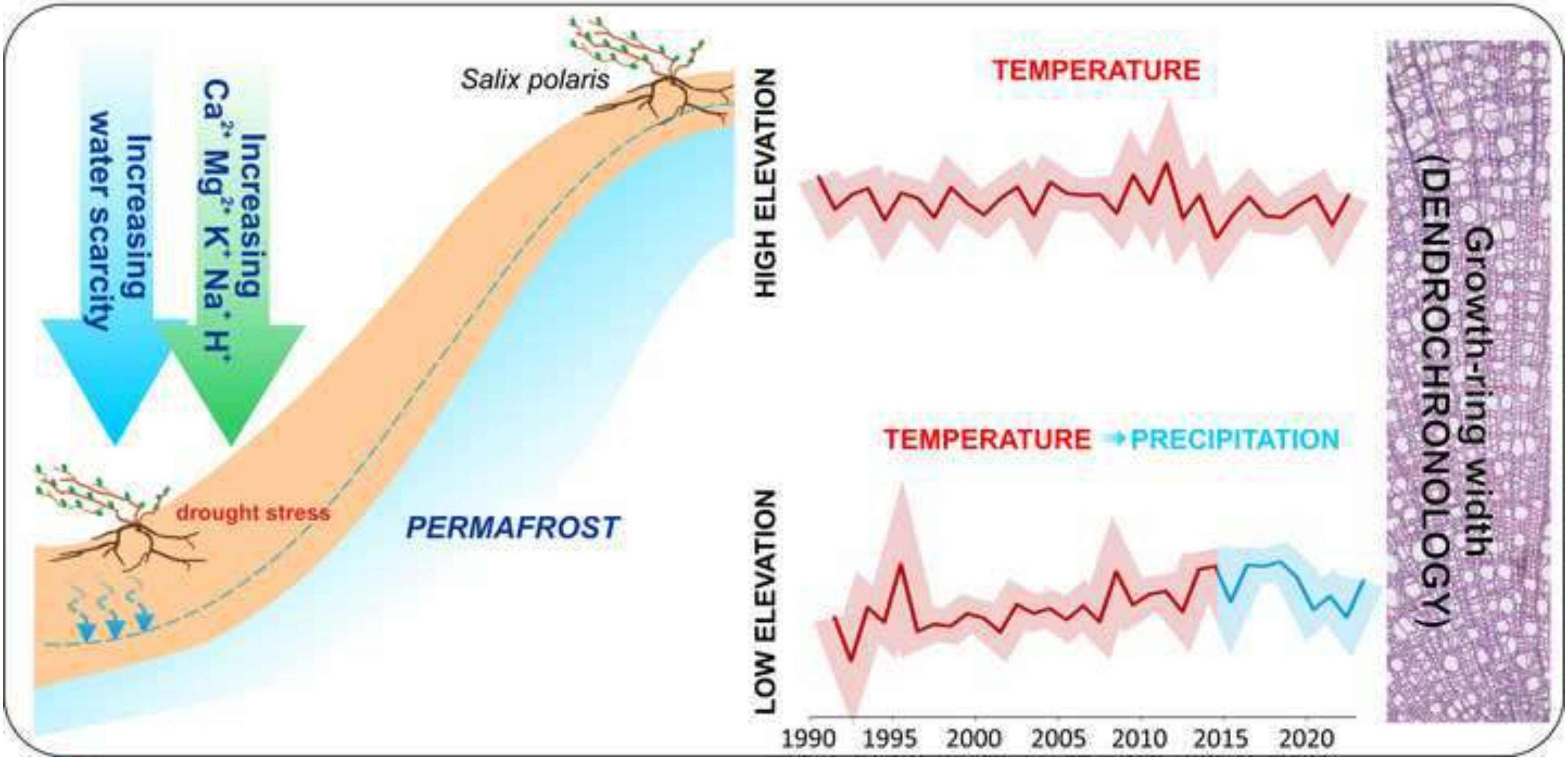
Corresponding Author:	Piotr Owczarek University of Wroclaw Institute of Geography and Regional Development POLAND
First Author:	Mohit Phulara
Order of Authors:	Mohit Phulara
	Magdalena Opała-Owczarek
	Wojciech Szymański
	Jacek Ślopek
	Michał Węgrzyn
	Ewa Łupikasza
	Bartosz Korabiewski
	Piotr Owczarek
Abstract:	Arctic regions are warming faster than the global average, leading to significant changes in permafrost, vegetation dynamics, and soil nutrient availability. Understanding these interactions is essential for predicting the rapidly changing behavior of tundra ecosystems. In central Spitsbergen, we examined the growth of Salix polaris across various elevations to assess the impact of local habitat conditions and climate change. Dendrochronological analyses revealed that low-elevation valley-bottom sites showed a strong positive correlation between June temperatures and ring growth (r = 0.69), supported by high soil moisture (up to 70%) and nutrient-rich soils. These areas exhibited higher productivity, referred to as 'greening,' with NDVI values reaching approximately 0.5. However, increased rain-on-snow (ROS) events and rapid soil drainage caused a late summer drought. In contrast, higher elevations experienced delayed yet sustained growth in mid-to-late summer, supported by permafrost moisture retention despite colder early summers. NDVI values at high elevations ranged from 0.0 to 1.5, with soil moisture peaking around 40%. These findings indicate that plants growing at low and high altitudes respond differently to climatic variables: at low altitudes, growth is driven by early summer warmth and moisture availability, while at high elevations it relies on mid-summer temperatures. The varied growth responses underscore the necessity of integrating multiple factors—such as soil chemistry, geomorphology, moisture variability, high-resolution imagery, and dendroclimatology—into predictive models. Relying solely on summer warmth is insufficient for understanding the complex growth behaviors in high-Arctic regions. Comprehensive approaches are necessary to accurately forecast future vegetation shifts and their ecological impacts in the High Arctic.
Opposed Reviewers:	

Highlights

- Growth of dwarf shrubs is strongly related to the local micro-habitat variability.
- Increased temperatures in the Arctic can have a various impact on plant growth.
- Depending on the altitude, a varying incremental response of the shrubs is observed
- Plants growing at lower altitudes are more susceptible to drought stress.
- Soil characteristics can modify the growth of dwarf shrubs but are not decisive.


Increasing
water scarcity
Increasing
Ca^{2+} Mg^{2+} K^{+} Na^{+} H^{+}
Salix polaris
drought stress
PERMAFROST
HIGH ELEVATION
TEMPERATURE
LOW ELEVATION
TEMPERATURE → PRECIPITATION
1990
1995
2000
2005
2010
2015
2020
Growth-ring width
(DENDROCHRONOLOGY)

Multiple factors controlling polar willow growth in the high Arctic (Svalbard): implications for future prediction of tundra productivity

Mohit Phulara[1], Magdalena Opała-Owczarek[1], Wojciech Szymański[2], Jacek Ślopek[3], Michał Węgrzyn[4], Ewa Łupikasza[1], Bartosz Korabiewski[3], Piotr Owczarek[3]*

[1] Institute of Earth Sciences, Faculty of Earth Sciences, University of Silesia in Katowice, Sosnowiec, Poland

[2] Institute of Geography and Spatial Management, Faculty of Geography and Geology, Jagiellonian University, Kraków, Poland

[3] Institute of Geography and Regional Development, Faculty of Earth Sciences and Environmental Management, University of Wroclaw, Wroclaw, Poland

[4] Institute of Botany, Faculty of Biology, Jagiellonian University, Kraków, Poland

*corresponding author: piotr.owczarek@uwr.edu.pl

Abstract

Arctic regions are warming faster than the global average, leading to significant changes in permafrost, vegetation dynamics, and soil nutrient availability. Understanding these interactions is essential for predicting the rapidly changing behavior of tundra ecosystems. In central Spitsbergen, we examined the growth of *Salix polaris* across various elevations to assess the impact of local habitat conditions and climate change. Dendrochronological analyses revealed that low-elevation valley-bottom sites showed a strong positive correlation between June temperatures and ring growth (r = 0.69), supported by high soil moisture (up to 70%) and nutrient-rich soils. These areas exhibited higher productivity, referred to as 'greening,' with NDVI values reaching approximately 0.5. However, increased rain-on-snow (ROS) events and rapid soil drainage caused a late summer drought. In contrast, higher elevations experienced delayed yet sustained growth in mid-to-late summer, supported by permafrost moisture retention despite colder early summers. NDVI values at high elevations ranged from 0.0 to 1.5, with soil moisture peaking around 40%. These findings indicate that plants growing at low and high altitudes respond differently to climatic variables: at low altitudes, growth is driven by early summer warmth and moisture availability, while at high elevations it relies on mid-summer temperatures. The varied growth responses underscore the necessity of integrating multiple factors—such as soil chemistry, geomorphology, moisture variability, high-resolution imagery, and dendroclimatology—into predictive models. Relying solely on summer warmth is insufficient for understanding the complex growth behaviors in high-Arctic regions. Comprehensive approaches are necessary to accurately forecast future vegetation shifts and their ecological impacts in the High Arctic.

Keywords: High Arctic, *Salix polaris*, dendrochronology, soil properties, topoclimate

1. Introduction

Arctic terrestrial ecosystems are susceptible to modern climate variations and reflect the effects of changes in air temperature, precipitation, snow cover, permafrost, and geomorphic processes activity. Large-scale warming in the Arctic has accelerated during recent decades and is occurring at a rate that is twice that of the global trend AMAP (2017). However, the climatic conditions in the Arctic are spatially highly variable, and inter-annual weather conditions, as well as the dynamics of biological, biogeochemical and geomorphic processes in terrestrial ecosystems, exhibit considerable variation (Raynolds et al., 2008;; Przybylak and Przybylak, 2016). This variability of environmental factors, including microtopography and microclimate, presents a significant challenge in assessing the impact of modern climate change on tundra vegetation. The effects of rapid warming are evident in increased primary productivity, termed "arctic greening," (Stenseth et al., 2003; Post et al., 2009). However, it should be noted that these effects are not uniform across the landscape. In some areas, a contrasting trend known as "arctic browning," characterized by decreased vegetation productivity and loss, complicates the narrative of a uniformly warming Arctic (Phoenix and Bjerke, 2016).

The direct impact of warming on vegetation in the Arctic is clear. Nevertheless, predictions of vegetative response to warming are confounded by observations of heterogeneous growth responses among tundra shrubs (Elmendorf et al., 2012; Epstein et al., 2012). This heterogeneity in response underscores the need to investigate the interplay of climatic and all other factors with plant growth in a more detailed manner.

The Svalbard Archipelago is a pertinent case study within the northern polar zone due to its relatively warm climate and observable increase in warm days conducive to plant growth (Przybylak et al., 2014). , Polar willow (*Salix polaris)* has emerged as a species of particular interest in dendrochronological research due to its widespread ecological amplitude and dominance across the varied habitats of Spitsbergen (Węgrzyn and Wietrzyk, 2015). Prior studies have focused predominantly on the relationship between *Salix polaris* growth and temperature, often using this species as a bioindicator for assessing climate impacts (Owczarek et al., 2013). These studies have revealed the importance of summer temperatures (Buchwal et al., 2013) but have also highlighted inconsistencies in the response of *Salix polaris* to climatic variations, suggesting that factors beyond temperature, such as precipitation and local microsite conditions, could play significant roles in determining growth (Schmidt et al., 2006; Zalatan and Gajewski, 2006; Owczarek and Opała, 2016; Opala-Owczarek et al., 2018; Owczarek et al., 2021).

Despite the value of traditional dendrochronological studies in elucidating the growth responses of Arctic shrub species to climate variables, a substantial gap remains in understanding the multifaceted influence of environmental factors on these processes. The growth and functionality of plants are profoundly affected by a range of environmental elements, including climatic aspects such as temperature and rainfall (Wodzicki, 2001; Begum et al., 2018), as well as non-climatic factors such as soil conditions and the occurrence of extreme events including geomorphological disturbances (Owczarek et al., 2013; Bräuning et al., 2016). However, the driving factors influencing tundra plant growth are not yet fully understood. It is thus evident that a comprehensive study integrating ground-based and satellite-derived observations and their linkage to a large variety of environmental factors is crucial.

Our research aims to deepen the understanding of how the diverse environmental conditions at different altitudes may influence the growth of *Salix polaris* in central Spitsbergen in the high Arctic Svalbard archipelago. We hypothesize that beyond the acknowledged macroclimatic influences, a range of microclimatic and edaphic factors play a significant role in shaping the growth patterns of this species. Considering the above research problems, the main research question we pose is: Is the incremental response of polar willow is homogeneous in the different morphological zones of central Spitsbergen? If not, what abiotic environmental factors affect growth and what are the possible implications in assessing greening or browning of the tundra? To achieve the research objectives, we employed coordinated multi-proxy methods including dendrochronological, meteorological, and soil properties analyses spanning scales from microhabitats to the broader landscape combined with satellite-derived data analysis.

2. Study area

The study was conducted in the central part of Spitsbergen, the largest island in the high Arctic Svalbard archipelago (Fig. 1A). Glaciers and ice caps cover approximately 57% of the archipelago (Nuth et al., 2013). The Central Spitsbergen exhibits the lowest glacial coverage, with less than 18% of the area covered by ice. The study sites are located in the Adventdalen area. The landscape of this part of central Spitsbergen is mainly characterized by wide plateaux at elevation 450 - 550 m a.s.l. above which isolated flat-topped peaks up to 1050 m a.s.l.. The elevated plateaux are often covered by rock debris with frost-patterned ground (Fig. 1B). In contrast, more intense erosional processes give rise to expansive U-shaped valleys with extensive braided river systems and alluvial cones (Fig. 1A,C). According to the Köppen classification system, the climate represents the tundra polar subtype (ET), with the average annual air temperature of –4.5°C and seasonal air temperatures varying between -11.7°C in winter and 5.2°C in summer. Compared to other parts of Spitsbergen, the Adventalen area receives very low precipitation, averaging 207.9 mm annually. Days with snowfall constitute about 50% of days with precipitation. The active layer of the permafrost ranges from 60 to 120 cm in thickness, underlying a landscape with diverse tundra vegetation adapted to local terrain relief and moisture (Watanabe et al., 2017; Szymański et al., 2022a). On plateaus, the dominant vegetation type is tundra classified as Cryptogam, herb barren. This habitat is characterized by dry to wet barren landscapes with very sparse, extremely low-growing plant cover. Prostrate shrubs less than 5 cm tall, such as *Dryas octopetala* and *Salix polaris*, along with graminoids and forbs, dominate lower elevations and valleys (Fig. 2A).

Following the methodological assumptions and the adopted research objectives, samples of polar willow were collected from areas with differing topographic, hydrological and soil conditions to facilitate the investigation of the impact of these factors on the plant's growth and development (Fig. 1A).

3. Material and methods

3.1. Vegetation plots and wood material

For each study site established at the polar willow sampling locations, vegetation communities were characterized using phytosociological relevés, each covering an area of 100 m². Relevé locations were selected following the fundamental principle of identifying uniform and homogeneous plant community surfaces, as described by Braun-Blanquet (1964). Unidentified taxa and fragments of biological soil crusts were collected for further identification and analysis in the laboratory. Based on the phytosociological relevés, plant communities were classified in terms of the ecological typology of plant habitats (Elvebakk, 1994) and syntaxonomy (Węgrzyn and Wietrzyk, 2015). At each study site, specimens of polar willow were collected for further dendrochronological analyses (Fig. 2A).

Salix polaris (Wahlenb.), known as polar willow, is widespread in the Svalbard archipelago, notably within south-western Spitsbergen and Edgeøya (Påhlsson, 1985Elvebakk, 1994; Rønning, 1996; Elvebakk, 1997). Its wide distribution across Spitsbergen makes it a suitable species for analyzing growth response variability due to its recognized potential in dendroclimatic and geomorphological studies (Buchwal et al., 2013; Owczarek et al., 2013; Opala-Owczarek et al., 2018). Visible parts are limited to dark green leaves and shoots (Fig. 2A). Branches are less than 1.2 cm in diameter, but distinct growth rings marked by rows of cells, are evident and significant for studying environmental conditions (Fig. 2C) (Owczarek, 2009; Owczarek et al., 2013). In total, during the 2022 and 2023 field campaigns, 157 samples of polar willow were collected. Samples were collected in 6 sites from both rocky debris plateaus of Breinosa and Sverdruphamaren, and the flat valley bottoms and lower parts of alluvial cones within Advendalen and Longyeardalen valleys (Fig. 1A).The samples including roots, root collars, and wooden branches (Fig. 2B) were collected from altitudes ranging between 67–459 meters above sea level (Table 1).

3.2. Dendrochronological processing and climate-growth interaction analysis

To accurately assess how topographical diversity and local factors influence the growth variability of *Salix polaris*, we sampled plants from climatically diverse sites. At each site, we randomly collected approximately 15-32 plant specimens of *Salix polaris*, depending on local availability. For laboratory analysis, we adapted well-established microscopic techniques for examining dwarf shrubs (Gärtner and Schweingruber, 2013). Given the prevalence of wedging and partially missing rings related to eccentric growth, at least two radii were manually measured using the WinDENDRO tree-ring system (Rinn, 2003), ensuring accuracy in our analysis of growth-ring variability. Cross-dating was conducted in three stages: first, within each cross-section; next, within each sample; and finally, across all sites. This process involved two steps: first, we conducted a visual analysis of the ring series using TSAPWin, then validated our findings statistically with COFECHA (Grissino-Mayer, 2001).

Pearson’s correlation analysis was used to examine the climate signals embedded in dwarf shrub growth rings. We analysed the standardized ring series against temperature and precipitation data to identify climatic patterns over a 16-month period, spanning June of the previous year to September of the current year. By extending our calculations across individual months and aggregate seasonal data, we aimed to pinpoint the climatic influences that shape the unique growth trajectories of these Arctic shrubs.

3.3. Geomorphological and soil analyses

Each research area, including the surroundings of designated vegetation plots, was subject to detailed geomorphological mapping. For the research, we paid special attention to landforms and processes that could either hinder or promote vegetation growth and plant productivity. Soil samples were collected from each designated vegetation plot from the surface layer (0-10 cm). All soil analyses were performed using fine-earth material (i.e. fraction <2 mm). In addition to the standard physical and chemical analyses, we examined the following elements: concentrations of exchangeable cations (Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}), concentration of plant available phosphorus (Pav), potassium (Kav), and magnesium (Mgav).

3.4. Remote sensing and NDVI analyses

The input data for calculating the NDVI for the study areas (Fig. 1) were high-resolution multispectral remote sensing data recorded by the commercial satellites WorldView-2 (Earth Online 2024a) and WorldView-3 (Earth Online 2024b). The main problem in using satellite imagery in studies of the Svalbard area (and polar regions in general) is the high cloud cover typically observed in July and August (Bednorz et al., 2014). Only a small number of satellite images contain useful data for the study areas (not obscured by clouds). For the Longyeardalen area, five satellite images recorded on 17.07.2020, 24.07.2020, 25.08.2020, 29.07.2021, and 14.08.2021 were selected for this study. For the Foxdalen area, seven satellite images recorded on 5.08.2011, 17.07.2013, 28.07.2019, 26.07.2020, 23.08.2020, 3.07.2021, and 8.08.2021 were selected for analysis. The rectified satellite imagery was used to calculate the NDVI index. The raster layers prepared in this way were further processed in GRASS GIS software (GRASS, 2024). The field locations of the measurement points (Fig. 1) were used to extract the NDVI values. Univariate statistics (minimum, maximum, mean, median, Q1 and Q3) of the NDVI index in the immediate vicinity of the collection site (in a circular buffer of 10m radius around the measurement point) were also calculated for these points.

3.5. Meteorological and sensor data

The closest meteorological station with long-term temperature and precipitation data is Svalbard Airport (78°25′N, 15°46′E), a coastal station located 4-15 km west of the study sites. Raw daily mean temperature (°C) and total precipitation sum (mm) data available for this station over the period 1971-2022 were obtained from the Norwegian Meteorological Institute (https://seklima.met.no) and recalculated into monthly data.

A temperature and moisture logger was installed in each vegetation plot to determine the variability of microclimate conditions. We recorded soil moisture and temperature at 15 minutes intervals at depth/height of -6, +2 and +15cm using the Temperature-Moisture-Sensors (TMS) (TOMST, www.tomst.com). They can thus capture the microclimatic conditions at that ground level, which is key to correctly identifying the variability of climatic conditions within the tundra community across different spatial scales and habitat types (Wild et al., 2019).

4. **Results**

4.1. Altitudinal distribution of vegetation and soil properties

All the studied topsoils showed loamy or sandy loam texture; however, the topsoils obtained from sites located in the valleys (i.e. low lying sites) showed slightly lower mean content of sand and slightly higher mean content of silt in comparison with topsoils obtained from the plateaus (i.e. high-elevated sites) (Table 1). The mean clay content was similar in topsoils from the valleys and plateaus. The mean content of rock fragments (fraction >2 mm) was substantially higher in topsoils on plateaus than in valleys (Table 1). All the studied topsoils were acidic. Topsoils from the valleys were characterized by slightly higher mean soil pH as well as higher SOC and TN content in relation to topsoils obtained from plateaus. The mean C/N ratio for valley topsoils was higher than that of plateau topsoils (Table 1). All the studied topsoils showed similar chemical composition; however, topsoils from sites located in the valleys were characterized by slightly lower mean content of SiO_2 and slightly higher mean content of Al_2O_3, Fe_2O_3, MgO, CaO, Na_2O, K_2O, TiO_2, and P_2O_5 in relation to topsoils obtained from the plateaus (Table 2). Mean cation exchange capacity (CEC) of the topsoils from the valleys was more than two times greater than in topsoils obtained from the plateaus (Table 3). Base cations, mainly Ca^{2+} and Mg^{2+} were the dominant exchangeable cations in all the studied topsoils. Topsoils occurring in the valleys showed clearly higher mean concentration of exchangeable Ca^{2+} and slightly higher mean concentration of Mg^{2+}, K^+, Na^+, and H^+ in comparison with the topsoils obtained from the plateaus (Table 3). On the other hand, plateau topsoils had a higher mean concentration of Al^{3+} and greater exchangeable acidity than valley topsoils. Mean base saturation was clearly higher in topsoils located in the valleys than on plateaus (Table 3). Topsoils occurring in the valleys showed clearly higher mean concentration of Kav and Mgav than topsoils obtained from the plateaus. In contrast, mean concentration of Pav was slightly lower in topsoils from the valleys in comparison with topsoils on plateaus (Table 3).

Phytosociological studies identified two main vegetation types (Supplement Table 1): mesic tundra in deeper parts of the Adventdalen valley and exposed ridge communities at higher elevations. The latter occurred in two variants, with moderate and very low vascular plant coverage.

Mesic tundra (the fresh tundra dominated by vascular plants, including dwarf shrubs) is a species-rich type of Arctic vegetation. It is characterized by moderate moisture levels, which distinguishes it from the extremely dry or very wet types of tundra. A total of 20 plant species were recorded at the studied sites in this community, with 5 species showing the highest coverage: *Salix polaris*, *Cassiope tetragona*, *Polygonum viviparum*, *Dryas octopetala*, and *Poa vivipara*. Among the cryptogamic species, mosses from dry or slightly moist habitats dominated: *Caliergon sarmentosum*, *Straminergon stramineum*, *Racomitrium lanuginosum*, *Sanionia uncinata*, and terricolous lichens: *Ochrolechia androgyna*, *O. frigida*.

The exposed ridge community develops on open mountain slopes and ridges, where intense winds limit snow accumulation, reducing winter frost protection for plants. At the studied sites in this community, a total of 11 vascular plant species were recorded in the rich variant and 7 in the poor variant. In both variants, the dominant species were *Salix polaris*, *Poa vivipara*, and *Luzula confusa*. *Cerastium arcticum* and *Luzula arcuata* appeared sporadically. Among the cryptogamic species, mosses from dry habitats dominated: *Polytrichum piliferum*, *Ptilidium ciliare*, *Racomitrium lanuginosum*, and crustose rock lichens: *Lecanora polytropa*, *Porpidia melinodes*, *Rhizocarpon geographicum*, and *Rh. reductum*; fruticose rock lichens: *Pseudephebe pubescens*, *Stereocaulon alpinum*, *Umbilicaria cylindrica*; ground lichens: *Collema cereniscum, Ochrolechia androgyna*.

4.2. Dendrochronological data and relationships between climate and growth-ring widths

High-resolution digital images of *Salix polaris* cross-sections from six sites enabled the construction of reliable growth-ring chronologies at five sites, spanning 30 to 39 years. (Table 4). The average width of an annual growth ring was 103.9 to 115.3µm at low elevation sites and 73.5 to 81.2 µm at high elevation sites. Specimens from high-elevation sites had a slightly better correlation between samples and higher average sensitivity, suggesting that dwarf shrubs from lower locations did not vary to the same degree from year to year as in the highest-located plateau. Missing and partially missing rings were most common at high-elevation sites due to extreme growth conditions, as at an altitude above 400 m, the growing season is even shorter than the short Arctic summer in the relatively warmer valleys of central Spitsbergen. Negative indicator years, common across all study sites, occurred in 2006 and 2014 and are discussed later in the text. Analyzing the course of the *Salix* growth-ring chronologies, characteristic trends were found, respectively increasing trend for sites located in the valley and decreasing but not statistically significant for sites located on the plateau (Fig. 3A). The previously apparent strong variation in variability from year to year has flattened out since the last 10 years, and reduced growth is evident at all sites.

Dendroclimatic analyses at different sites yielded diverse results, enabling insightful interpretations of the factors influencing polar willow growth in Central Spitsbergen. Our analysis of various microsite conditions suggests that the growth response of this species is influenced by more factors than a single climate driver – specifically the positive effect of July temperature. We grouped the results for two types of sites: low and high elevated (Fig. 3A). At low-elevation sites, June temperature (r=0.69) is the primary factor promoting growth, while temperature plays a lesser role in the subsequent summer months. High June temperatures positively affect polar willow growth by accelerating snowmelt, enabling early growth initiation, and ensuring adequate moisture availability. For July and August, the highest correlation values were obtained between the growth width and the amount of precipitation, indicating higher water demand during the short Arctic summer with relatively constant air temperature (mean T_{JJA}(1976-2023)= 5.2°C (SD±1)). A statistically significant negative correlation was also observed with spring precipitation, particularly in March and April. During this period, solid precipitation dominates, increasing snow cover and delaying the onset of the growth period, which may result in narrower rings.

At high-elevation sites, July and August temperatures, rather than June temperatures, are the main weather variables positively associated with ring growth (Fig. 3A). At approximately 450 m elevation, subzero temperatures are still common in June. Warm winters or the onset of warm spells in winter may negatively impact growth. This occurred in 2014, when we recorded the most pronounced negative pointer year in our dendrochronological series across multiple sites, despite normal summer conditions (dev.T_{JJA} =+0.4°C from the long-term average 1976-2023) (Fig. 3B). February of 2014 was the warmest of all long-term meteorological series (dev.T_{Feb} =+10.8°C from the long-term average 1976-2023), many days with temperatures near 0, and several consecutive days (February 9-14th) with positive temperatures were recorded (Fig. 3B). The impact of warm winter and rain-on-snow (ROS) was also evident in 2006, though its effect on willow growth varied across sites. Low growth, unrelated to the primary climatic driver, mainly occurs at low-elevation sites and at only one high-elevation site (Foxfonna).

4.3. NDVI index

Elevation strongly influences NDVI values and their variability across the analysed research sites (Fig. 4). At lower-elevation sites, NDVI values measured during equivalent periods are 2 to 3 times higher than at higher-elevation sites (Fig. 4). At the FOX04 site, the NDVI determined for its location, for most of the analyzed satellite scenes in both July and August, did not exceed 0.1, taking an average value of about 0.05. At this site, an NDVI value of 0.121 was recorded only in August 2021. Analyzing the average values of the NDVI index in the vicinity of the measurement point, it can be seen that this index took on average values near 0.05 or 0.03 if records from the year 2021 are not included. NDVI variability at site FOX04 in 2021 differed from previous years. The interquartile range for 2021 is an order of magnitude smaller than that recorded in 2011-2020. The range of extreme values of the NDVI index for the surroundings of this site is similar for the 2011-2020 records and is about 0.19. For satellite images from 2021, the range of extreme values, as well as the variation expressed by the interquartile range, is smaller than that recorded in earlier years. A significantly higher NDVI value was observed during this period at site LYR 06 (LYR07), which is located at a lower altitude. At this site, NDVI exceeded 0.3 in most analyzed satellite scenes in both July and August. However, a low value for this index was observed in July 2013.

For the Longyearbyen area, we obtained satellite imagery from July and August, for 2020 and 2021 only. However, as observed at the FOX sites, there are also substantial differences in NDVI between the upper and lower sites (Fig. 4). NDVI values at high elevation sites ranged from 0.0 to 1.5, and a slight increase is observed in 2021 compared to 2020 (Fig. 4). As shown in Figure 4, the lower-elevation sites exhibit not only higher not only higher NDVI values but also greater variability. At the LYR01 site and its surroundings in July 2020, average NDVI values remained negative. NDVI at the site and in its surroundings became positive only in late August of that year. Values close to 0.5 were recorded. The images recorded in 2021 were from late July and mid-

August. The average values of the NDVI index were in the range of 0.4-0.5. At site LYR08, located at a similar elevation, average NDVI values ranged from 0.3-0.5.

4.4. Variability of soil moisture and ground temperature

Significant variability in soil moisture and topoclimatic conditions across morphologically and altitudinally diverse research sites can markedly influence tundra plant growth and, consequently, NDVI. Detailed measurements at six research sites revealed a clear relationship between temperature variation and altitude. They provided important information on soil moisture variation, which is crucial in areas with permafrost and the appearance of drought stress in the second phase of the growing season. This variability in soil moisture and temperature is well represented by two measurement sites FOX04 and LYR01, which are considered typical within the measurement network established in 2022. Figure 5 shows the results of continuous monitoring of soil moisture and temperature at the analysed sites. Annual soil moisture variability is similar across all sites, with a stable winter minimum followed by a sharp increase in early summer (first half of June). The winter minimum corresponds to the frozen state of the ground and is 10 – 18 % at FOX04 and 5 – 19% at LYR01. Soil moisture increases rapidly during the initial phase of snowmelt, while the ground remains frozen, preventing deep infiltration. In 2023, soil moisture at site FOX04 peaked at 40% in the second half of June, while at site LYR01, located at a lower elevation, it reached 70% during the same period, although the increase in soil water content started much earlier (Fig. 5). These maximum values are representative of near-surface porosity. At the lower site, soil moisture exceeded 50% from June 10 to early July, whereas at the upper site, the period of maximum water saturation—linked to snowmelt—was much shorter, lasting about one week. The measured variable period in summer corresponds to a snow-free and frost-free state, which allows coupling between precipitation and soil moisture. At the upper site, soil moisture fluctuates significantly (15–40%), indicating a rapid response to precipitation due to a relatively shallow active permafrost layer. At the lower site, soil moisture rapidly declines to a range of 10–15%. This phenomenon is attributed to the rapid escape of water into the deeper parts of the active layer. Topoclimatic conditions also differ significantly between the analysed sites, directly influencing the length of the growing season (Fig. 5). In the lower site, the average annual air temperature in the observation year 2023 was -1.92°C, while at the upper site it was -4.83°C. During summer (June-August), the values were, respectively, 8.86 and 5.94°C. It is interesting to note the variation in ground temperature at a depth of 6 cm (Fig. 5). The average summer temperature at the lower site is slightly lower, at 4.34°C, compared to 5.35°C at the upper site.

5. Discussion

5.1. Heterogeneous growth of polar willow at spatial scales

Earlier works rather indicated the consistency of the dendrochronological curves across Svalbard (Le Moullec et al., 2020), leaving aside the impact of differences in habitat conditions, especially microclimatic conditions related to altitude, that can strongly influence the embedded climatic signal. However, our findings reveal substantial site-level variability in *Salix polaris* growth. At lower elevations, rapid snowmelt and warm early-summer temperatures foster ring formation, yet well-drained valley soils can induce seasonal drought stress that constrains overall productivity. Water deficit in July causes precipitation to be the limiting factor in summer growth. Owczarek et al. (2021) also noted that water deficit in July makes precipitation the limiting factor for summer growth in their analysis of polar willow growth on Bear Island. In contrast, higher-elevation sites display a delayed but positive response to rising mid-to-late summer temperatures, underpinned by permafrost layers that retain moisture and mitigate water deficits (; Hansen et al., 2014). These observations align with studies emphasizing the importance of summer warmth for

Arctic shrub growth (Forbes et al., 2010; Beil et al., 2015; Büntgen et al., 2015; Weijers et al., 2017). The results emphasized the importance of microtopography in dwarf shrub growth, as already indicated in preliminary studies conducted in the southern Spitsbergen (Owczarek and Opała, 2016; Opala-Owczarek et al., 2018).

Observed changes in the limiting factors for shrub growth are important in assessing and predicting the process referred to as greening or browning of the tundra. Extreme winter warming and rain-on-snow (ROS) events can damage tundra vegetation and contribute to localized "browning" (Phoenix and Bjerke, 2016; Bjerke et al., 2017). Such events impede oxygen diffusion, cause mechanical shoot breakage, and reduce annual ring formation (Bokhorst et al., 2011; AMAP, 2017). In contrast, widespread "greening" has been documented throughout the Arctic in response to extended growing seasons and warmer summers (Karlsen et al., 2024). Svalbard in particular shows notable increases in shrub coverage tied to rising annual soil temperatures and improved summer moisture conditions (Berner et al., 2020; Myers-Smith et al., 2020). These dual processes underscore the complexity of Arctic vegetation responses: while warming generally enhances plant productivity, short-term winter disturbances can trigger browning episodes with lasting local effects (Bokhorst et al., 2012; Phoenix and Bjerke, 2016). However, it should be noted that observed drought stress in low elevation sites, not previously recorded in central Spitsbergen, suggests that the greening process may weaken in the future. Ongoing warming in the Arctic has led to both extended growing seasons and more frequent drought events (Migała et al., 2024). At lower elevations, rapid soil drainage heightens moisture deficits, which may intensify browning trends and ultimately restrict the expansion of *S. polaris*. Conversely, higher elevations receive more precipitation, and permafrost layers help maintain soil moisture, resulting in comparatively stable growth (Callaghan and Jonasson, 1995; Migała et al., 2014). Nevertheless, negative trends in SPEI signals progressive drying in certain parts of Svalbard (Migała et al., 2024), and the frequency of ROS events is projected to rise (Bintanja and Andry, 2017).

In the Longyearbyen area, NDVI Index from 2020 and 2021 revealed earlier and more pronounced "green-up" at lower-elevation sites, whereas higher-elevation sites remained less productive overall but still showed small year-to-year gains. Notably, LYR01 displayed negative NDVI in early July 2020 before increasing to moderate values (~0.5) by late August, highlighting rapid phenological shifts within a single season. These findings resonate with previous greening trends reported for Svalbard (Karlsen et al., 2024) but also confirm that local factors—topography, soil moisture, and snowmelt timing—can drive significant variation in productivity (Macias-Fauria et al., 2012; Raynolds et al., 2014).

5.2. Problems in assessing dominant growth factors of dwarf shrubs across the Arctic

The Arctic environment is characterized by a very high degree of microtopographical and microclimatic diversity, as well as variations in the physico-chemical characteristics of the topsoil and its hydrological conditions. The identification of only one growth factor in different parts of the Arctic, even in a relatively small Arctic archipelago such as Svalbard, therefore raises many concerns.

In our study, *S. polaris* growth in Central Spitsbergen does not adhere to a single, uniform trajectory; instead, it arises from the multifaceted interplay of climatic, edaphic, and geomorphological variables. At lower elevations, higher nutrient availability and relatively warm early summers generally stimulate rapid growth. Under varying topoclimatic conditions, soil composition emerges as one of the fundamental drivers. Topsoils occurring in lower elevations showed higher mean concentrations of exchangeable Ca^{2+}, Mg^{2+}, K^{+}, Na^{+}, and H^{+} in comparison with the topsoils found on the plateaus, which is relevant to the growth rate of dwarf shrubs.

Moreover, the physical properties of the soil, such as a higher content of fine particles, may favour the growth of *S. Polaris* in lower-elevation sites. Higher organic matter, enriched base cations, and finer textures retain moisture for a longer portion of the growing season, supporting more vigorous *S. polaris* populations (Convey et al., 2018; Sannel, 2020; Du et al., 2022). By contrast, plateau soils often exhibit greater acidity and are strewn with rock fragments, which accelerate water drainage and deplete nutrients.

These patterns align with the findings of Owczarek et al. (2013), who highlighted the significance of geomorphological processes in shaping soil and vegetation structures across Svalbard. Additionally, the vegetation itself can alter topsoil temperatures, creating microfeedbacks that preserve or reduce soil water content (Szymański et al., 2022b). Small but significant differences in soil chemistry—particularly in exchangeable acidity—can thus translate into major contrasts in *S. polaris* root and shoot development.

Elements that make it difficult to identify the main factor influencing dwarf shrub growth include winter weather disturbances and extreme precipitation and temperature events, which occur more frequently in the Arctic. Winter processes also exert significant control over *S. polaris* performance. Frequent ROS episodes can form ice sheaths that physically damage stems and restrict root-zone oxygen, diminishing annual ring widths. Intermittent thaw-freeze cycles—particularly at mid- and high-elevation sites with inconsistent snow cover, add to these stresses by hindering resource mobilization (Owczarek and Opała, 2016). Our observations indicate that the timing and length of these winter stressors differ considerably among sites, intensifying the contrast in early-season growth between elevations.

Similar winter-driven impacts have been documented across the Arctic (Forchhammer, 2017), suggesting that they may become more influential as climate change induces milder winters.

Although a well-developed snowpack can insulate plants (Hallinger et al., 2010;), it also risks delaying melt-out and shortening the effective growing season (Schmidt et al., 2006;). In the present study area, variations in snow depth, precipitation type, and ice formation interact with site-level properties—such as slope aspect and soil drainage—to produce local pockets of success or failure for *S. polaris*. These patterns underscore that winter conditions can be as critical as summer warmth in shaping Arctic shrub growth trajectories.

The length of the vegetation period emerges as a central factor in explaining spatial growth disparities. Based on the data obtained from soil temperature sensors mounted at different altitudes, we found a marked difference in the number of positive-degree days. Earlier snowmelt at lower elevations prolongs photosynthetic activity, contributing to thicker ring increments (Hudson and Henry, 2009; Hudson et al., 2011). Higher-elevation sites, however, are confined to a shorter growing window, with late snowmelt and cooler microclimates limiting the duration of active development.

These observations are in line with broader Arctic studies attributing earlier greening to rising temperatures and diminishing sea ice (Forbes et al., 2010; Macias-Fauria et al., 2012; Karlsen et al., 2024). Yet, pronounced site-specific NDVI fluctuations also highlight the role of local parameters—surface water, snow cover, and soil characteristics—in causing abrupt shifts between “greening” and “browning” even over short distances (Kirpotin et al., 2009; Moskalenko, 2013). Employing high-resolution imagery (Miles and Esau, 2016) was key to detecting these subtle differences, reinforcing that *S. polaris* responses to climate warming are shaped by a suite of factors operating from micro- to landscape- scale. However, further comprehensive studies are necessary, including ground-level studies coupled with satellite-derived data. Our research has shown the influence of various factors on the growth of polar willow. This growth is heterogeneous and combining dendrochronological data in pan-Arctic or even just regional transects should be very careful.

6. Conclusion

It was pointed out that the growth of dwarf shrubs like *Salix polaris* is not only the effect of the temperature variation of one summer month. Instead, it is significantly affected by local microhabitat conditions, which are in turn shaped by changing thermal and moisture regimes, including those that occur during the preceding winter dormancy period. In a morphologically diverse area in Central Spitsbergen, we found two distinct shrub growth trends. At low altitudes, drought stress appeared to be the limiting factor, and in late summer, precipitation playing a key role. This was in contrast to the higher altitude sites, where the main factor responsible for growth was summer temperature.

This multifaceted interplay became evident: early-summer warmth does drive ring formation, but factors such as soil drainage, snowmelt timing, and rain-on-snow (ROS) events during winter exert equally important influences on subsequent dwarf shrub performance. Consequently, the complex patterns of greening and browning observed across Arctic landscapes arise from a combination of favorable growing-season conditions and episodic stressors, including soil water deficits, ice encasement, and freeze–thaw cycles.

Overall, our study underscores that local microhabitat conditions are crucial for understanding *Salix polaris* growth in a warming Arctic. Its growth is driven by a complex interplay of temperature, soil composition, moisture balance, geomorphology, and winter microclimatic extremes, so focusing on a single factor may overlook key interactions. Future research should integrate longer-term data, broader geographic sampling, and advanced remote sensing techniques to better predict vegetation patterns and ecosystem resilience, thereby enhancing our understanding of how changing environmental factors drive spatially variable growth responses in *Salix polaris* and offering clearer insights into the future of Arctic landscapes.

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Captions:

Fig. 1. (A) Location of the study sites in Central Spitsbergen (Svalbard Archipelago), (B) typical plateau surface at the elevation 450 - 500 m a.s.l. covered with coarse-grained weathered material (FOX04 site), (C) wide Advent valley floor with flat alluvial-deluvial cones in its marginal zones (FOX06 site).

Fig. 2. (A) *Salix polaris* colony with dark green leaves, growing on a deluvial cone in the Advent valley, (B) complete individual of *Salix polaris*, including root system, root collar and wooden

branches collected for laboratory analyses, (C) microscopic cross-section of *Salix polaris* with distinct growth rings boundaries marked by cell rows.

Fig. 3. (A) Growth-ring chronology of *Salix polaris* growing at high and low elevation sites and correlation and response function analysis with climate data, (B) air temperature and precipitation in 2006 and 2014, when a negative year was commonly marked in *Salix polaris* growth pattern

Fig. 4. NDVI index in 10m-buffer around research sites located at high and low elevations.

Fig. 5. Temporal evolution of the measured soil moisture and ground and air temperature at two research sites located in high and low elevations.

Table. 1. Main characteristics of research sites and texture and basic chemical properties of the studied topsoils.

Site code		Elevation (m a.s.l.)	Aspect and main geomorphic characteristics	Rock fragments	Sand	Silt	Clay	Soil texture*	pH	SOC[a]	TN[b]	C/N
				(%)					(H_2O)	(%)		
LYR01	Low elevation sites	67	E-SE distal part of flat alluvial cone	30	49	44	7	Loam	5.71	2.58	0.17	16
LYR08		76	W-NW distal part of flat alluvial cone	30	42	47	11	Loam	6.56	2.65	0.17	15
FOX06		75	N distal part of flat alluvialslope	5	45	49	6	Sandy loam	6.26	5.36	0.42	13
			Mean	**22**	**45**	**47**	**8**		**6.18**	**3.53**	**0.25**	**15**
LYR03	High elevation sites	418	Flat plateau covered by coarse-grained weathered material	60	65	29	6	Sandy loam	5.87	1.63	0.17	10
LYR04		459	Flat plateau with distinct patterned ground	40	46	43	11	Loam	5.92	0.58	0.07	8
FOX04		451	N flattened slope covered by coarse-grained material and solifluction lobes	50	58	36	6	Sandy loam	5.87	1.13	0.12	9
			Mean	**50**	**56**	**36**	**8**		**5.89**	**1.11**	**0.12**	**9**

* - according to U.S. Department of Agriculture

a - soil organic carbon

b - total nitrogen

Table. 2. Chemical composition of the studied topsoils.

Site code	SiO_2	Al_2O_3	Fe_2O_3	MgO	CaO	Na_2O	K_2O	TiO_2	P_2O_5	MnO
					(%)					
LYR01	66.55	12.50	5.34	0.74	0.52	1.65	2.66	0.68	0.14	0.04
LYR08	62.51	14.24	6.80	1.06	0.48	1.56	2.48	0.80	0.16	0.05
FOX06	54.18	15.08	6.52	1.35	0.96	1.44	2.48	0.80	0.22	0.06
Mean	**61.08**	**13.94**	**6.22**	**1.05**	**0.65**	**1.55**	**2.54**	**0.76**	**0.17**	**0.05**
LYR03	69.75	11.30	5.99	0.73	0.31	1.45	2.39	0.58	0.16	0.05
LYR04	75.99	10.11	4.58	0.60	0.22	1.46	2.19	0.59	0.09	0.05
FOX04	75.85	9.65	4.16	0.57	0.31	1.37	2.10	0.62	0.11	0.04
Mean	**73.86**	**10.35**	**4.91**	**0.63**	**0.28**	**1.43**	**2.23**	**0.60**	**0.12**	**0.05**

Table 3. Exchangeable cations, exchangeable acidity (H), cation exchange capacity (CEC), base saturation (BS) as well as plant available potassium (Kav), magnesium (Mgav), and phosphorus (Pav) in the studied topsoils.

Sample	Ca^{2+}	Mg^{2+}	K^+	Na^+	H^+	Al^{3+}	H	CEC	BS	Kav	Mgav	Pav
				(cmol kg^{-1})					(%)		(mg 100 g^{-1})	
LYR01	6.99	2.01	0.20	0.12	0.26	0.05	0.31	9.63	96.78	7.71	38.91	0.44
LYR08	7.85	2.48	0.18	0.07	0.09	0.00	0.09	10.67	99.16	6.14	46.25	0.38
FOX06	15.25	3.41	0.22	0.17	0.18	0.00	0.18	19.23	99.06	8.07	60.67	0.94
Mean	**10.03**	**2.63**	**0.20**	**0.12**	**0.18**	**0.02**	**0.19**	**13.18**	**98.33**	**7.31**	**48.61**	**0.59**
LYR03	3.30	1.83	0.18	0.08	0.13	1.27	1.40	6.79	79.38	5.52	38.32	0.06
LYR04	2.32	1.22	0.09	0.07	0.13	1.36	1.49	5.19	71.29	2.50	26.72	1.32
FOX04	3.74	1.54	0.14	0.05	0.18	0.13	0.31	5.78	94.64	5.55	31.59	0.87
Mean	**3.12**	**1.53**	**0.14**	**0.07**	**0.15**	**0.92**	**1.07**	**5.92**	**81.77**	**4.52**	**32.21**	**0.75**

Table. 4. Growth-ring chronology statistics.

Site code	Site information	Time span (AD)	Maximum/Mean age	Number of series/included in chronology	Mean correlation with master chronology	Mean sensitivity	Mean growth ring width (µm)	Maximum growth ring width (µm)	Problems
LYR01	Low elevation sites - mesic tundra community	1989-2022	43/26	27/13	.527	.391	110.1	463.3	-
LYR08		1992-2022	31/24	28/18	.543	.520	103.9	398.0	Missing rings, especially in 2011
FOX06		1989-2022	34/22	25/14	.413	0.333	115.3	595.0	Incomplete sequences, possibly due to dead or partially dead individuals (grazing?)
LYR03	High elevation sites - exposed ridges community	1988-2022	35/25	30/20	.549	.545	81.2	225.5	Missing rings, especially in 2015
LYR04				15/0					Wood material in very poor condition, rapid decomposition without the ability to make microscopic cross-sections. Lack of main shoots, a large number of small and thin roots and wooden shoots
FOX04		1983-2022	40/24	32/14	.546	0.467	73.5	319.34	Missing rings due to extreme growth conditions

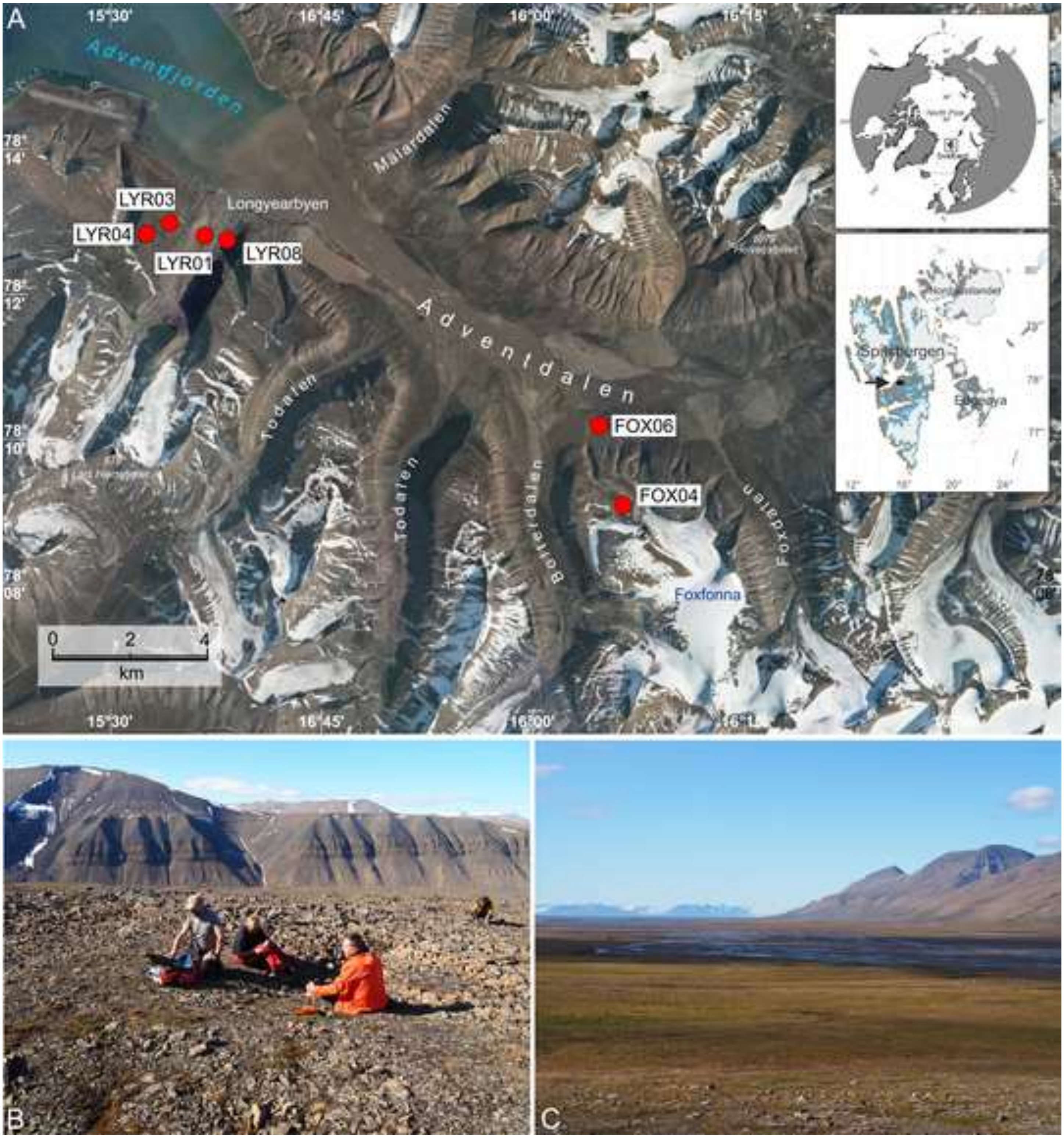
A
15°30'
16°45'
16°00'
16°15'
Adventfjorden
Longyearbyen
LYR03
LYR04
LYR01
LYR08
Mälardalen
Adventdalen
Todalen
Bolterdalen
Foxdalen
FOX06
FOX04
Foxfonna
78° 14'
78° 12'
78° 10'
78° 08'
0
2
4
km
Spitsbergen
Nordaustlandet
Edgeøya
B
C

Figure 2

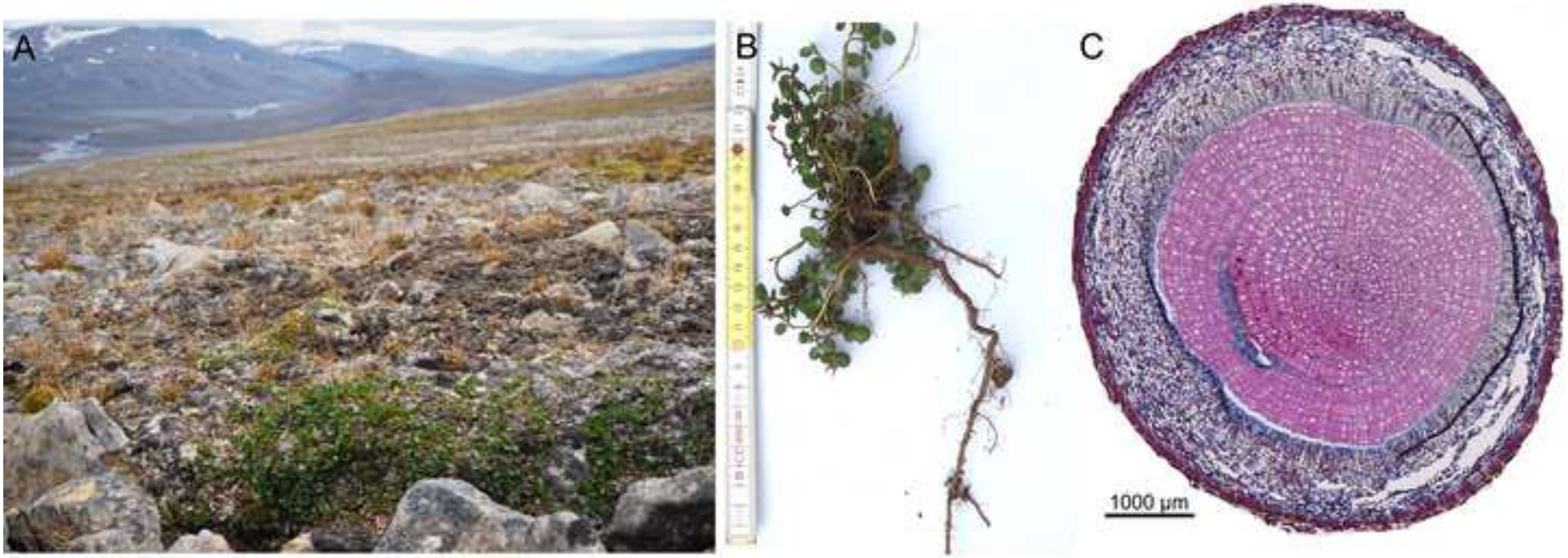

Figure 3

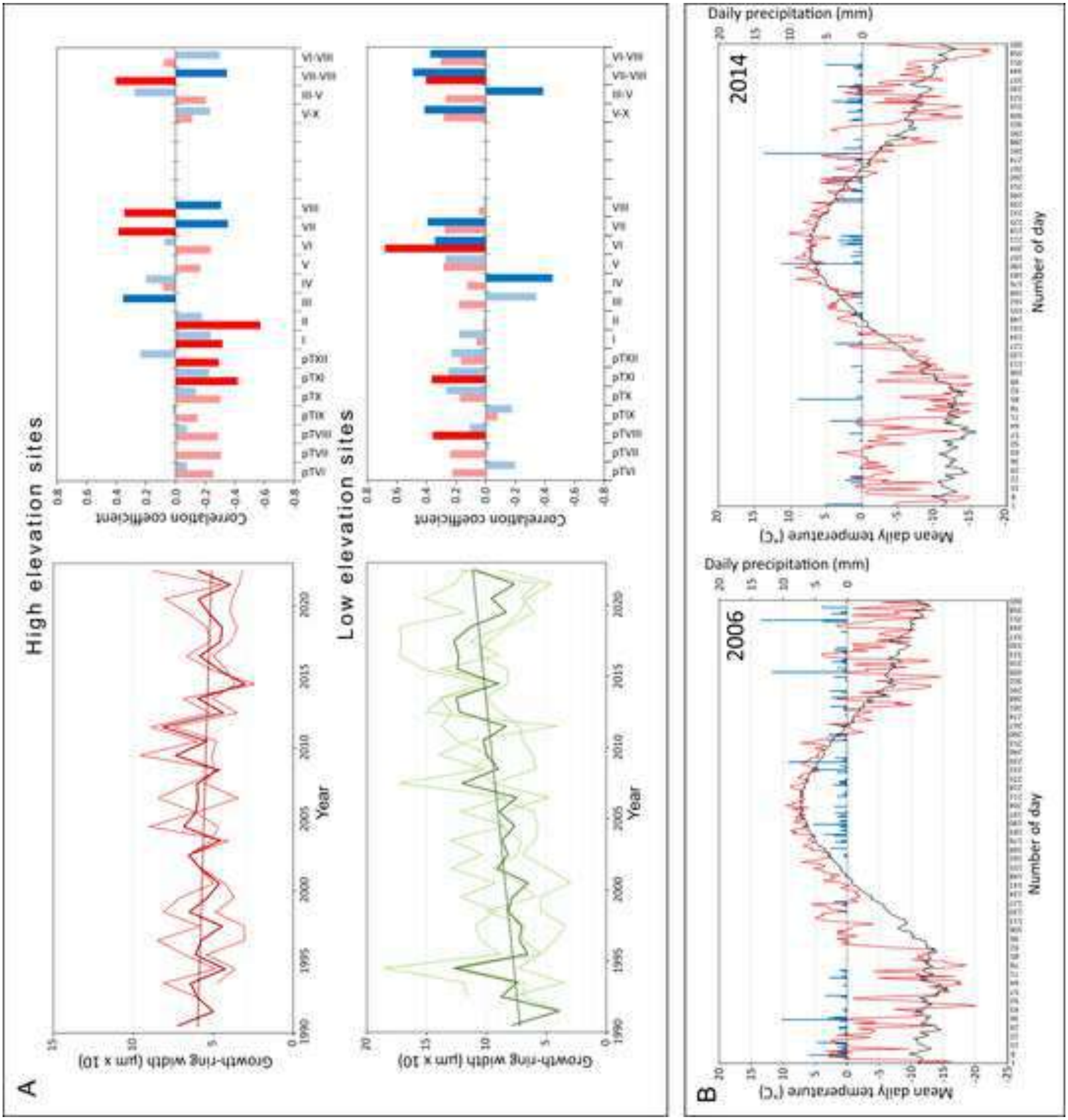
A
High elevation sites
Low elevation sites
Growth-ring width (µm x 10)
Year
1990
1995
2000
2005
2010
2015
2020
Correlation coefficient
pTVI
pTVII
pTVIII
pTIX
pTX
pTXI
pTXII
I
II
III
IV
V
VI
VII
VIII
V-X
III-V
VII-VIII
VI-VIII
B
2006
2014
Mean daily temperature (°C)
Daily precipitation (mm)
Number of day

Figure 4

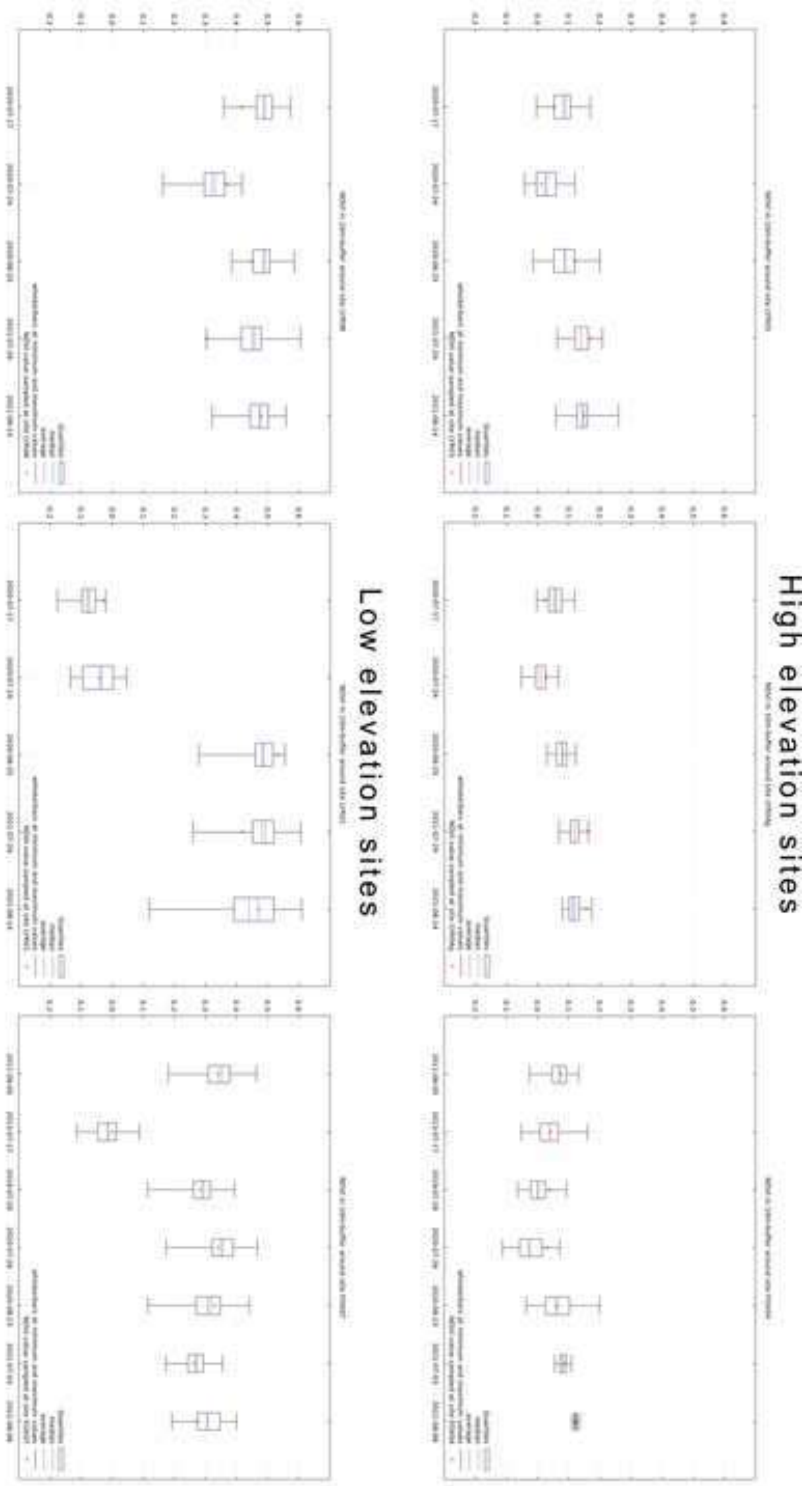

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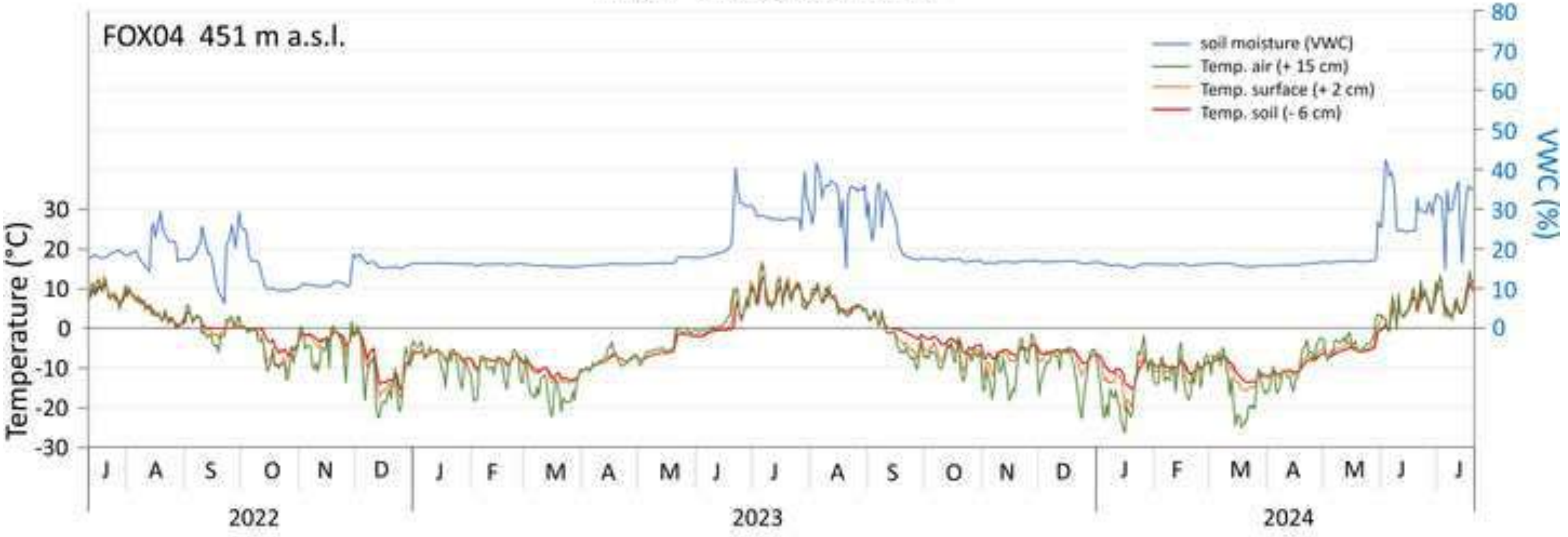
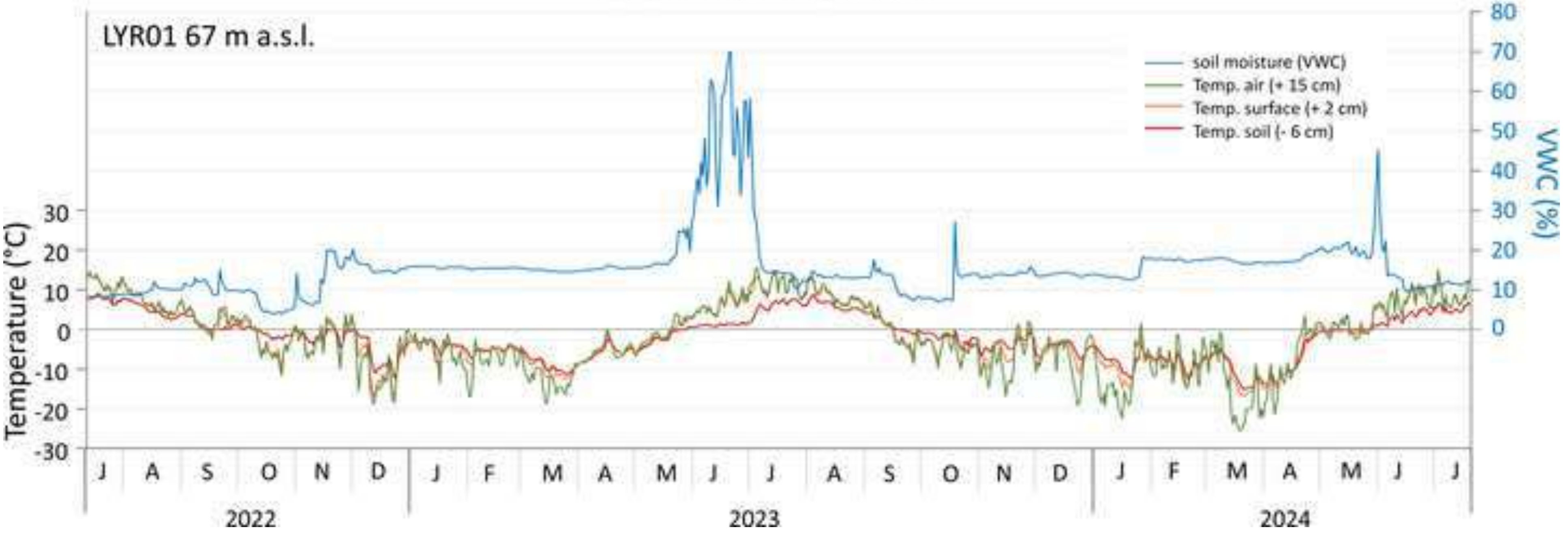
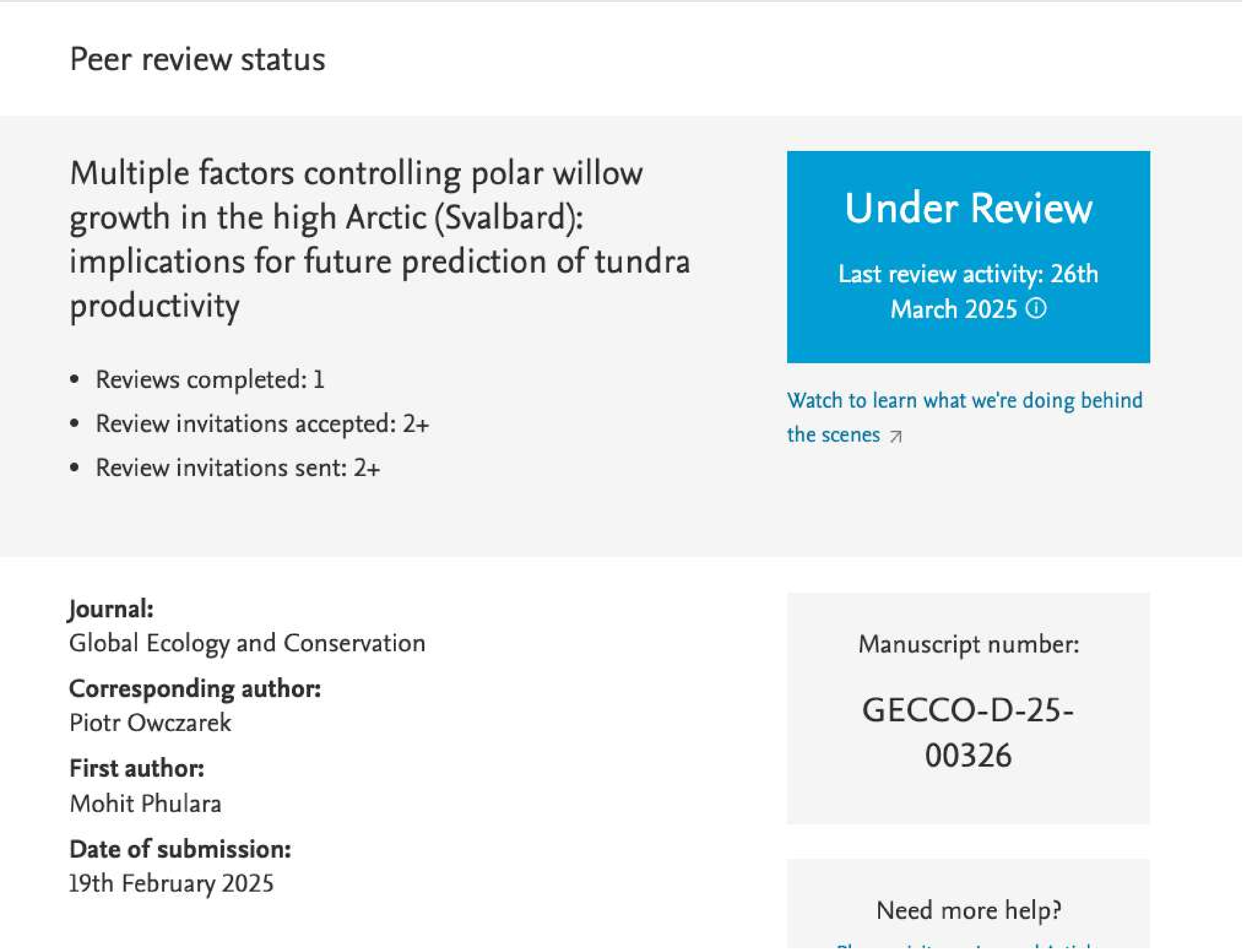
Figure 5

High elevation site



Low elevation site





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Multiple factors controlling polar willow growth in the high Arctic (Svalbard): implications for future prediction of tundra productivity

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Article IV

Varied Growth Response of High Alpine Rhododendron myrtifolium and Forest Zone Tree Species to Climate Warming in the Eastern Carpathians, Ukraine

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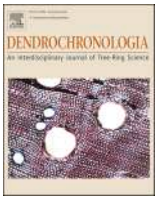

Varied growth response of high alpine *Rhododendron myrtifolium* and forest zone tree species to climate warming in the Eastern Carpathians, Ukraine

Piotr Owczarek [a], Mohit Phulara [b], Pavlo Shuber [c], Bartosz Korabiewski [a], Marek Błaś [a], Magdalena Opała-Owczarek [b],*

[a] *Institute of Geography and Regional Development, University of Wroclaw, Wroclaw, Poland*
[b] *Institute of Earth Sciences, Faculty of Natural Sciences, University of Silesia in Katowice, Sosnowiec, Poland*
[c] *Faculty of Geography, Ivan Franko National University of Lviv, Lviv, Ukraine*

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ABSTRACT

Plants growing along altitudinal transects in alpine and mountainous areas respond differently to climatic conditions. The present study is centred on the unique and ecologically significant species, *Rhododendron myrtifolium* Schott & Kotschy, an evergreen clump-forming or prostrate dwarf shrub. This high-mountain endemic plant grows at several localities in isolated massifs of the Eastern Carpathians, but the greatest numbers of sites can be found in the subalpine and alpine belts of the Chornohora range. The main objectives of this study were (1) to assess the dendrochronological potential of *Rhododendron myrtifolium* as a new species in dendrochronological research and (2) to compare the growth response of *R. myrtifolium* (sampling elevation: 1800–1950 m a.s.l.) with *Picea abies* Karst. (1350–1500 m a.s.l.) and *Abies alba* Mill. (950–1050 m a.s.l.) collected from the upper and lower forest belts. Tree-ring material from 97 trees and shrubs enabled the construction of three site chronologies from sites located within the altitudinal transect. The longest chronology, covering the previous 184 years, was developed for fir. The chronology for the rhododendron was the shortest at 66 years. This species is the most sensitive of the three species analysed. The highest positive r-value (r=0.71) was obtained between the rhododendron chronology and the warm-season temperature (from March to July). Also, the growth of this species was significantly positively correlated with the summer temperature (r=0.50). In contrast, fir and spruce demonstrated a similar inverse relationship with August temperatures.

1. Introduction

The altitudinal distribution of plant species demonstrates a clear relationship between climate, plant growth and the distribution pattern of vegetation. Temperature, precipitation and other climate variables are key determinants of plant growth through diverse direct and indirect mechanisms (Viner et al., 2006). In alpine and mountainous areas, plants growing along altitudinal transects respond differently to climatic conditions depending on altitude. While this is mainly related to climatic variables, other environmental components such as morphological factors, gravitational disturbances and human activities can create a challenging ecological landscape (Kharal et al., 2017; Körner, 2003; Oberhuber et al., 2020; Schweingruber, 1996; Opała-Owczarek et al., 2018, 2023). Nowadays, rapid climate change is bringing about significant transformations of forest and alpine ecosystems (Büntgen et al., 2015; Dawes et al., 2013). High-altitude forests and alpine communities, often regarded as temperature-limited environments, are experiencing a warming that is more rapid than the global average (Körner, 2012; Pepin et al., 2015). Consequently, plants growing at high elevations, and thus at the very edge of their natural distributions, are responding extremely sensitively to environmental change. For this reason, a proper understanding of the response of the various vegetation types in the different altitudinal zones is particularly important if we wish to understand this response to changes in the natural environment at the landscape level.

The Eastern Carpathian mountains in Ukraine provide a unique natural setting with diverse geomorphic features that categorize it into distinct ecological units with common lithological, structural and geomorphic characteristics, and also typical altitudinal vegetation patterns (Cheval et al., 2014, Melnyk, 1999, 2009). Dendrochronological research in the Ukrainian Carpathians has been conducted in two areas, the Chornohora and Gorgany mountain ranges, the focus being on spruce and stone pine trees. The dendrochronological analyses span the

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* Corresponding author.
E-mail address: magdalena.opala@us.edu.pl (M. Opała-Owczarek).

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last c. 100–250 years. Kaczka and Büntgen (2006) tested a spruce tree-ring width chronology from Mt. Hoverla for spatial autocorrelation and climate sensitivity and reported a low but statistically significant correlation with mean June-July seasonal temperatures. Recently, the Chornohora range was also investigated for snow-avalanche activity on the basis of dendrochronological data (Decaulne et al., 2023). Growth dynamics (Holubchak et al., 2019), the influence of carbon-containing greenhouse gases on the dynamics of radial growth (Moroz et al., 2020) and the forest disturbance regime (Trotsiuk et al., 2014) were reconstructed on the basis of dendrochronological records from the Gorgany Mountains. To date, researchers have not yet investigated the dendroclimatological responses of plants above the treeline. In our opinion, this is the most important gap in the dendrochronological analysis of the Eastern Carpathians.

The great potential for research into shrub vegetation above the upper forest limit was highlighted by studies carried out in other mountain massifs in Europe (Bär et al., 2006; Francon et al., 2017; Carrer et al., 2019; Francon et al., 2020, 2021; Fontana et al., 2021) and Asia (Liang and Eckstein, 2009; Opała et al., 2013; Lu et al., 2015; Tiwari et al., 2017; Wang et al., 2023). The present study centres on the unique, endemic and ecologically significant species, *Rhododendron myrtifolium* Schott & Kotschy, an evergreen clump-forming or prostrate dwarf shrub that can grow to a height of 50 cm. Clonal spread takes place by the rooting and separation of creeping lateral branches (Sosnovsky et al., 2021). This species has a distinctive distribution encompassing the Eastern and Southern Carpathians, with scattered, isolated populations in the Northern Balkans (Garden 1980; Chamberlain et al., 1996; Cox and Cox 1997; Boratyński et al., 2006). The stronghold of *R. myrtifolium* in the Ukrainian Carpathians lies mainly in the subalpine Chornohora range, as first documented by Weigl (1888) and described by Środoń (1948). Today, the habitats of *R. myrtifolium* are under significant threat, primarily because of abiotic stresses and the shift of upper forest limits taking place in the Carpathians, a situation highlighted by Voloshchuk and Shumik (2012). *R. myrtifolium* has never been examined from the dendrochronological point of view, although several studies have addressed the taxonomy, morphology, ecology and leaf architecture of this plant (Hayes et al., 1951, Cox and Cox 1997, Boratyński et al., 2016, Voloschuk and Prokopiv 2011, Sosnovsky et al., 2017, 2021). The radial growth of high-elevation *Rhododendron* taxa, examined in other subalpine mountain areas, is highly responsive to annual and seasonal temperature changes and notably sensitive to other climate variables. Thus, these evergreen alpine shrubs, which can live for more than a century, have frequently been used to examine long-term climate-growth relationships (Dhyani et al., 2023; Francon et al., 2017; Francon et al., 2020; Francon et al., 2021; Panthi et al., 2021; Piccinelli et al., 2023). Our research aimed to provide a comprehensive assessment of the current state of this remarkable species growing in the subalpine zone of the Ukrainian Carpathians and to contribute to the collective efforts for its conservation and sustainable management. As indicated above, the ecophysiological characteristics of *R. myrtifolium* and its responses to environmental impacts remain largely unexplored. We consider that it offers a unique opportunity to expand the present dendrochronological network into extreme environments beyond the survival limit of trees. However, a comprehensive understanding of the climatic response of this species can only be gained by analysing the responses of other species growing along the same altitudinal transect. We therefore addressed the following research questions: (1) Can data from *Rhododendron myrtifolium* growing in the highest altitude range in the Eastern Carpathians be used for dendrochronological analyses? If so, (2) are contemporary climate changes being reflected in its growth-ring widths? (3) Is there a convergence in growth and climatic responses between the lower forest belt (*Abies alba* Mill.), the upper forest belt (*Picea abies* Kars.) and the subalpine and alpine belt (*Rhododendron myrtyfolium*)?

2. Materials and methods

2.1. Study area

The study area is located in the Eastern Carpathians (Fig. 1A,B). This part of the Carpathian arc lies mainly in eastern Ukraine. These mountains run from north-west to south-east and feature an asymmetric relief. Chornohora is one of the main ranges of the Eastern Carpathians. Culminating at more than 2000 m a.s.l., it is the highest Carpathian range built of Cretaceous – Paleogene flysch formations (Rogoziński and Krobicki, 2006, Karabiniuk et al., 2022). The main ridge of Chornohora is more than 40 km long. The highest peak is Hoverla (2061 m a.s.l.) (Fig. 1C), which rises more than 1000 m above the surrounding valley bottoms of the River Prut to the east and the Rivers White and Black Tisza to the west. The north-eastern slopes of the ridges tend to be steeper owing to their distinctive geological structure and the influence of Pleistocene glaciations (Matoshko, 2004; Kłapyta, 2008; Kłapyta et al., 2021). The northeastern slopes often feature glacial cirques with steep walls and rocky outcrops, in contrast to the southwestern slopes, which were unaffected by glaciers and present a gentler terrain (Kłapyta et al., 2021). Pleistocene glaciation forms with deep valleys cutting through the asymmetric slopes of the massif are one of the most characteristic aspects of the relief of this part of the Carpathians (Fig. 1B,C).

The climate of Chornohora is influenced mainly by the western atmospheric circulation. It has continental features and varies according to the elevation above sea level. The temperature of the coldest month of February ranges from - 8°C at altitudes of 450–850 m a.s.l. to - 12°C at 1500–2000 m a.s.l., July temperatures range from +14°C to +7°C, respectively, and the annual precipitation at these altitudes is from 900 mm to 2000 mm, respectively (Miller, 1963; Melnyk, 1999). Since the 1980 s, temperatures have been increasing by about 0.5°C/decade (Pozhyzhevs'ka Meteorological Station, 1451 m a.s.l.) (Fig. 2), a rise that has been even more pronounced during the summer seasons JJA (0.74°C/decade). Simultaneously, summer precipitation JJA has been decreasing, from 516 mm (1961–1990 mean) to 438 mm (1991–2020 mean) (Fig. 2).

2.2. Woody material and sample collection

Vertical climatic differentiation has resulted in the development of vegetation belts (Melnyk, 1999, 2009) (Fig. 1C): (1) the lower forest - from 500 to 1200 m a.s.l. - with beech forests, and admixtures of fir and sycamore; (2) the upper forest - from 1200 to 1550 m a.s.l. - with spruce forests; (3) the subalpine belt - from 1550 to 1850 m a.s.l. - with dwarf pine and black alder thickets; (4) the alpine belt - from 1850 to 2061 m a.s.l. - with alpine meadows (Polonyna - a local geographic term used in the Eastern Carpathians to describe areas of montane meadows) and rhododendron patches. Although the human impact on the environment at present is insignificant (Melnyk, 2009; Szponar et al., 2011), there has been intensive deforestation of the area in the past, leading to significant loss of trees from the upper and lower forest belts. The beech forest has been largely replaced by spruce monocultures, whereas in the upper forest, spruce is often second-growth and has survived in its natural state in only a few places.

Samples were collected from different vegetation belts. In 2019, 30 cores were collected from fir trees (*Abies alba* Mill.) (ABAL) in the lower forest belt in the Prut valley, at altitudes from 950 to 1050 m a.s.l. During two field campaigns in 2015 and 2019, 40 spruce (*Picea abies* Karst.) (PCAB) cores were collected from the Maryshevska ridge at 1350 – 1450 m a.s.l. The most important aspect of our field research was the sampling of the Eastern Carpathian rhododendron (*Rhododendron myrtifolium*) (RHMY) (Fig. 1D,E). There are a large number of localities of *R. myrtifolium* in the subalpine and alpine belts of Chornohora, mainly at altitudes between 1500 and 1900 m a.s.l., and reaching the highest elevation at 2030 m a.s.l. on Hoverla (Boratyński et al., 2006; Voloshchuk and Shumik, 2012). This plant often forms a community consisting

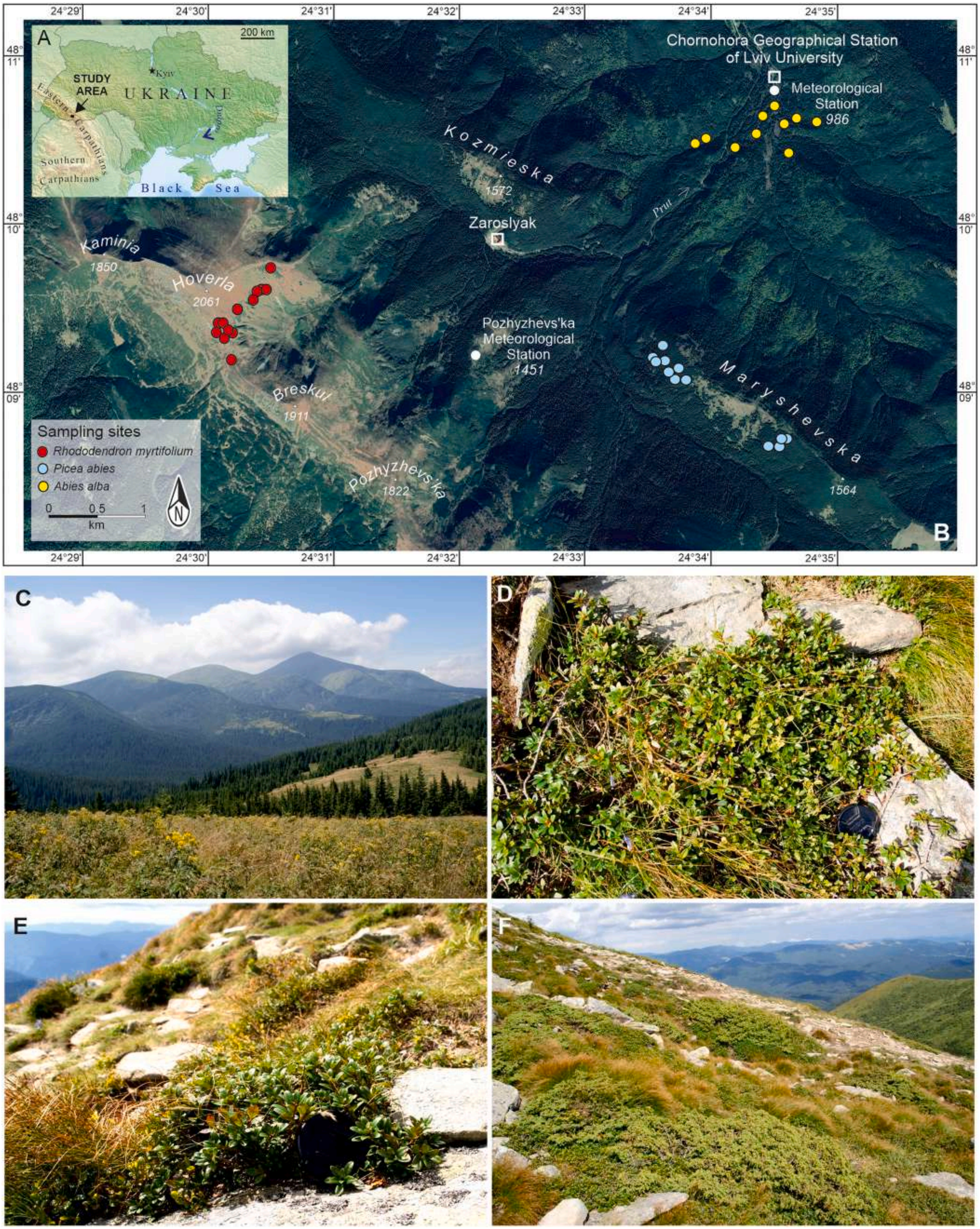

Fig. 1. (A) Location of the study area in the Eastern Carpathians in Ukraine, (B) Location of the sampling sites on the Chornohora ridge and in the upper Prut River valley (background map from Google Earth, 2023 CNS/Airbus/ Maxar Technologies, Retrieved November 4, 2023), (C) General view of the Hoverla massif (2061 m a.s.l.) from the Polonyna Maryshevska with the boundaries of the vegetation belts clearly distinguishable; in the foreground, the tree line in the transition to the subalpine zone, (D, E) Specimens of the evergreen prostrate dwarf shrub *Rhododendron myrtifolium* (Schott & Kotschy) growing at c. 1950 m a.s.l. on the south-eastern slopes of Hoverla, (F) Alpine plant communities dominated by *Juniperus communis* and *Rhododendron myrtifolium* in the high elevations of the Chornohora ridge.

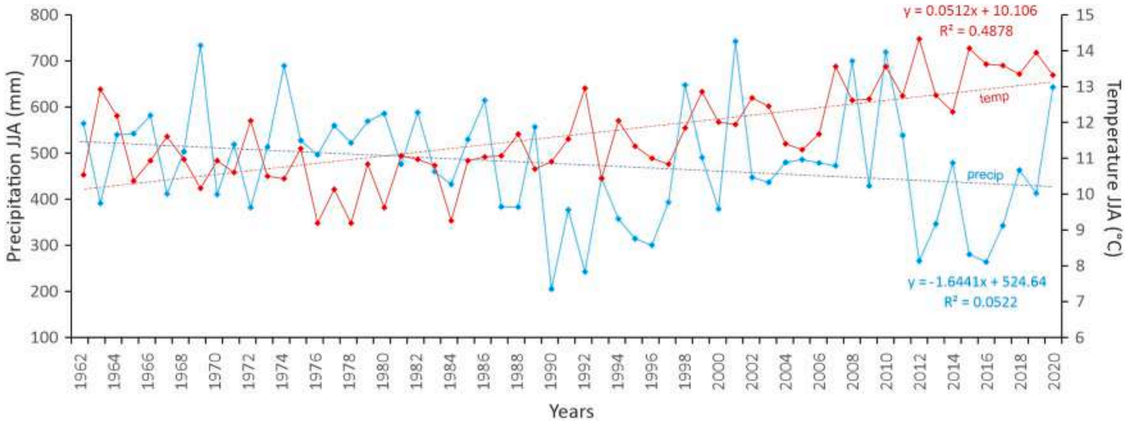

Fig. 2. Summer (JJA) average temperature and precipitation at the Pozhyzhevs'ka Meteorological Station, 1451 m a.s.l. for the period 1962 – 2020.

of other species from the *Ericaceae* family. However, especially on slopes with a southerly exposure, *Juniperus communis* L. growing alongside rhododendron patches is a distinct admixture in the transition zone between the subalpine and alpine zones (Fig. 1F). 35 specimens of *R. myrtifolium*, including roots and woody branches were collected in 2019 from the eastern and south-eastern slopes of Hoverla at altitudes of 1800–1950 m a.s.l.

2.3. *Sample processing*

This is the first time that the Eastern Carpathian rhododendron (*Rhododendron myrtifolium*), endemic to the Eastern Carpathians, has been used in dendrochronological studies (Căprar et al., 2014, Kliment et al., 2016). Whole specimens, including the root system and woody shoots, were taken for laboratory analysis. Two or three cross-sections (65 in total) were cut from each root and shoot. The samples were processed according to the dendrochronological protocol used for preparing wood samples with very small growth rates to measure the

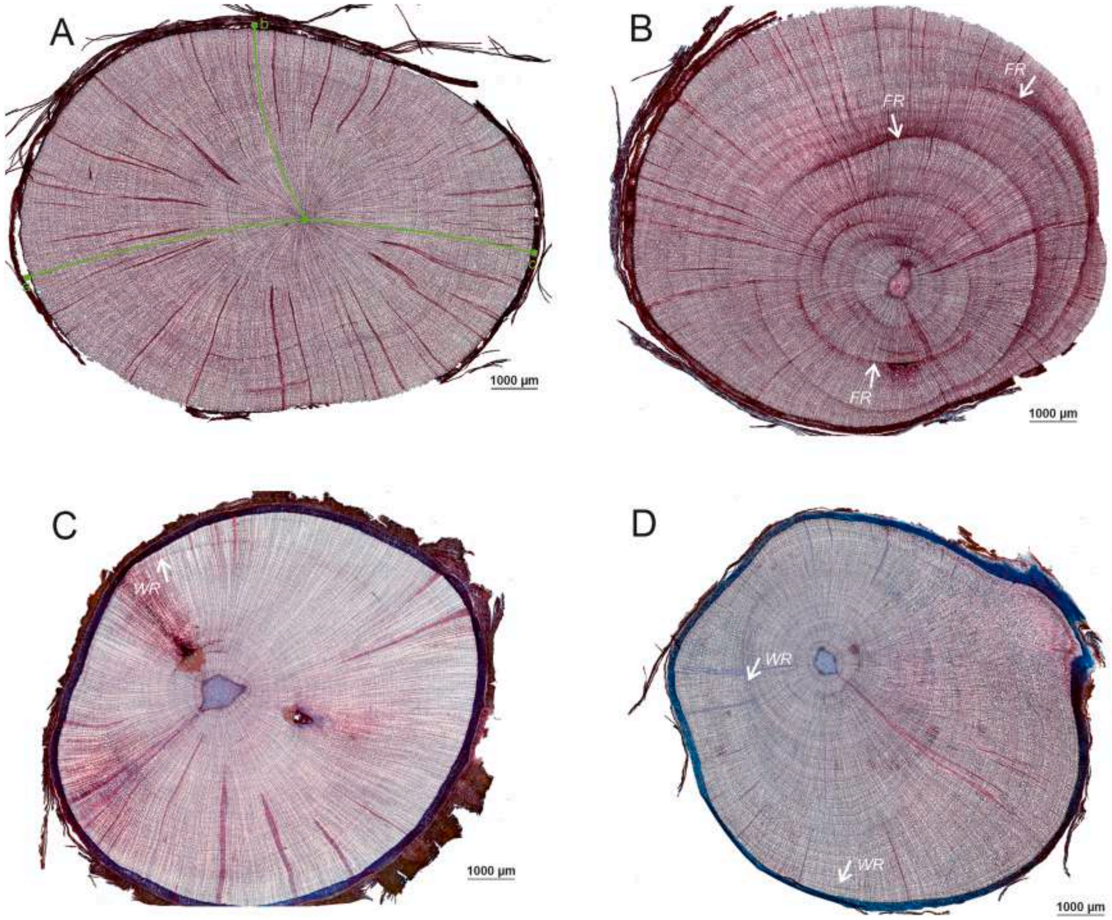

Fig. 3. Microscopic cross-sections of *R. myrtifolium* with distinct growth ring boundaries highlighted by more frequent vessels in the earlywood, (A) Cross-section of an *R. myrtifolium* root; note the measurement lines along the three radii, (B) Cross-section of *R. myrtifolium* branch with distinct frost rings (*FR*), (C, D) Cross sections of *R. myrtifolium* with distinct eccentricity and wedging rings (*WR*).

growth-ring widths (Bär et al., 2006; Gärtner and Schweingruber, 2013; Owczarek et al., 2013; Myers-Smith et al., 2015b). For each cross-section, we prepared a 20-μm thick micro-section using a GSL 1 sledge microtome (Gärtner et al., 2015) (Fig. 3 A,B,C,D). The micro-sections were stained with safranin (1% w/v in 70% v/v ethanol) and Astra blue (1% w/v in 100% ethanol) to highlight the ring boundaries and further permanently fixed with Canada balsam (Gärtner and Schweingruber, 2013). This process aimed to distinguish lignified and non-lignified tissues with particular focus on narrow and irregular ring boundaries. Digital photographs of the micro cross-sections were taken using a Leica DFC420C camera connected to a Leica DM4500B microscope. Subsequently, multiple images taken at 10× magnification were stitched together using PTGui software (New House Internet Services B. V., Rotterdam, NL) to create single high-resolution images for each cross-section. This step was vital for accurately identifying annual ring borders and measuring ring widths. A measuring track was determined, beginning from the pith and following the xylem rays towards the cambium. If there was cross-sectional irregularity and pronounced eccentricity, measurements were performed along multiple radii (Fig. 3A).

In addition, 30 cores were taken from fir trees and 40 cores from spruce trees using a Pressler borer. All the tree samples were processed using standard procedures: air drying, mounting the cores into wooden blocks and polishing the surfaces (Stokes, 1996). Next, the cores were scanned in a high-definition optical scanner (EPSON Perfection V700 Photo Scanner) with 2400 DPI optical resolution, and the annual ring widths (TRW) were measured using semi-automatic image-analysis software WinDendro (Regent Instruments Inc. 2006).

2.4. *Chronology building and climate-growth analysis*

Samples from a given site were cross-dated, the results being corroborated with COFECHA software (Grissino-Mayer, 2001). Finally, the master chronology was created as the average of the best-matched samples. The growth-ring width sequences of fir and spruce exhibited an age trend (decreasing trend), while the individual rhododendron series generally indicated an increasing trend, although a flat curve was present in a few samples. Raw chronologies were compared to give insights into shrub growth trends and its potential drivers. In contrast, we used residual chronologies for the dendroclimatic analyses. TRW series were standardized and transformed with ARSTAN software (Cook and Holmes, 1996). The ring-width data from both species were standardized using double-detrending process based on a negative exponential or linear regression, followed by a fitting of a cubic smoothing spline with a 50% frequency response at 32 years (Cook and Peters, 1981). The measured values were divided by the fitted curve values to obtain a standardized series. To compare *R. myrtifolium* shrub growth patterns with tree species, Pearson's correlations were calculated between all the chronologies.

Extreme years were identified on the basis of standard deviations of raw ring width chronologies of three species. Extreme years were defined as calendar years where TRW exceeded the ±1 standard deviation threshold. For the final analysis with climatic conditions, we used pointer years that overlapped between the species analysed. This was based on a visual comparison of positive and negative pointer years as described by Schweingruber (1988).

Meteorological data for 1961–2020 from the Pozhyzhevs′ka Meteorological Station, the nearest one to the study area, were used for the dendroclimatological analyses. Pearson's correlation analyses were used to explore the climate-growth relationships. A 95% confidence level criterion was applied to determine the statistical significance of the correlations. These analyses were examined for two climate variables – mean air temperature and monthly precipitation sums – for the 16 months from the June of the previous growth year to the September of the following growth year. Calculations were also made for individual months and seasons. Changes over time were analysed using moving correlation analysis in the yearly moving time intervals of a 25-year time window.

3. Results

3.1. *Growth-ring chronologies*

The tree-ring material from 97 trees and shrubs enabled the construction of three chronologies for sites located within the elevational transect from 950 to 1950 m (Table 1, Fig. 4, Fig. 5). The longest chronology, covering the previous 184 years, was developed for fir (Fig. 5C). The chronology for the rhododendron shrubs was the shortest with a length of 66 years (Fig. 5A). This species is characterized by the narrowest growth rings and the highest mean sensitivity of the three species investigated (Table 1). As the annual rings of *Rhododendron myrtifolium* are semi-ring-porous, the boundaries were well defined by relatively large vessels in the earlywood. Growth-ring widths in the samples ranged from relatively wide (250 μm) to extremely narrow (less than 20 μm). Owing to the low synchronicity within the samples, fifteen of these had to be rejected from further analysis. Microscopic analysis of *Rhododendron myrtifolium* showed that frost rings occurred infrequently (Fig. 3B), but that high percentages of wedging rings and growth eccentricity were common (Fig. 3C,D).

Analysis of the growth ring width time series revealed a convergence in growth within the forest belt species *Abies alba* and *Picea abies* (Fig. 4). This is confirmed by the high correlation coefficient between chronologies for trees (r=0.90). In contrast, the correlation between tree species and rhododendron chronologies is low (r=-0.44 and −0.46 for fir and spruce, respectively). For the subalpine *Rhododendron myrtifolium*, growth fluctuations in tandem with other species occurred only in certain periods and years, e.g. slow growth in 1970, 1984–1985, 1990, 2002, 2009–2010, 2014 and 2018, and rapid growth in 2000 and 2017 (Fig. 4). Common occurrence of pointer years for this three species were related to the occurrence of characteristic pattern of climatic conditions. The negative years can be divided into four groups: (1) the occurrence of very strong frost in May and September accompanied by the dry summer months (1970, 1981, 1990), (2) a normal year with very strong frost in April and September (2002), (3) cold winter and summer and dry August (1984–1985), (4) warmest winter (2014) or spring (2018) accompanied by dry August. Positive years were associated with relatively warm April-July and precipitation near multi-year average. Despite the occurrence of some coinciding years in growth patterns, the long-term courses of these chronologies exhibit opposing trends: downward for species from the forest belt and upward for sub-alpine zone species.

3.2. *Relationships between climate and tree-ring widths*

The highest positive r-value (r=0.71) was obtained between the rhododendron chronology and the warm-season temperature (March – July) (Fig. 6A). The growth of this species was significantly positively correlated with summer temperature (r=0.50), the highest monthly r-value being for August (r=0.65). For most months except March, there was no significant relationship for precipitation. A positive correlation with the March precipitation was found for fir (r=0.35) (Fig. 6C) and there was also a weak but significant summer precipitation signal for this species. For spruce, a positive correlation was found with winter precipitation (Fig. 6B). The growth of both tree species was similarly dependent on temperature, and was negatively correlated with the August temperature, although the correlations were not as strong as for rhododendron (spruce −0.29, fir −0.24) (Fig. 6B,C).

In general, the climate signal, calculated over the 60 years from 1961 to 2020, of trees growing in the Ukrainian Carpathians was rather weak, whereas the rhododendron shrubs growing above the treeline exhibited a clear climatic signal. These results prompted us to look at how this growth-climate relationship has changed over time.

The moving correlation analysis points to a temporal change in the dendroclimatic reactions among the three species. The correlation

Table 1
Main dendrochronological characteristics of analysed species.

Species	Altitude of sampling (m a.s.l.)	Vegetation belt	Number of samples (collected/used in chronology)	Time span	Correlation with master chronology	Mean sensitivity	Auto correlation filtered/ unfiltered
Rhododendron myrtifolium	1800–1950	Subalpine /alpine	35/20	1953–2019	0.400	0.379	0.330/0.22
Picea abies	1350–1500	Upper forest	32/25	1906–2012	0.508	0.155	0.916/-0.25
Abies alba	950–1050	Lower forest	30/21	1835–2019	0.470	0.174	0.861/0.038

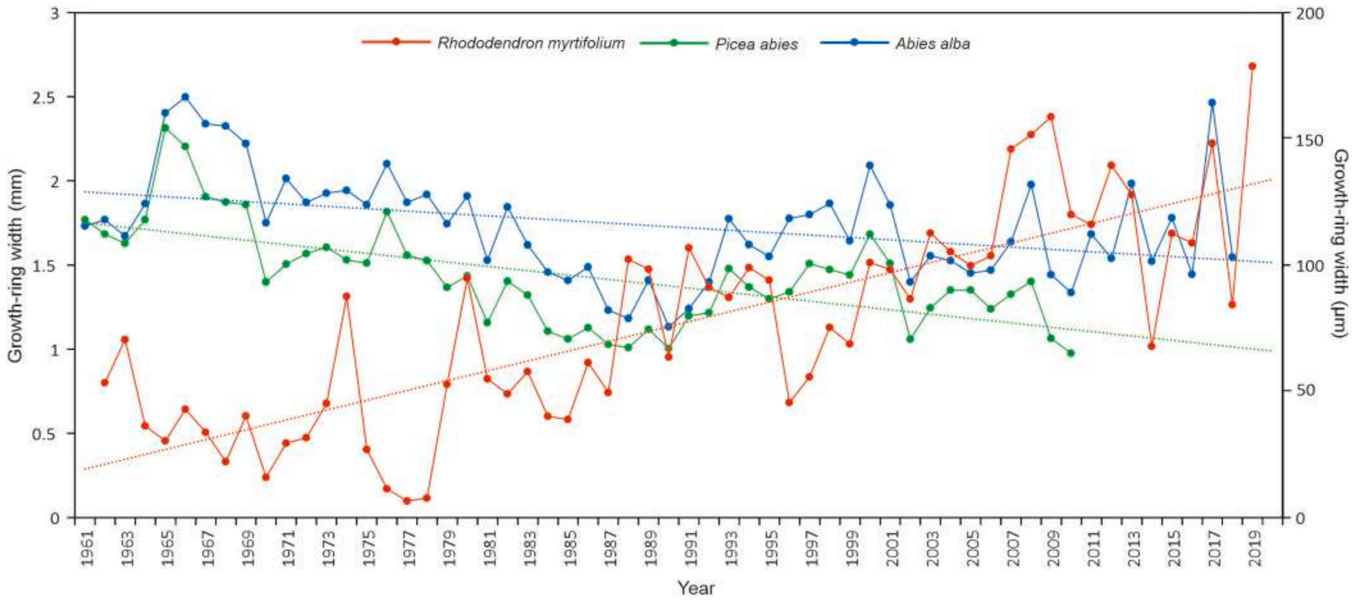

Fig. 4. Growth trends for 1961–2019 of the growth-ring width chronologies of the three species analysed.

between the annual growth rings of RHMY and summer temperature has increased in the last three decades (Table 2). In the same period, the negative correlation between PCAB and summer temperature has also increased. The rainfall signal has changed from a negative to a positive effect on rhododendron growth. The ABAL precipitation signal (March to July), which had remained stable over a long period of time, has also changed in the last ten years (Fig. 7).

4. Discussion

Structurally and functionally, woody plants respond to mountain and alpine environments by adapting to the physical constraints of these ecosystems (Körner, 2003). Although temperature and humidity are the basic climatic factors restricting or promoting plant growth along an altitudinal transect, there are many others in the alpine zone that influence growth, including microtopography, micrometeorological conditions or soil properties (Körner, 2003; Myers-Smith et al., 2015b; Opala-Owczarek et al., 2018; Owczarek and Opała-Owczarek, 2016). Hence, in order to carry out a reliable, comprehensive assessment of the climatic response of plants growing in an altitudinal transect, a multi-species or single-species approach should be used (Büntgen et al., 2007; Frank and Esper, 2005; García-Suárez et al., 2009; Leonelli et al., 2016; Opała-Owczarek et al., 2023). In the case examined here, the principal task was to develop the first dendrochronological scale for a previously unexplored shrub species, i.e. *Rhododendron myrtifolium*, and to determine its climatic response. This was an attempt to redress this information gap regarding the dendroclimatic response of plants from the subalpine zone of the Eastern Carpathians.

The observed relationships, i.e. the positive, ever stronger correlation between rhododendron shrub growth rings and summer temperature, and the ever larger annual increments during recent decades, indicate that the Eastern Carpathian rhododendron is in good condition, despite the warming climate. Increasing temperatures above the tree line are having a beneficial effect on its growth. It can therefore be conservatively estimated that further increases in temperature will enable this species to expand. Our study has revealed a robust positive correlation between rhododendron shrub growth rings and summer temperatures, aligning with previous findings from the Arctic and the Alps (Hoch, 2014; Korner, 2003; Kudo and Suzuki, 1999; Molau et al., 2005; Wheeler et al., 2016; Wipf, 2010) and emphasizing the critical role of temperature in driving alpine vegetation growth. Moreover, Francon et al. (2017) noted a climate-growth association in *R. ferrugineum* similar to treeline *Picea abies* trees in their study region and identified May–July temperatures as key growth-limiting factors. Francon et al. (2020) further highlighted the sensitivity of *R. ferrugineum* to local weather conditions, underscoring its potential as an indicator for documenting the response of alpine vegetation to global warming. Our findings also concur with Panthi et al. (2021), who revealed a positive relationship between the radial growth of *R. campanulatum* and temperatures throughout the year, and very considerable sensitivity to winter minimum temperatures, suggesting potential benefits from future winter warming. In contrast, Dhyani et al. (2023) show the negative effect of increasing temperature on the growth of *R. arboreum* in the West Indian Himalayan region. They show not only the positive correlation with precipitation and the negative correlation with temperature in June-August, but also the complex interaction between regional climate and shrub growth.

In the rhododendrons we studied, we found an increase in the growth-ring width with age. The growth pattern of rhododendrons varies, depending on the species and location. An age-related growth

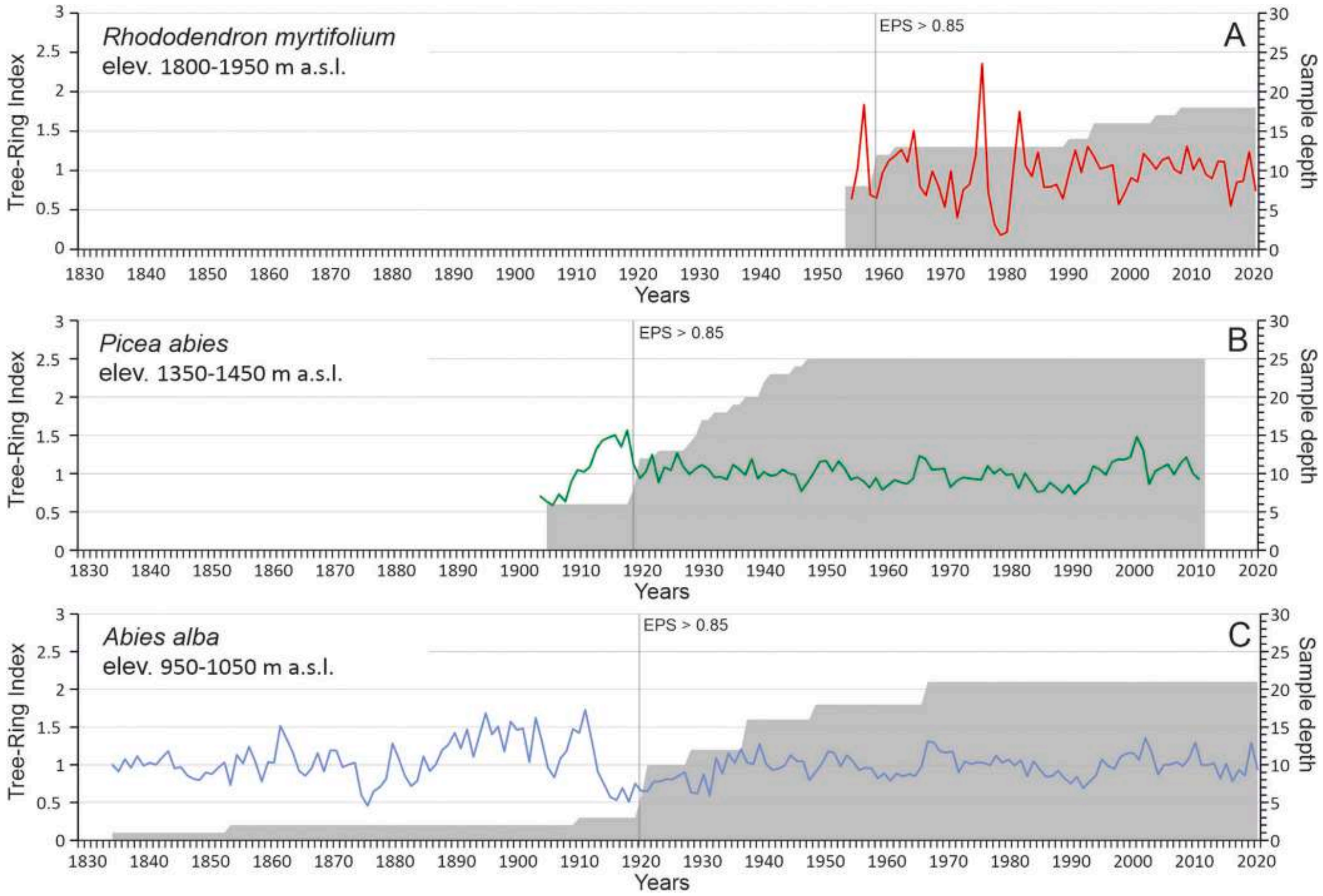

Fig. 5. Indexed chronologies of (A) *Rhododendron myrtifolium*, (B) *Picea abies*, (C) *Abies alba*, and the corresponding sample replications.

trend was found in the Alps (Francon et al., 2017, Piccinelli et al., 2023). In the high mountains of Asia, the ring-widths of rhododendrons collected in the Eastern Tibetan Plateau tended to decrease with increasing age (Lu et al., 2015, Wang et al., 2023), but no age-trend was reported in the Himalayas (Panthi et al., 2021). Increasing growth-ring width with age was reported in shrub and dwarf shrub species from polar areas, where annual growth rings were wider and tracked more closely the increase in spring and summer temperatures (Myers-Smith et al., 2015). It should be noted, however, that despite this positive correlation between summer temperature and rhododendron growth, the signal is weakening somewhat. Although the positive effects of warming on dwarf shrub growth in the Arctic and alpine environments have been well documented (Ackerman et al., 2018; Forbes et al., 2010; Myers-Smith et al., 2015a; Van Der Wal and Stien, 2014; Weijers et al., 2017), the reverse processes have begun to appear during the last few years. This may be due to drought stress as both temperatures and soil water deficiency increase (Opala-Owczarek et al., 2018; Owczarek et al., 2021).

Our results indicate the possibility of drought stress and deteriorating growth conditions in the forest zone. At the same time, while climatic conditions for rhododendrons are improving, the growth of forest tree species is being impaired. It seems that the latter will suffer from increasingly higher temperatures and the associated drought stress. Sidor et al. (2015) reported that tree growth at high altitudes in the Eastern Carpathians is predominantly constrained by summer temperatures. However, this climatic signal is diminishing with decreasing altitude and rising mean temperatures. At lower elevations, spruce growth is influenced primarily by summer precipitation, whereas at intermediate elevations there is no statistically significant correlation with climatic variables. It is noteworthy that June and July temperatures are having a positive effect at elevations above 1300 m a.s.l. but a negative one below 1000 m a.s.l. However, spruce displays a heightened response to temperature, both in the current and previous growing seasons, as well as to soil water deficit (Bouriaud and Popa, 2009). On the other hand, fir emerges as the least sensitive species in this context. Popa (2003) highlights a positive and significant influence of winter temperatures on the current growth of a mixed spruce-fir stand in the Eastern Carpathians, approximately 300 km away from our study area. However, contrasting findings emerge from the Hoverla region chronologies, where Kaczka and Büntgen (2006) reported no significant response to monthly temperatures but discovered evident correlations with the seasonal June-August and July-August means. In particular, the spruce chronologies from Hoverla, as presented in this study, are closely correlated with other sub-groups, i.e. in other parts of the Carpathians, and demonstrate a heightened response to summer temperatures (Kaczka and Büntgen, 2006).

Our research relating to the convergence in growth and climatic response between the lower and upper forest belts, and the subalpine and alpine belts, leads to the conclusion that there are periods and single years where the signals overlap for the three species analysed here. This is the first such comparison for plant species from the Eastern Carpathians. We found characteristic patterns of climatic conditions which led to development of negative pointer years in all analysed species.

5. Conclusions

This study presents the first 66-year chronology for the dwarf shrub *Rhododendron myrtifolium* from the Eastern Carpathians, revealing its considerable dendroclimatological potential. Despite its shorter timespan in comparison with the fir and spruce chronologies, RHMY

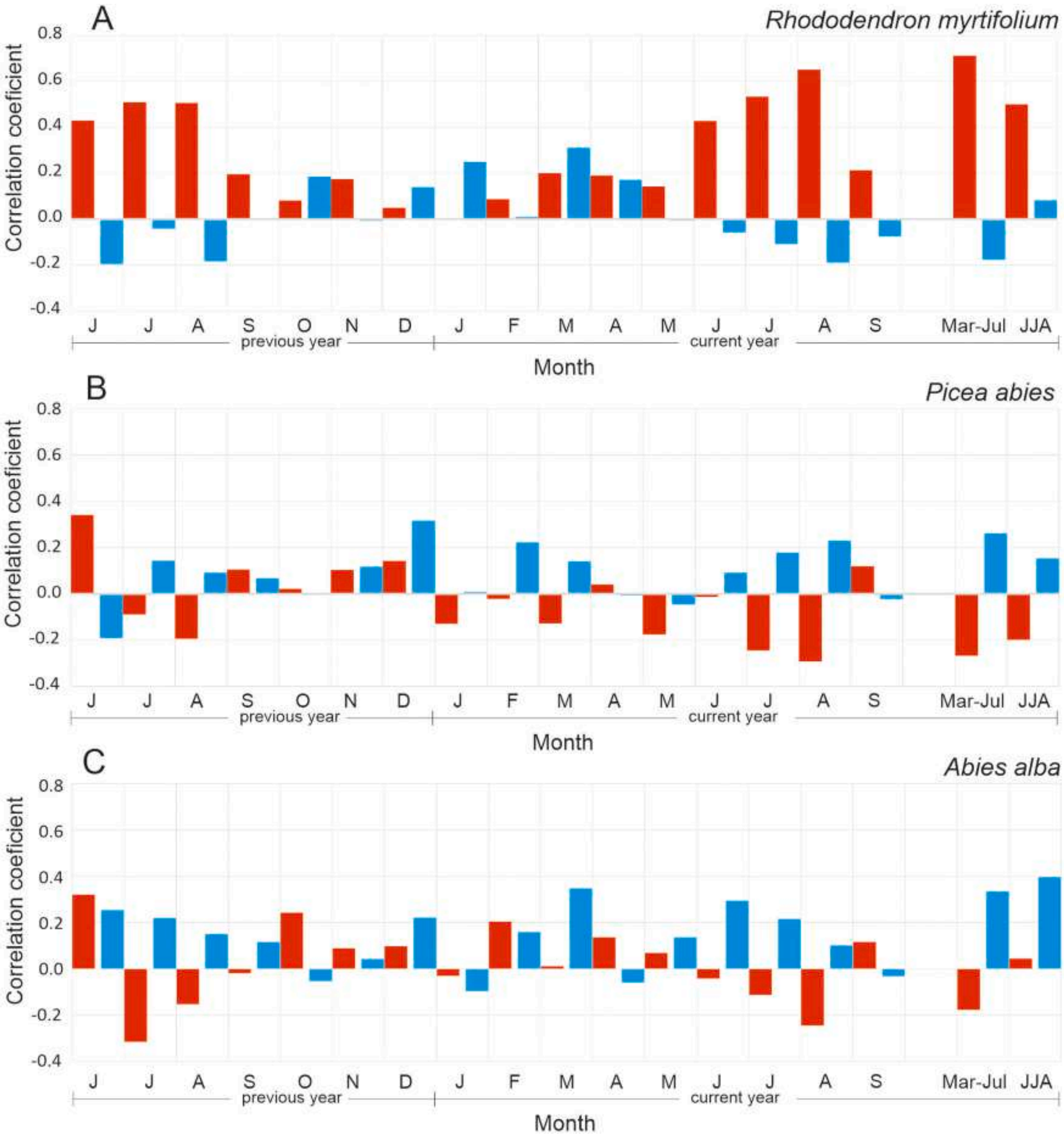

Fig. 6. Correlation between the growth-ring width indices of (A) *Rhododendron myrtifolium,* (B) *Picea abies* and (C) *Abies alba*, and the monthly mean temperature and monthly total precipitation from the previous June to the current September during 1960–2020. The meteorological data were kindly supplied by the Pozhyzhevsʹka Meteorological Station.

Table 2
Correlation values between chronologies for three analysed species and selected climate variables calculated for two different time periods.

Period	Rhododendron myrtifolium	Picea abies	Abies alba	Period	Rhododendron myrtifolium	Picea abies	Abies alba
Temperature $_{\text{August}}$				Temperature $_{\text{Summer}}$			
1962–1991	0.38	-0.19	-0.21	1962–1991	0.27	-0.05	-0.19
1991–2020	0.47	-0.21	0.22	1991–2020	0.59	-0.46	0.01
Precipitation $_{\text{Winter}}$				Precipitation $_{\text{March-July}}$			
1962–1991	-0.37	0.41	0.41	1962–1991	-0.36	0.34	0.45
1991–2020	0.57	-0.16	0.03	1991–2020	0.25	0.1	0.22

characteristically exhibited the narrowest growth rings and a greater sensitivity. There was a strong positive correlation (r=0.71) between the RHMY chronology and warm-season temperatures, with the highest correlation for August (r=0.65). In contrast, the two tree species, fir and spruce, demonstrated a shared dependence on temperature, being negatively correlated with August temperatures. Our findings suggest a positive and increasingly stronger correlation between rhododendron shrub growth and summer temperature, indicating that Eastern Carpathian rhododendrons are thriving in the era of climate warming. These insights contribute to the broader discourse on climate-driven vegetation dynamics, offering valuable information for policymakers in formulating adaptation measures for forest management, particularly in the context of protecting the vulnerable communities of this region from the anticipated adverse impacts of future droughts. Thus, our study

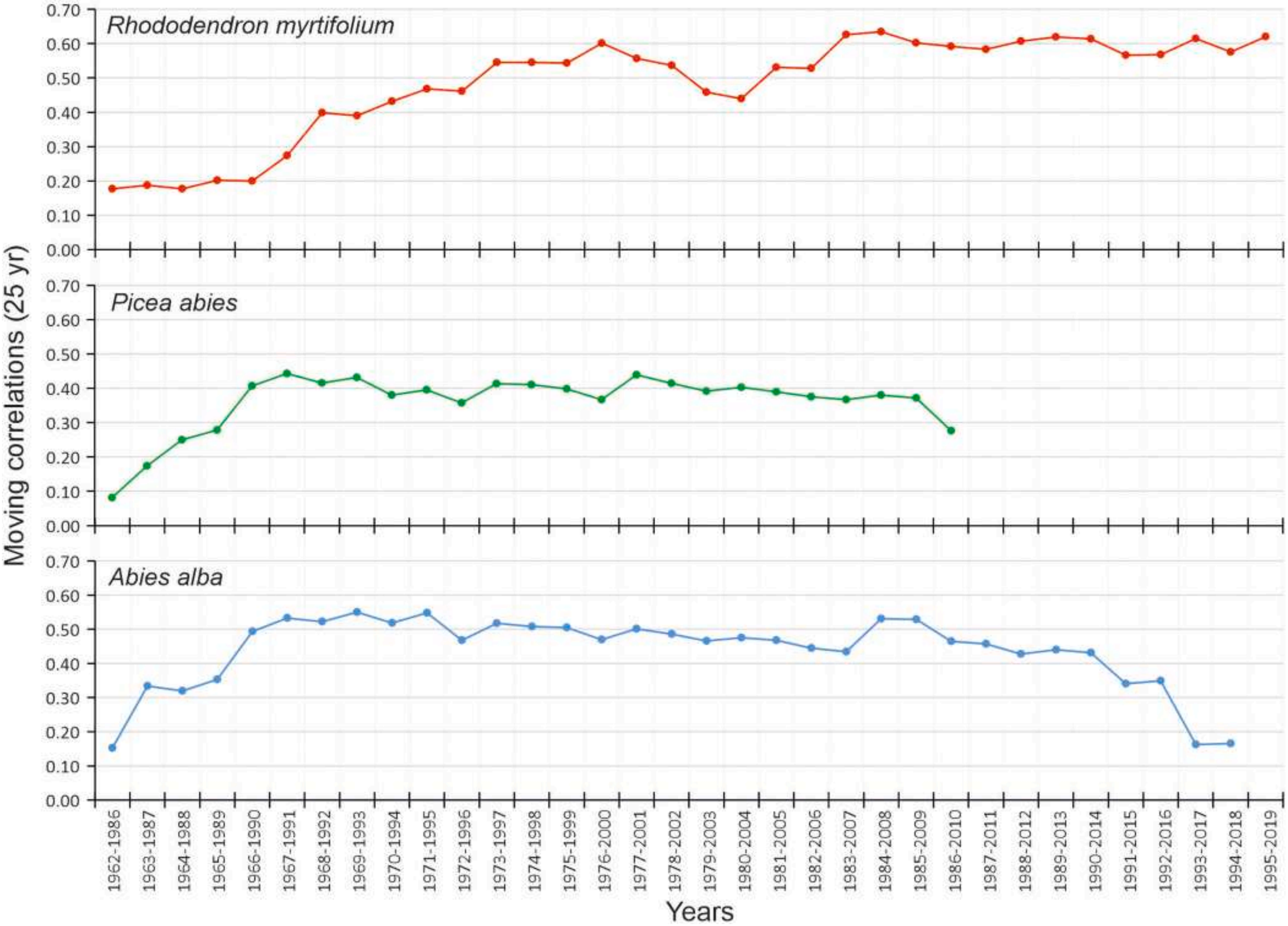

Fig. 7. Moving correlation between growth-ring width of *Rhododendron myrtifolium, Picea abies, Abies alba* and summer temperature.

emphasizes the complex responses of various rhododendron species to climate changes, highlighting the need for a thorough understanding of local and regional factors that shape their growth patterns amid ongoing global warming. Future research should explore the detailed anatomical traits of rhododendron species and examine the combined effects of diverse environmental factors specific to study sites.

CRediT authorship contribution statement

Piotr Owczarek: Writing – original draft, Visualization, Investigation, Conceptualization. **Mohit Phulara:** Writing – original draft, Formal analysis. **Pavlo Shuber:** Resources, Investigation. **Magdalena Opala-Owczarek:** Writing – original draft, Validation, Resources, Methodology, Formal analysis, Conceptualization. **Bartosz Korabiewski:** Investigation. **Marek Błaś:** Resources.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Article V

Tracing Aphid Infestations through Wood Anatomical Markers: Insights from Rhododendron campanulatum Species of the Himalayan Region

Dendrochronologia

Tracing aphid infestations through wood anatomical markers Insights from Rhododendron campanulatum D.Don of the Himalayan region

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Corresponding Author:	Holger Gärtner Swiss Federal Institute for Forest Snow and Landscape Research WSL Birmensdorf, SWITZERLAND
First Author:	MOHIT PHULARA
Order of Authors:	MOHIT PHULARA
	Magdalena Opała-Owczarek
	Piotr Owczarek
	Alexander Bast
	Indra Dutt Bhatt
	Holger Gärtner
Abstract:	Recent climatic shifts have led to a noticeable increase in temperatures across the high-altitude ecosystems of the Himalayas, particularly in winter. This warming is altering growing conditions for many species, including aphids, found at higher altitudes where they were previously rare. As air temperatures increase, aphids develop more rapidly, extending their active periods and winter survival, and changing their geographical distribution and abundance. In this study, we analyzed the anatomical structure of Rhododendron campanulatum D.Don tree rings to detect aphid infestations in the higher elevational range of the Himalayas. Microscopic examination of wood sections from branches and increment cores from the main trunk revealed sapwood alterations caused by aphid activities. Our findings show that aphids were active at elevations between 3100 and 3400 m a.s.l., and preferred younger trees over mature ones after a certain age period. Hence, the pattern of aphid infestation is influenced not solely by rising temperatures, as previously assumed, nor is it significantly affected by altitude changes. Instead, it is notably impacted by the age of the samples. These anatomical markers highlight the impact of aphids and broader ecological shifts affecting plant resilience and forest health. Thus, this study urges collaboration among wood anatomists, entomologists, and ecologists to understand aphid life cycles, host preferences, and ecological interactions in the Himalayas. These findings are crucial for biodiversity conservation in the region and could affect ecological management strategies in other mountain regions worldwide.
Suggested Reviewers:	Alan Crivellaro Prof., University of Torino alan.crivellaro@unito.it
	Ingo Heinrich Helmholtz-Zentrum Potsdam GFZ ingo.heinrich@dainst.de
Opposed Reviewers:	

Tracing aphid infestations through wood anatomical markers: Insights from *Rhododendron campanulatum* D.Don of the Himalayan region

Mohit Phulara[1], Magdalena Opała-Owczarek[1], Piotr Owczarek[2], Alexander Bast[3,4], Indra Dutt Bhatt[5], Holger Gärtner[6]*

[1] Institute of Earth Sciences, Faculty of Natural Sciences, University of Silesia in Katowice, Sosnowiec, Poland
[2] Institute of Geography and Regional Development, University of Wroclaw, Wroclaw, Poland
[3] WSL Institute for Snow and Avalanche Research SLF, Alpine Environment and Natural Hazards / Permafrost, Flüelastrasse 11, 7260 Davos Dorf, Switzerland
[4] Climate Change, Extremes and Natural Hazards in Alpine Regions Research Center CERC, Flüelastrasse 11, 7260 Davos Dorf, Switzerland
[5] Center for Biodiversity Conservation and Management (CBCM), G. B. Pant National Institute of Himalayan Environment (NIHE), Kosi-Katarmal, Almora, Uttarakhand, India
[6] Swiss Federal Research Institute WSL, Forest Dynamics, Dendrosciences, Birmensdorf, Switzerland

*** Correspondence:**
holger.gaertner@wsl.ch

Abstract

Recent climatic shifts have led to a noticeable increase in temperatures across the high-altitude ecosystems of the Himalayas, particularly in winter. This warming is altering growing conditions for many species, including aphids, found at higher altitudes where they were previously rare. As air temperatures increase, aphids develop more rapidly, extending their active periods and winter survival, and changing their geographical distribution and abundance. In this study, we analyzed the anatomical structure of *Rhododendron campanulatum* D.Don tree rings to detect aphid infestations in the higher elevational range of the Himalayas. Microscopic examination of wood sections from branches and increment cores from the main trunk revealed sapwood alterations caused by aphid activities. Our findings show that aphids were active at elevations between 3100 and 3400 m a.s.l., and preferred younger trees over mature ones after a certain age period. Hence, the pattern of aphid infestation is influenced not solely by rising temperatures, as previously assumed, nor is it significantly affected by altitude changes. Instead, it is notably impacted by the age of the samples. These anatomical markers highlight the impact of aphids and broader ecological shifts affecting plant resilience and forest health. Thus, this study urges collaboration among wood anatomists, entomologists, and ecologists to understand aphid life cycles, host preferences, and ecological interactions in the Himalayas. These findings are crucial for biodiversity conservation in the region and could affect ecological management strategies in other mountain regions worldwide.

Keywords: tree-rings, anatomical markers, discrete features, insect infestation, xylem distortion

1. Introduction

Mountain ecosystems around the world are facing profound ecological changes as global warming intensifies. The Himalayan region warms three times faster than the global average (Xu et al., 2009; Schickhoff et al., 2015). This accelerated warming, especially notable during the winter months, raises substantial concerns about the region's biodiversity and the resilience of its native species. For this, the Himalayas, characterized by unique altitudinal gradients and distinct ecological zones, are witnessing transformative changes in species composition and biodiversity (Change, 2007; Singh et al., 2011).

The effects of these temperature increases are clearly visible at the treeline, where shifts in vegetation patterns act as early indicators of broader ecological changes affecting the entire region (Körner and Paulsen, 2004; Gaire et al., 2017). As mean annual temperatures continue to rise, the treeline and its associated vegetative bands shift upwards, altering natural habitats and disrupting the balance of flora and fauna. Among the most affected plants in the Himalayas are the *Rhododendron* species (*Ericaceae*), predominating the subalpine to alpine transition zones of the Indian Himalayan Region—a recognized global biodiversity hotspot (Conservation International, 2004). *Rhododendron*, a subdominant taxon, thrives across a broad temperature range of 4.3–11.6 °C, although it is notably absent from the region's warm temperate zones. Among others, the bell-flowered rhododendron (*Rhododendron campanulatum* D.Don) is migrating upwards along altitudinal gradients at an estimated rate of 1.4 meters per year in response to rising temperatures (Singh and Negi, 2018). Further studies in the western Himalayas have recorded an upward shift of treeline species over ten years of 19m on south- and 14m north-facing slopes (Bhasha Dubey et al., 2003). Such phenological and geographical shifts underscore the adaptability and vulnerability of these key floral species under the stress of changing climatic conditions. The upward migration and expansion of these species into new altitudinal zones indicates broader ecological shifts within these fragile high-altitude ecosystems (Zhang et al., 2020). Furthermore, under warmer conditions, especially evergreen Rhododendron leaves are anticipated to become more nitrogen-enriched, which could boost the abundance and activity of feeding herbivores (Pöyry et al., 2011).

Parallel to these vegetative changes, insect populations, particularly aphids, are also undergoing significant transformations due to global warming. Insect populations in general are expected to expand their range to higher latitudes and elevations, potentially increasing herbivory pressure (Parmesan et al., 1999; Conrad et al., 2004). Among the one million known insect species, almost 50% are herbivores, including aphids. These insects are phloem-feeders belonging to the family *Aphididae* (Hemiptera). Over 4000 aphid species have been described, many of which are known to impact plant health significantly (AFG, 1998). Warmer climates have been shown to influence the developmental cycles of aphids, leading to faster development, higher overwintering survival, and increased reproductive rates (Harrington et al., 2001; Bale et al., 2002). Aphids, being poikilothermic, respond markedly to these climatic changes, often with one to five additional reproductive cycles per season for every 2°C increase in temperature (Yamamura and Kiritani, 1998; Harrington et al., 2007). These changes are not isolated to aphids alone but reflect a broader trend among herbivorous insects, whose altered phenology can advance the timing of larval and adult emergence, particularly in regions experiencing significant temperature increases.

The ability of aphids to alternate between woody primary and herbaceous secondary host plants enhances their exploitation of favorable food resources in different seasons. This ecological flexibility plays a crucial role in the fitness and survival of aphid species (Mackenzie and Dixon, 1991). As host plants expand their range northwards due to climate change, the migration of aphids to these new areas is expected to lag. However, as many southern plant species are already establishing themselves in Northern Europe, their specific aphids will inevitably follow, colonizing these plants as they become more prevalent.

The impact of global warming on aphid distribution was further highlighted in 2014, where four specimens of an Asiatic aphid species associated with Rhododendron spp. were captured at various locations across England, marking the first observation of this species in natural habitats within Britain. This significant finding underscores the shifting dynamics of aphid populations in response to changing environmental conditions (Wieczorek et al., 2019). Despite their global prevalence as significant agricultural and forestry pests, very little work has been conducted on the biology and life cycle of aphids in the Himalayas, leaving a substantial gap in understanding their impact on high-altitude ecosystems (Chakrabarti, 2021). The unique environmental conditions of the Himalayas present distinct challenges that are not as well-documented. Studies by a pioneer entomologist (Chakrabarti et al., 1983) documented major aphids in the Himalayan range during the 1980s. Moreover, recent research, including from the Kargil district of UT Ladakh, has revealed that 14 aphid species infest 37 medicinal plant species, indicating that even palatable, high-altitude plants are affected (Ali et al., 2023). In dendroecological research, advanced wood anatomical techniques allow for detailed analysis of the inter- and intra-annual variability of cellular structures. This is crucial for understanding the adaptation and growth responses of woody species to diverse climatic conditions (Prendin et al., 2017; Pandey et al., 2018; Puchi et al., 2020). Discrete features in the wood anatomical structure of woody species, such as frost rings, resin pockets, reaction wood or insect scars as aphid traces, are vitally used as markers in dendroecology for studying environmental events with high temporal resolution (Fig. 1).

The ability to analyze these markers underlines the longstanding value of wood anatomy in environmental research (Speer, 2010). Based on our comprehensive literature review, this study is the first to trace aphid infestation systematically through wood anatomical markers.

The actual ecological opinion in the higher Himalayas by anonymous experts suggests that aphids do not inhabit high-altitude regions, affect younger trees (10~15yrs) only so they cannot be in matured one and cannot infest those species that are perceived as unpalatable. By examining aphid activity across different altitudes, particularly in a higher altitude region of North-western Himalaya, this research aims to test those perceptions, reevaluate the ecological strategies, and highlight the impacts of aphids in Himalaya.

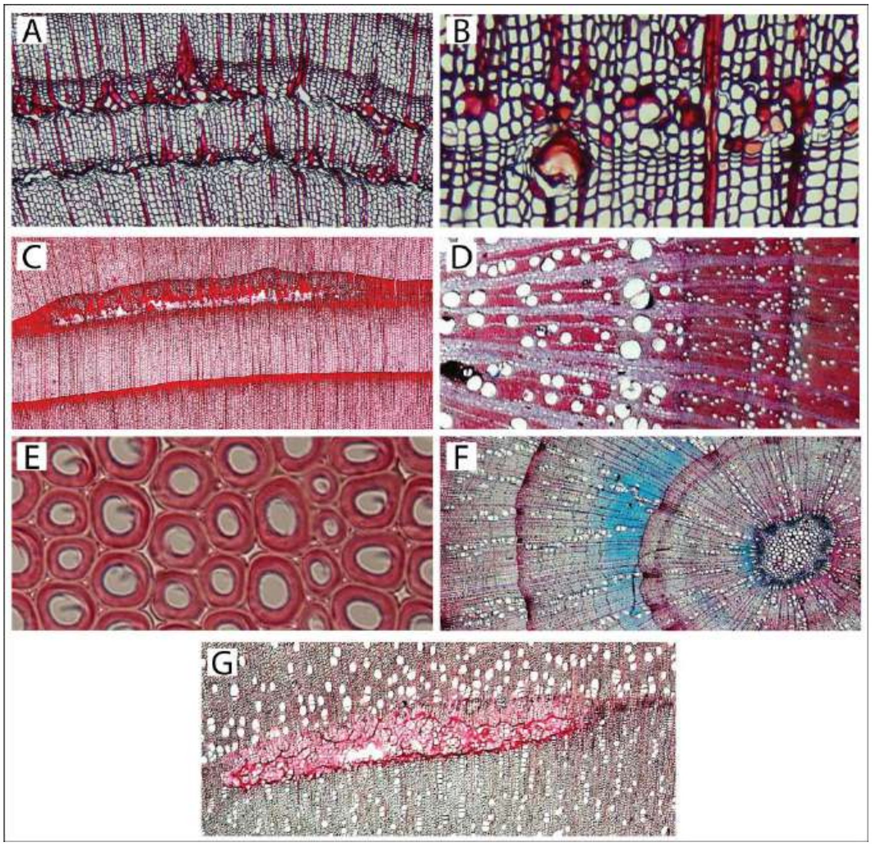

Fig. 1.

2. Material and Methods

2.1 Study Site

This study was conducted in the Western Himalayas within the Garhwal divisions at Rudraprayag (30°14.0' N, 79°13.0' E) (Fig. 2). Sampling was done across elevations ranging from 3100 to 3400 m a.s.l., encompassing ecological zones from subalpine forests to alpine meadows (Champion and Seth, 1968). The study site features a more diverse composition of dominant woody species near the treeline, including *Abies spectabilis* D.Don*, Betula utilis* D.Don*, Sorbus foliolosa* (Wall.) Spach*, Prunus cornuta* (Wall. ex. Royle) Steud*.*, and *Rhododendron campanulatum* D.Don (Malik and Nautiyal, 2016; Chandra et al., 2018). The study area is underlain by weathering bedrocks predominantly composed of crystalline and metamorphic rocks, supplemented by Paleozoic sedimentary deposits (Gansser, 1964). The soil exhibits a sandy loam texture and is acidic, with a pH ranging from 4.9 to 5.6 (Nautiyal et al., 2001).

The region typically experiences snow cover from December to March and receives the bulk of its annual precipitation during July and August. The growing season extends from mid-May to late October, with climatic conditions typical of high-altitude environments, including cold temperatures, intense solar radiation, low atmospheric pressure, and high wind speeds. In the studied region, rising temperatures associated with global climate change are leading to consistently high soil moisture levels during the growing period of the plants (mid-April to mid-October) (Joshi et al., 2018; Tewari et al., 2018). Additionally, sites with earlier snowmelt tend to exhibit higher productivity and greater species richness compared to areas where snowmelt is delayed (Litaor et al., 2008; Nabe-Nielsen et al., 2017). Past studies in the region indicate that the climate is primarily influenced by monsoon circulation, with easterly winds prevailing during the summer and westerly winds dominating from October to March. Additionally, recent research has highlighted a decline in the Temperature-Lapse Rate (TLR) in the area, which is attributed to global warming. This trend is associated with elevation-dependent warming (EDW), where warming occurs at a higher rate at elevated areas compared to lower elevations (Joshi et al., 2018).

The temperature trends in the studied region from 1950 to 2020 (Fig. 3), highlights mean annual air temperature (MAAT), spring, and winter temperatures. Spring temperatures display the highest year-to-year fluctuations but show a gradual warming trend, especially after the 1980s. Winter temperatures exhibit a steadier increase with less variability, while the MAAT reflects an overall rise of 1–2°C over the period. These trends suggest increased spring temperature variability due to shifts in snowmelt timing, precipitation patterns, and climatic events, which may disrupt ecosystems and seasonal cycles. The steady rise in winter temperatures points to milder winters, potentially reducing snowpack and altering hydrological cycles.

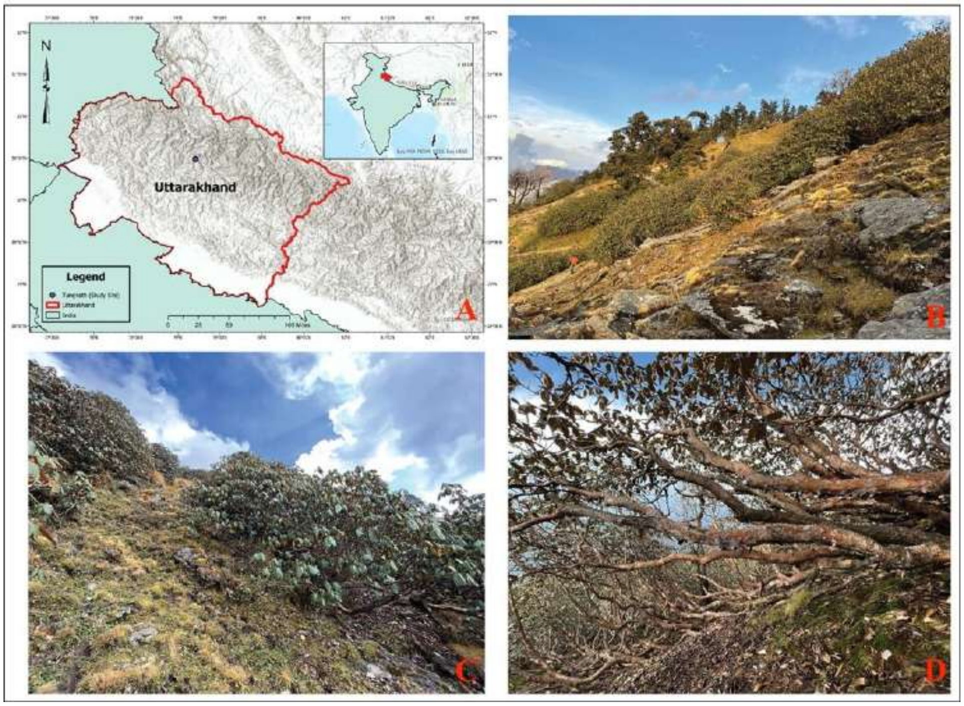

Fig. 2.

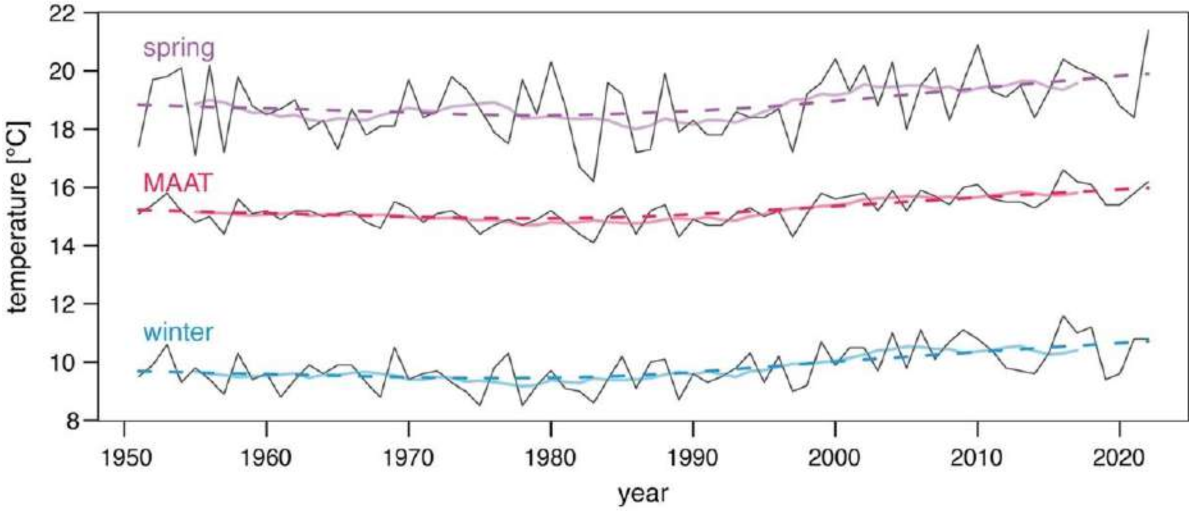

Fig. 3.

2.2 Species studied

Rhododendron campanulatum D.Don is a shrub or small tree (Fig. 2D) up to 8 m tall (referred to as a tree hereafter) that produces striking bell-shaped flowers during April–May, followed by fruiting in June and subsequent seed dispersal (Bisht et al., 2014). It is a timberline krummholz species, characterized by its crooked growth form, and serves as a biogeographical example of a sub-dominant taxon found in subalpine to cold temperate zones (Tiwari and Chauhan, 2006). Notably, this Rhododendron species is distinctive in its ability to form large, uniform stands across the timberline regions of the Central and Western Himalayas (Vetaas, 2002).

In the studied region, *R. campanulatum* appears to benefit from the warming trend, as its seedlings and saplings are often found beyond the timberline and treeline (Singh et al., 2021). This species exhibited the highest leaf area and leaf mass compared to other species, and its lower specific leaf area suggests thicker leaves, potentially as an adaptation to the stressful high-altitude conditions (Körner, 2012). Qualitative observations from various arboreta have identified that a major challenge for the survival of *R. campanulatum* is the early growth during late winter or early spring, which is often followed by sudden frost events (Vetaas, 2002). Notably, *R. campanulatum* is the only tree species observed to recruit seedlings and saplings beyond the treeline at 3280 m asl at this site, a pattern not seen in any other species (Adhikari et al., 2012; Singh and Negi, 2018).

2.3 Sample Collection and Preparation

In November 2022, samples were collected randomly from 20 trees by excising discs approximately 3 cm thick from three branches of each targeted *R. campanulatum* tree, i.e. six discs per tree. In addition, increment cores (5 mm) were taken from the main trunk of the targeted trees. The two discs of each branch were taken at a distance of approximately 25 cm. We prioritized mature trees with thick trunks or branches suitable for dendrochronological analysis. Sampling was organized into three distinct elevation bands: 3100–3200 m a.s.l. (low altitude), 3200–3300 m a.s.l. (mid altitude), and 3300–3400 m a.s.l. (high altitude). Those collected discs were initially stored in paper bags in the field and later transferred to plastic bags containing 50% ethanol for preservation. The samples were then processed for microscopic inspection following standard procedures (Gärtner and Schweingruber, 2013). All disks were cut on the cross-sectional level to prepare micro sections of 15-20 µm thickness using a GSL1 sliding microtome (Gärtner et al., 2014). Digital imaging of the prepared sections was done using a Zeiss slide scanner Axio Z1(state company, city, country; URL), resulting in high-resolution micro-photos taken at 100 x magnification. The images were then used to visually determine the aphid traces and their position within the annual ring.

A core-microtome was used to prepare all increment core surfaces (Gärtner and Nievergelt, 2010). To ensure precise cutting without damaging the delicate cell walls, a non-Newtonian fluid was added to the surface of the cores while cutting (Schneider and Gärtner, 2022). The cut core surfaces were digitized using the image-capturing system Skippy

(Gärtner et al., 2024). The resulting high-resolution images of the cores were stitched to a single panorama using PTGui (New House Internet Services B.V., Rotterdam, The Netherlands), which is then used for further observation and analysis.

2.4 Aphid traces

Aphids are insects that feed on phloem sap by penetrating the phloem of woody plants with their piercing-sucking mouthparts (stylets). When feeding on phloem sap, they occasionally also have to feed on xylem sap because the Aphids need to alleviate the osmotic effects of ingested phloem sap, the concentration of which exceeds by far that of xylem vessels (Buchanan et al., 2015). To reach the sap-transporting vessels in the xylem, the stylets of the aphids penetrate the (active) cambium. The mechanical stress is comparable to the so-called pinning procedure (Gärtner and Farahat, 2021). In contrast to the impact of the pinning needle, the small size of the stylet is not destroying but disturbing the cambium cells. The following growth reaction results in a locally limited formation of callous tissue, returning to the host plant's common cell structure after a few cell rows. As a result, the xylem of the respective ring shows a tangentially elongated, radially flat zone of callous tissue surrounded by the regular cell structure of the xylem (Fig. 4E2). This structure, called aphid trace, is characteristic for disturbances caused by aphids and differs from other cambial damages caused by mechanical impacts such as woundings by hailstorms or even frost rings (Fig. 4E1). These aphid traces, clearly visible in cross-sectional microsections of the xylem rings of the host plant, can be used to analyze the temporal and spatial occurrence of aphids at respective sites.

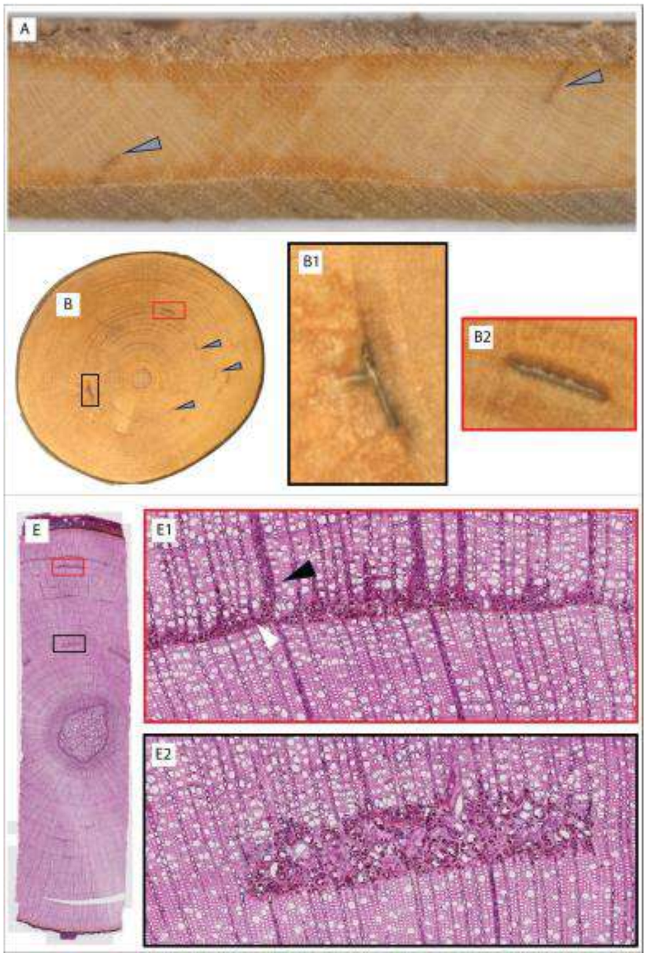

Fig. 4.

2.5 Statistical analysis of detected aphid traces

A visual exploration of our data suggested a potential temporal change in the number of aphid-affected samples. Hence, to reconstruct the pattern of aphid infestation, we applied segmented (piecewise) regression to detect and model these temporal changes and identify specific breakpoints, i.e., years where significant shifts in the number of affected samples occurred. We performed statistical analysis on all the data, which were subsequently divided into different altitude groups (low, mid, high) to examine how infestation rates vary with altitude. Segmented regression models are a specialized type of regression where piecewise linear segments represent the relationship between the response variable and the explanatory variable (Muggeo, 2003, 2008). These segments are connected at unknown points, known as breakpoints, estimated as part of the model. For detailed information on segmented regression modelling, we refer to (Muggeo, 2003).

First, we fitted a simple linear regression model, where the dependent variable, the square root of the number of affected samples, was modelled as a function of the independent variable, year. The square root transformation of the dependent variable was applied to stabilize variance and meet the assumptions of the regression models (Stahel, 2013). We performed a Davies test to assess the presence of significant structural changes in the linear relationship, i.e., a change in the slope (Muggeo, 2003). The test provided strong evidence (Table 1) for a change in slope, prompting further exploration using segmented regression.

To identify candidate breakpoints, we applied a Lowess smoother to the data (Cleveland, 1979). Visual inspection of the smoothed curve guided our selection of initial guesses for potential breakpoints, representing years where the slope of the relationship between the variables might change. These initial estimates were then used as starting points for the optimization process to determine the actual breakpoints in the segmented regression model.

We applied diagnostic plots to assess the fit of the segmented regression model and to ensure that the regression assumptions were met (Stahel, 2013; Fox and Weisberg, 2018). For this, we (i) plotted residuals versus fitted values to detect potential non-linearity, heteroscedasticity and outliers, (ii) plotted residuals over time to check if residuals exhibit patterns over time, and (iii) used quantile-quantile plots to assess if residuals are approximately normally distributed.

We used the open-source software R (R-Core-Team, 2023) within the Rstudio environment (Posit-Team, 2023) for our analyses and visualizations. To perform the Davies test and apply segmented regression models, we utilized the functions *segmented* and *davies test* from the R-package “segmented” (Muggeo, 2008; Muggeo, 2024).

Table 1: Significance levels for the analyses at different altitudes

Statistical Analysis	P-value (Davies Test)
All sites	9.934335e-18
Low Altitude	1.014156e-14
Mid Altitude	2.041814e-10
High Altitude	1.026187e-09

3. Results

3.1 Tracing of Aphid Infestation

By carefully examining aphid traces within tree rings across a large sample size exceeding 100 specimens, our study reveals consistent aphid activity in *R. campanulatum*, with traces distributed throughout growth rings, as shown in the macro-sections of the disc (Fig. 4, B2). The aphid traces were initially visible after disc polishing and cutting the cores

(Fig. 4, A), but they were distinctly observed and differentiated from other disturbances in micro sections (Fig. 4, E2), showing their prevalence at the boundaries of both earlywood and latewood rings. This pattern indicates peak aphid activity aligns with critical physiological phases— either in early spring or onset of dormancy during late summer, but mostly in the latewood boundary.

We observed fluctuations in aphid trace frequency over time; however, no consistent relationship was found between aphid activity and seasonal temperatures (winter and spring). The data showed no clear or significant trend that would justify graphical representation. Hence, our major findings underline only a uniform presence of aphids at high altitudes of the Himalayan site over the past decades (1951 onwards; Fig. 4 & 5), testing previous assumptions about high altitude limitations.

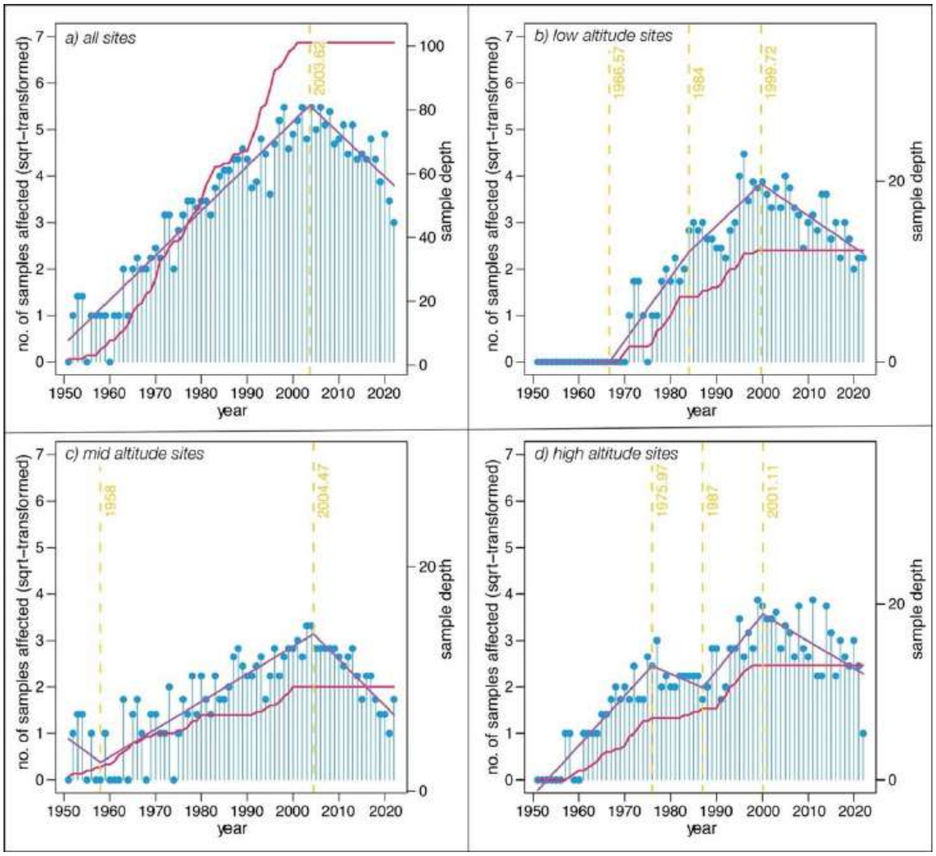

Fig. 5.

We then grouped our data based on the altitudinal range of the low, mid and high altitude sites to identify any noticeable patterns in infestation behavior (Fig. 5). Our results show an apparent increase in aphid infestation from the early stages of tree growth through to the period spanning up to 2000s paralleled by an increase of sample depth (Fig. 5) and followed by a subsequent decline of aphid traces when sample depth stays constant. While aphids are present across all sites within the 3100-3400 m a.s.l. range, there appear to be fewer older tree samples at lower altitudes due to anthropogenic pressure of human activities such as cutting these older trees for fuelwood.

The segmented regression analysis reveals a temporal change in aphid infestation on studied *R. campanulatum* across varying altitudes. Across **all sites (a)**, infestation levels increased steadily, peaking around 2003 and suggesting an upward trend that eventually stabilized. At **low altitudes (b)**, infestations began slightly later, around 1966, and rose quickly, peaking by 1984, followed by stabilization, likely due to favorable early conditions. At **mid-altitudes (c)**, infestations increased from 1958, peaking around 2004. **High-altitude sites (d)** exhibited two notable breakpoints, one in 1975 and another in 1987, followed by a decrease and increase respectively. Despite the different breakpoints, the overall shape of the curves remains broadly consistent. As all sites share a common breakpoint somewhere between 2000 and 2004, followed by a decline.: Rising phase → Peak → Decline/Stabilization phase

This suggests that the driving forces behind these trends may be similar across altitude gradients.

This plateau or variations in infestations across elevations post-peak may be attributed to factors such as host resistance, natural population regulation, changes in environmental conditions or other micro-climatic influences.

4. Discussion

It is generally assumed that lower temperatures and less stable climate conditions at higher elevations are not suitable for insect survival and breeding (Bale et al., 2002; Rasmann et al., 2014), but the recent rise in global warming is likely to provide new opportunities to introduce insects at higher altitude (Walther et al., 2009; Roques, 2010). As our study found the existence of aphids in a higher elevational range of the Himalayas from the 1950s until 2022. Following the suggestions of Cui et al. (2022), future studies should focus on the intensity and frequency of interactions rather than the rate itself to shed new light on plant-insect interactions in cold-limited regions. Our study highlights a most likely constant frequency and intensity of aphid infestations for a high elevational range (3100-3400 m a.s.l) and for a more extended period. This challenges the perception that high-altitude conditions are unsuitable for aphid survival and activity.

Aphids, known for their obligate phytophagous nature, establish close relationships with their host plants and exhibit a remarkable ability to select specific hosts (Eastop, 1978), and they do infest various medicinal and aromatic plants globally (EL-KORDY et al., 1999; Amin et al., 2017; Rohini et al., 2018). As in our case, we found traces of aphid infestations on *Rhododendron campanulatum*, a plant of high medicinal value (Bhattacharyya, 2011). Its conservation and preservation for future needs are imperative. The trend of aphid infestations increasing initially and then decreasing could also be linked to the Allee threshold, where populations below a minimum density are likely to go extinct (Lande, 1993; Liebhold and Tobin, 2008). In cases of Allee effects, populations might fail to expand in large favorable areas due to dissemination and decreased population density (Roques et al., 2008). As younger trees, being more nutrient-rich, may attract more aphids initially.

As stated in the results, our analysis shows no pronounced correlation between air temperature (winter and spring) trends and aphid infestation rates, aligning with the understanding that temperature effects on insects differ among habitats (Bale et al., 2002). While the direct impact of temperature increases is most pronounced in extreme environments like the Arctic, the interaction between temperature and other factors, such as rainfall, may be significant in tropical regions (Hodkinson and Bird, 1998; Vernon et al., 1998; Convey and Block, 2013). In contrary to this, the present study exploring these interactions, which would be valuable for future research. Predicting the effects of temperature increases on insect communities is complex, as global warming affects all associated organisms, resulting in cascading effects (Rouault et al., 2006; Hance et al., 2007; Bidart-Bouzat and Imeh-Nathaniel, 2008; Netherer and Schopf, 2010). The impact of temperature on insects varies across species, depending on their environments, life histories, and adaptive capacities, with their response to rising temperatures determined by whether the temperatures remain within or exceed the species' suitable range (Bale et al., 2002; Chen ChiaYu et al., 2013).

Similarly, altitudinal variation also did not affect the aphid infestation trends; infestation patterns were consistent across all three altitudes, increasing initially as long as younger trees are added to the samples and declining sample depth, i.e., all sample trees matured. Younger plants tend to be more susceptible to damage from feeding and viruses than older plants (Harrington and Clark, 2010). However, in our study aphid infestations persist even as the trees mature but later shows a declining trend towards maturity. As Scott-Brown et al. (2016) found that older leaves of *Rhododendron simsii* at an altitude beyond 400 m a.s.l exhibited greater leaf damage compared to younger leaves due to their lower trichome density and diterpenoid concentration. Furthermore, our research clearly shows the previously unnoticed presence of aphids at high altitudes above 3200m a.sl., in the Himalayan region that dates back to 1951. This might not even be the starting point, since the maximum age of our samples was 71 years. Although temperature plays a role in infestation dynamics, our findings suggest that tree age classification may also significantly impact infestation trends more than any direct temperature changes. Contrary to Cui et al. (2022), who observed increasing aphid frequency with elevation, our findings suggest that tree age has a more significant influence on aphid infestation rates than environmental factors such as temperature and altitude. Similarly, Altmann and Claros (2015) noted that insect abundance and leaf damage increase with altitude, but our study emphasizes the complexity of mechanisms governing insect abundance and plant damage, requiring further analysis. Previous studies by Hullé et al. (2010) suggested higher temperatures are generally advantageous for aphids, especially for cosmopolitan pest species. However, our findings indicate a potential deviation in indigenous aphid species in temperate zones, where temperature increases may exceed their optimal conditions, leading to declining infestation rates (Durak et al., 2016). Such studies can be considered in future Himalayan research for a detailed understanding of altitudinal dependent aphid infestation in plants.

Several studies have been done in recent decades that examined the shifting treeline, reduced livestock grazing, phenological changes, and other climate change impacts in the studied region (Singh et al., 2021; Chandra et al., 2022; Singh et al., 2023), but a significant gap remains in understanding insect outbreaks, particularly aphid infestations. As over the past two decades, atmospheric temperatures during the growing season have risen by approximately 1°C (Singh and Negi, 2018), consistent with the accelerated warming observed across the Himalayas, particularly at higher altitudes. While treeline shifts have often been attributed to rising temperatures, their progression is likely constrained by nutrient limitations at higher elevations, as foliar nitrogen and soil organic carbon decrease with altitude (Müller et al., 2016; Drollinger et al., 2017). Despite lower nutrient availability, *R. campanulatum* appears to persist and even advance into alpine meadows (Singh et al., 2021), contributing to treeline densification. This species benefits from winter snowmelt, which mitigates water stress during spring and early summer (Tewari et al., 2018). However, phenological disruptions, such as reduced or complete absence of flowering in *R. arboreum* population at studied region under warming conditions (Chandra et al., 2022), suggest that rising temperatures may exceed physiological thresholds for some treeline plants.

Since in the late 1980s, the pioneer entomologists Lt. A.K. Ghosh and S. Chakrabarty recorded multiple aphid species by visual inspection of their presence, including on *Rhododendron* plants from the nearby region of Trijuginarayan, justifies our observations from 1951 onwards reinforcing these findings. However, since then, no studies have been conducted on either the aphid species or the region, resulting in a complete ignorance of this biotic pressure. As similar to the IUCN's long-standing negligence of this bio-monitor treeline species *R. campanulatum*, which has recently been taken under evaluation in 2024, this issue requires urgent and focused study.

While climatic factors have been extensively studied, the role of biotic stressors, particularly aphid infestations, remains underexplored. Our analysis of wood anatomical markers revealed that aphid activity in *R. campanulatum* has persisted at high altitudes since at least 1951. This long-term evidence highlights the resilience of aphid populations in extreme environments and their potential to influence plant health and ecosystem dynamics. Aphids, although causing minimal direct tissue damage, can significantly reduce plant vigor when infestation levels are high (Foyer et al., 2016). Unlike earlier studies linking aphid abundance to elevation and temperature (Cui et al., 2022), our findings suggest that host plant characteristics, such as tree age and nutrient availability, could also play a more significant role in aphid infestation trends. Younger trees, rich in nutrients, may act as more suitable hosts, aligning with studies showing higher insect herbivory in juvenile plants (Harrington and Clark, 2010).

Although our study is limited by the sampling strategy, which focused on older, thick-trunked trees intended for dendroclimatology studies. This approach may have excluded younger trees that could provide more detailed insights into aphid population dynamics. Additionally, the lack of direct observational data on aphid activity limits our ability to establish causal relationships between climatic variables and infestation trends. Due to the lack of past information for either for aphids or for host-interactions in the region or for the particular species, certain ecological interactions may remain undetected. However, despite all these limitations, the consistent traces of aphid activity observed in our samples provide valuable baseline data for understanding long-term trends. This work contributes to existing knowledge and enhances future research directions by documenting previously unrecognized aphid activity, revealed for the first time through this approach.

Given the accelerating impact of climate change on alpine ecosystems, it becomes crucial to investigate how biotic stressors like aphid herbivory interact with abiotic changes to influence ecosystem function and resilience. *R. campanulatum*, as a key treeline species and an integral component of high-altitude Himalayan biodiversity, warrants conservation strategies that address both biotic and abiotic pressures. By advancing our understanding of these intricate interactions, future research can contribute to the development of informed, sustainable management practices for fragile mountain ecosystems under a changing climate. Conservation efforts by the local people, foresters, and researchers become crucial to address these immediate concerns.

5. Conclusions

Our study shows that the aphid infestations in *Rhododendron campanulatum* D. Don are widespread in the Himalayas, affecting both earlywood and latewood, contrary to previous estimations. This highlights aphids' adaptability to high altitudes and extreme conditions. Despite the rise in global temperature, increased herbivory pressure suggests significant impacts on alpine ecosystems along with the impact on the species' abundance. Conservation strategies need to be developed to address both environmental changes and pest pressures. This is the first study to trace aphid infestations using wood anatomical markers, showing their presence from 1951 onwards at 3100-3400 m a.s.l., with a preference for younger trees. Urgent collaboration among wood anatomists, entomologists and ecologists is needed to address this issue.

Based on our observations and interpretations, future research directions should focus on i) sampling strategies for reconstruction: Future sampling should include younger samples, as aphids tend to prefer younger trees over mature ones after a certain age. Additionally, samples of the mixed plant species are essential, as aphids frequently change hosts after a certain period, ii) capturing full scope of potential ecological impacts, future studies should also consider daily and seasonal temperature fluctuations in relation to aphids. iii) Investigating mechanisms behind breakpoints (e.g., host resistance, predator-prey dynamics) that could clarify drivers of aphid population shifts. Understanding these temperature variations is crucial because aphids can complete their entire lifecycle in one month or less at high temperatures.

Thus, our findings underscore the necessity for updated conservation strategies and long-term ecological monitoring to preserve the biodiversity of the Himalayan region.

Acknowledgement

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Figure captions:

Fig. 1. Discrete features within the anatomical structure of woody plants. **A:** Two frost rings in *Larix sibirica*; **B:** Callous tissue caused by a wood pecker in the earlywood of *Pinus sylvestris*; **C:** Resin pocket in the latewood of *Picea abies*; **D:** Structural change in the anatomical structure in a root of *Prunus amygdalus* caused by sudden exposure of the root; **E:** Compression wood in a ring of *Larix decidua*; **F:** Tension wood in a branch of *Carpinus betulus*; **G:** Aphid trace in the latewood of *Salix alba*.

Fig. 2. **(A)** Map showing the location of the study area in the Indian Western Himalaya, with the Tungnath region highlighted as the main study location, **(B)** showing the forest landscape dominated by the studied treeline species, highlighting its distribution at the ecological treeline, **(C)** the characteristic krummholz growth form and overall height of the species in the studied region, and **(D)** close-up view of the branching structure and growth pattern of the species, adapted to its high-altitude environment.

Fig. 3. Mean annual air temperature (MAAT) (red line), spring (purple line) and winter (blue line) temperature development for the study site within the Rudraprayag district in the Western Himalayas (30.4885° N, 79.2168° E) for the period 1951-2022. Spring temperatures represent the mean values of March, April and May, while winter temperatures are based on December, January and February. The solid lines show the 10-year running means, and the dashed lines show a lowess smoother applied to the data. Temperature data are from the CRU TS v4.06 gridded dataset.

Fig. 4. Aphid traces and other disturbances. **A**: Cut surface of a *Rhododendron campanulatum* increment core showing two distinct aphid traces (grey arrows). **B**: Polished surface of a *Rhododendron campanulatum* disk. Grey arrows indicate aphid traces. The black rectangular in B indicates a (closed) wound (magnified in B1). The red rectangular in B highlights an aphid trace (magnified in B2). **E**: Micro section of *Rhododendron campanulatum*. The red rectangular highlights a frost-ring, the black rectangular shows an aphid trace. **E1**: Magnified frost-ring, showing the bend rays (black arrow) and a layer of collapsed cells (white arrow) due to the frost event. **E2**: Magnified aphid trace, showing the locally restricted callous tissue (irregular cells) transferring back to regular cell structure after a few cell rows.

Fig. 5. Reconstruction of aphid infestation in *Rhododendron campanulatum* D.DON samples from 1951 to 2022 using segmented regression analysis. Panel **(a)** shows the number of infested aphid traces per year across the entire sampled elevation range (3100–3400 m a.s.l.), while panels **(b), (c),** and **(d)** present the number of aphid traces observed at low-altitude sites (3100–3200 m a.s.l.), mid-altitude sites (3200–3300 m a.s.l.), and high-altitude sites (3300–3400 m a.s.l.), respectively. Blue bars with dots represent the number of infested samples per year, the red solid line indicates the accumulated sample depth, and the purple line represents the segmented regression model fit. Breakpoint years, signifying changes, are marked by yellow dotted lines and annotated with yellow numbers. Note that the number of affected samples has been transformed by square root.

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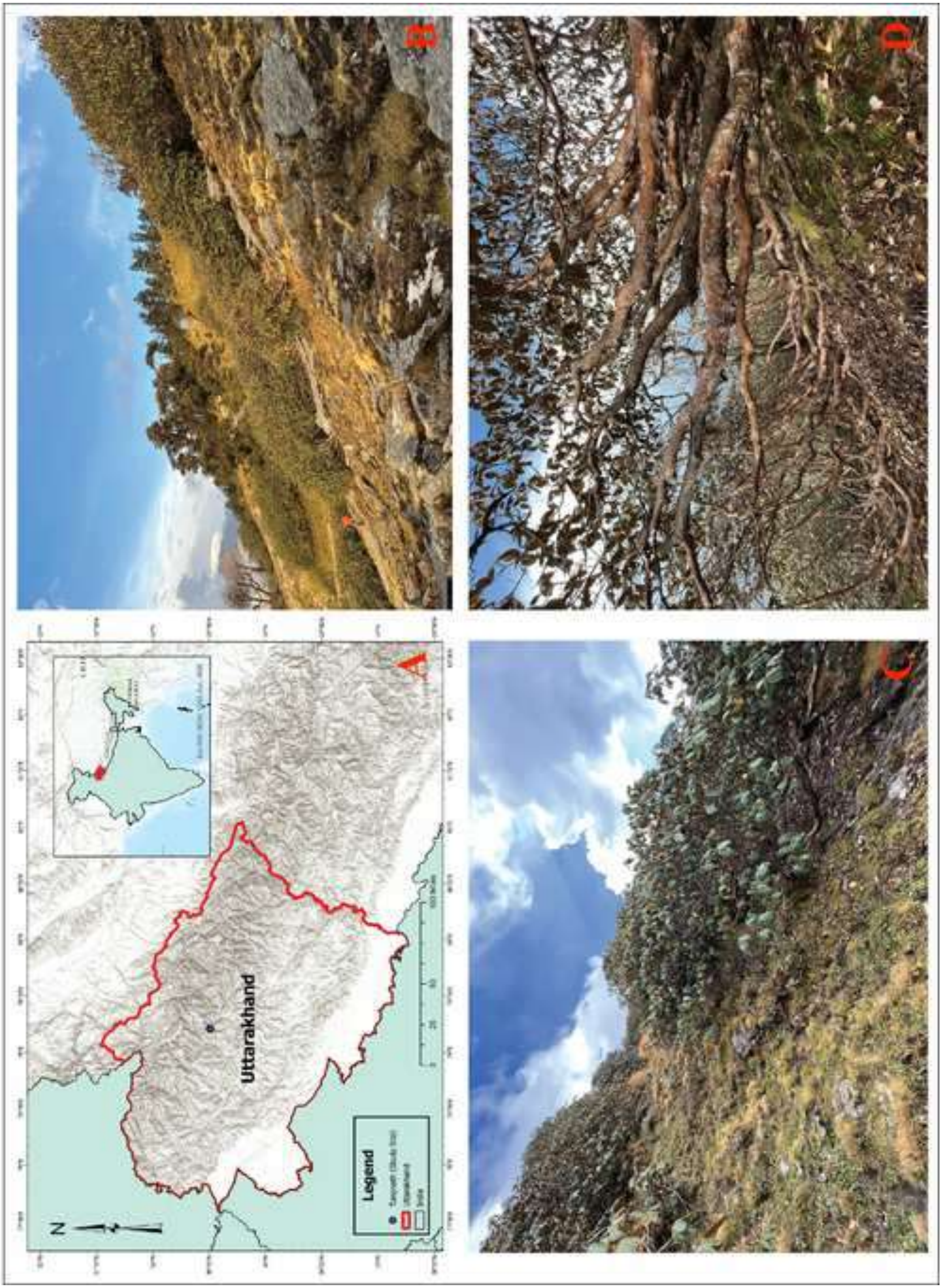
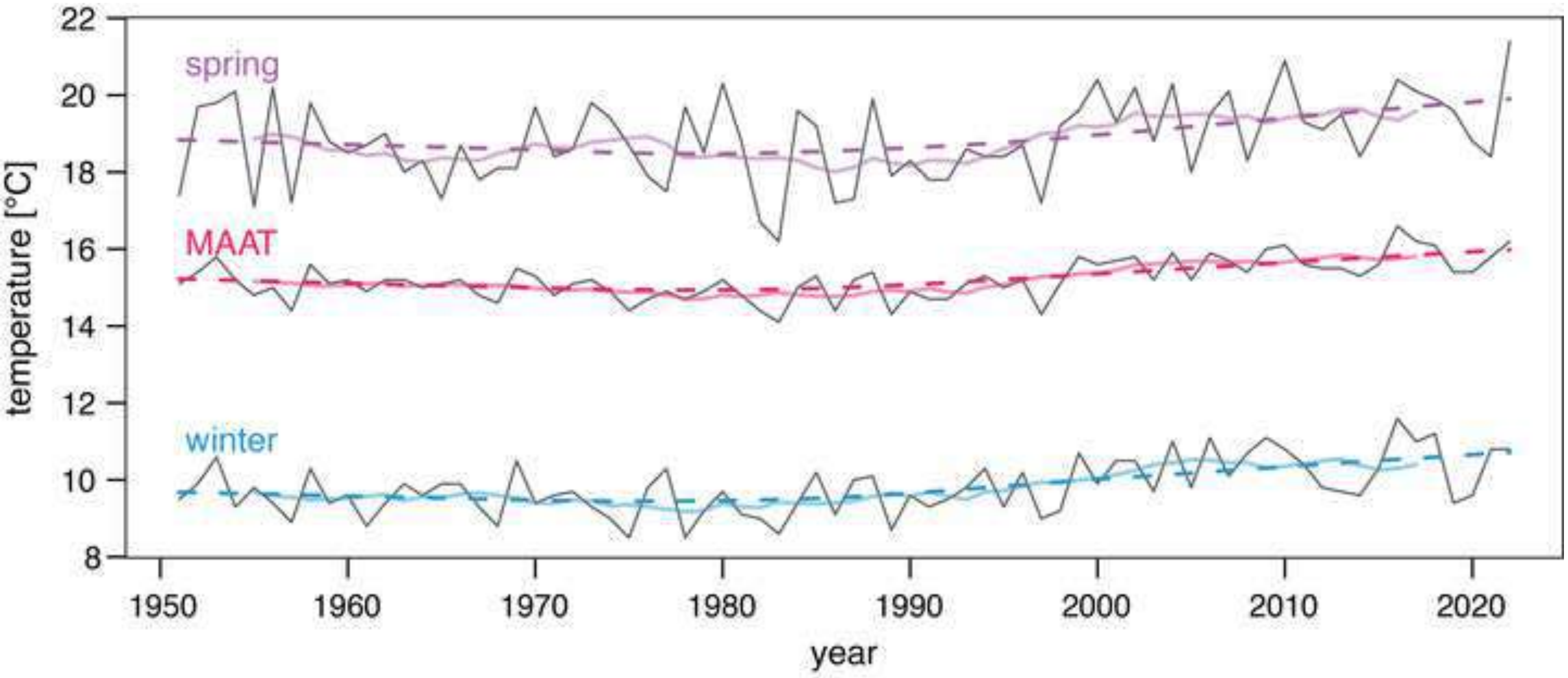
Figure_2

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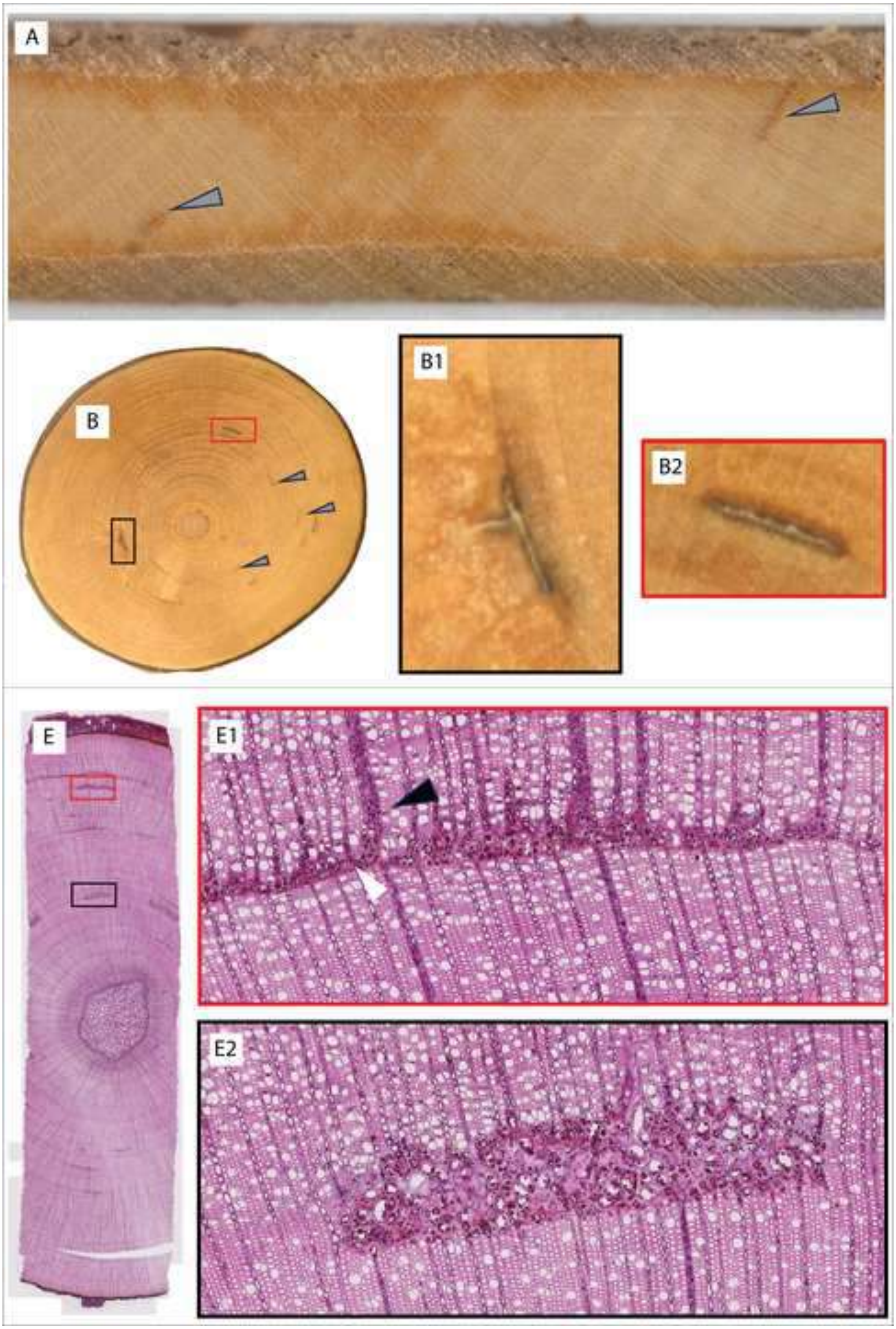
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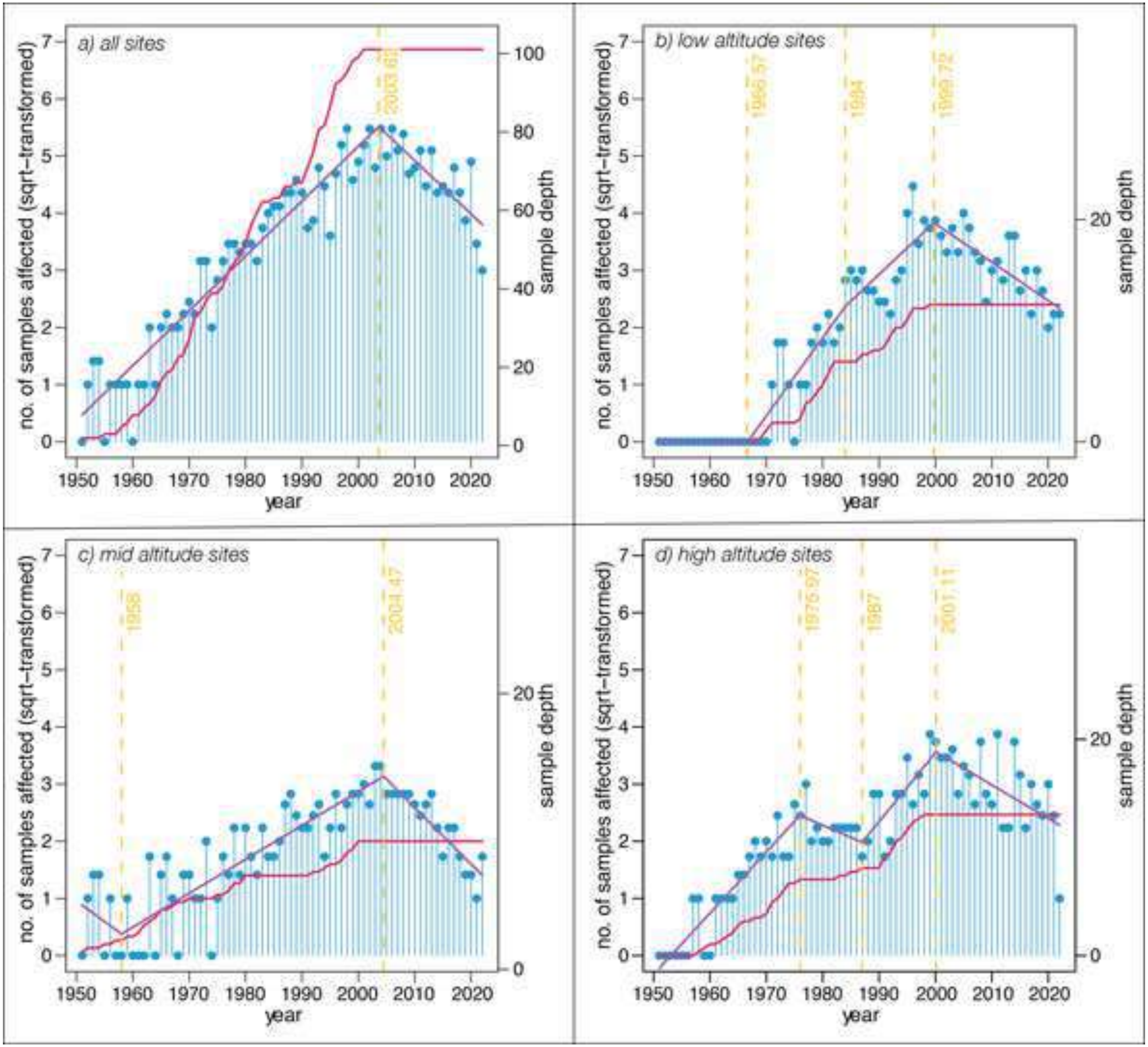

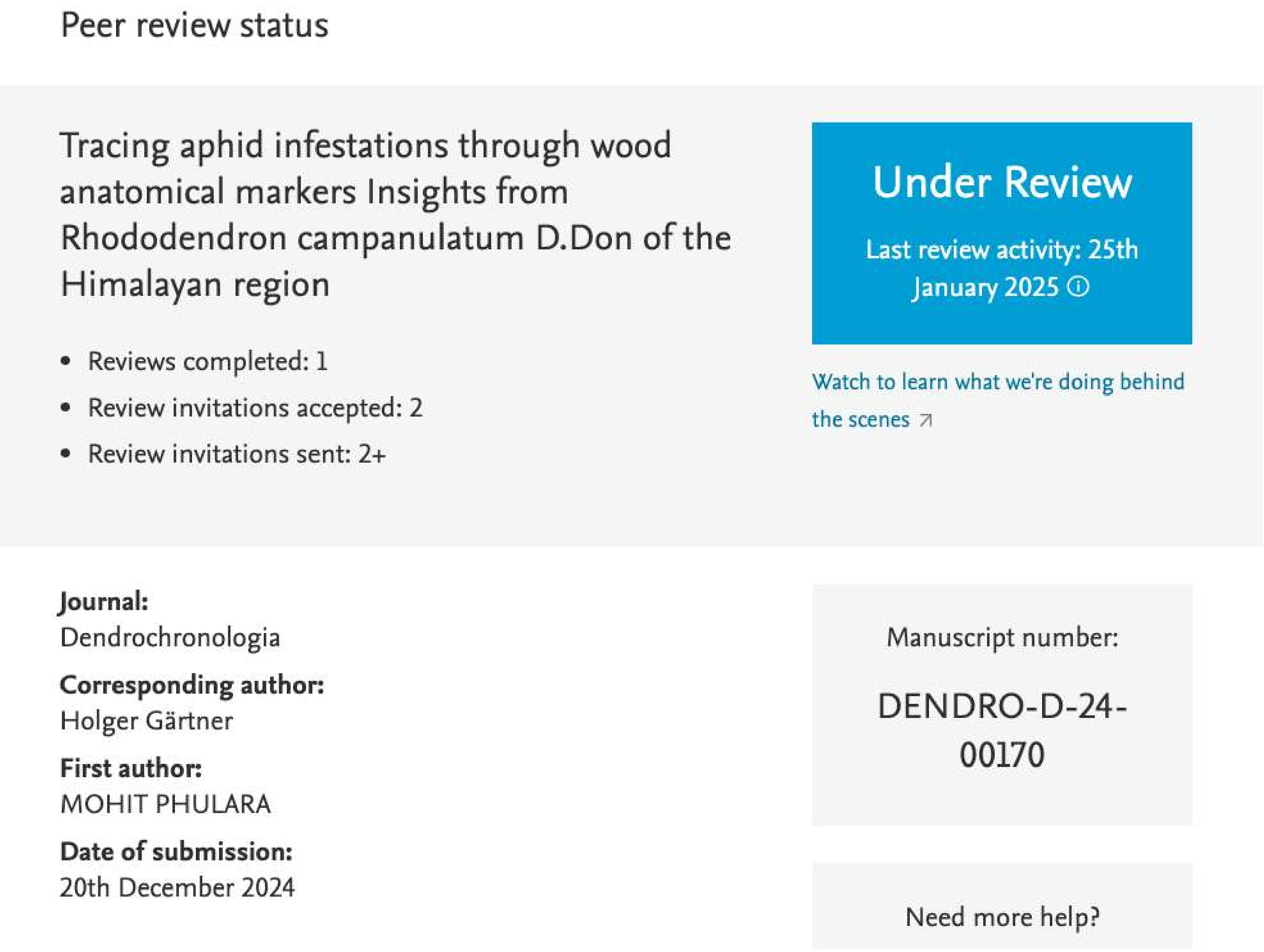

Peer review status

Tracing aphid infestations through wood anatomical markers Insights from Rhododendron campanulatum D.Don of the Himalayan region

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Corresponding author:
Holger Gärtner

First author:
MOHIT PHULARA

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Need more help?

Declaration of My Contribution and Co-authors' Contributions

Sosnowiec, 21/03/2025

Mohit Phulara
First and last name of co-author of the publication

Institute of Earth Sciences, University of Silesia in Katowice
Affiliation

A STATEMENT OF THE APPLICANT'S AUTHOR OF THEIR CONTRIBUTION TO THE WORK

I declare that for the following works:

I. **Phulara, M**., Opała-Owczarek, M., & Owczarek, P. (2022). Climatic signals on growth ring variation in *Salix herbacea*: Comparing two contrasting sites in Iceland. *Atmosphere, 13*(5), 718.

My participation consisted of preparing thin sections and measuring samples, contributing in dendrochronological and dendroclimatic analyses, and to the conceptualization of the study and methodology design. I also prepared some figures to visualize this work effectively. Furthermore, I wrote the initial draft of the thesis—incorporating critical analytical insights—and played a key role in the final review and editing process.

II. **Phulara, M.,** Balzano, A., Opała-Owczarek, M., Owczarek, P., & Merela, M. (2024). Insights from roots to stems: Comparative wood anatomy and dendroclimatic investigation of two *Salix* species in Iceland. *Forests, 15*(10), 1707.

My participation consisted of establishing a collaborative partnership with the University of Ljubljana and initiating the conceptualization of the research idea alongside my co-authors. I prepared the samples according to the established method at the University of Ljubljana (UL) laboratory, contributed to the dendrochronological and dendroclimatic analyses, and performed the relevant statistical analyses. Additionally, I prepared all the figures used in the study, drafted the initial version of the manuscript, and contributed significantly to the final review through detailed writing, editing, and refinement of the text.

III. **Phulara, M.,** Opała-Owczarek, M., Szymański, W., Ślopek, J., Węgrzyn, M., Łupikasza, E., Korabiewski, B., & Owczarek, P. (2025). Multiple factors controlling polar willow growth in the High Arctic (Svalbard): Implications for future prediction of tundra productivity. Manuscript under review in *Global Ecology and Conservation.*

My participation consisted of participating in the field research, collecting samples for laboratory analysis, preparing thin sections and measuring samples, as well as contributing to dendrochronological and dendroclimatic analyses. I co-contributed in conceptualizing the study and prepared initial sections of the manuscript, including the Introduction and Methodology. After receiving results and substantive contributions from co-authors, I integrated these into the manuscript, performed the final refinement, and prepared the text of Discussion and Conclusions. I too contributed significantly to the final manuscript review, including thorough editing and refinement of the text.

IV. Owczarek, P., **Phulara, M.,** Shuber, P., Korabiewski, B., Błaś, M., & Opała-Owczarek, M. (2024). Varied growth response of high alpine *Rhododendron myrtifolium* and forest zone tree species to climate warming in the Eastern Carpathians, Ukraine. *Dendrochronologia, 85*, 126198.

My participation consisted of preparing thin sections and measuring shrub samples of *Rhododendron myrtifolium*, as well as contributing to dendrochronological and dendroclimatic analyses that were required for this study. Additionally, I co-contributed in the conceptual framework of the research and prepared initial sections of the manuscript, including the Introduction and Methodology. Finally, I also conducted an extensive review and editing of the entire manuscript.

V. Phulara, M., Opała-Owczarek, M., Owczarek, P., Bast, A., Bhatt, I. D., & Gärtner, H. (2025). Tracing aphid infestations through wood anatomical markers: Insights from *Rhododendron campanulatum* D. Don of the Himalayan region. Manuscript under review in *Dendrochronologia.*

My participation included establishing collaborative partnerships with the Swiss Federal Research Institute (WSL) and the Gobind Ballabh Pant National Institute of Himalayan Environment (GBPNIHE), as well as co-leading the conceptualization and overall design of this research article alongside my co-authors. I conducted fieldwork in the Himalaya region to collect the necessary samples and successfully secured NAWA-Bekker funding for my laboratory visit to WSL. At the WSL laboratory, I prepared thin sections according to established protocols and measured samples using WinCELL software. Furthermore, I drafted the initial manuscript, integrated contributions from all authors, and played a key role in finalizing the text through comprehensive review, writing, detailed editing, and refinement.

Signed by /
Podpisano przez:

Mohit Phulara
Uniwersytet
Śląski

Date / Data:
2025-03-27 09:14

....

Signature of the author of the publication

Załącznik nr 10
do pisma okólnego nr 2
Prorektora ds. nauki i finansów
z dnia 19 lutego 2024 r.

OŚWIADCZENIE

WSPOŁAUTORA OSOBY UBIEGAJĄEJ SIĘ O WŁASNYM WKŁADZIE W POWSTAWANIE PRACY

Miejsce Wrocław, dnia 23.03.2025

Piotr Owczarek
Imię i nazwisko współautora publikacji

Instytut Geografii i Rozwoju Regionalnego, Uniwersytet Wrocławski
Afiliacja

OŚWIADCZENIE

Oświadczam, że w pracy:

Phulara, M., Opała-Owczarek, M., & Owczarek, P. (2022). Climatic signals on growth ring variation in *Salix herbacea*: Comparing two contrasting sites in Iceland. *Atmosphere*, *13*(5), 718.

(autorzy, rok wydania, tytuł, czasopismo lub wydawca, tom, strony)

Mój udział polegał na: uczestnictwie w badaniach terenowych, zebraniu materiału badawczego w terenie, przygotowaniu treści artykułu (obszar badań, część wprowadzenia i dyskusji wyników), przygotowaniu rycin.

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Podpis współautora publikacji

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z dnia 19 lutego 2024 r.

OSWIADCZENIE

WSPÓŁAUTORA OSOBY UBIEGAJĄCEJ SIĘ O WŁASNYM WKŁADZIE W POWSTAWANIE PRACY

Katowice . dnia 23.03.2025 r.

Magdalena Opała-Owczarek
imię i nazwisko współautora publikacji

Uniwersytet Śląski w Katowicach
Afiliacja

OŚWIADCZENIE

Oświadczam, że w pracy:

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Mój udział polegał na: pozyskaniu środków finansowych na badania, kierowaniu projektami naukowymi częściowo obejmującymi badania opisane w pracy, przygotowaniu koncepcji publikacji, uczestnictwie w badaniach terenowych, przygotowanie fragmentów manuskryptu, wykonaniu wstępnej analizy dendroklimatycznej i współudziale w opracowaniu statystycznym skal dendrochronologicznych, współudziale w przygotowaniu odpowiedzi na recenzje.

....
Podpis współautora publikacji

UNIVERSITY
OF LJUBLJANA
BF
Biotechnical
Faculty
Department of Wood Science
and Technology

A STATEMENT OF THE APPLICANT'S CO-AUTHOR OF THEIR CONTRIBUTION TO THE WORK

Location: Ljubljana, date 3.3.2025

Assoc. prof. dr. Maks Merela;
University of Ljubljana, Biotechnical Faculty, Department of Wood Science and Technology

STATEMENT

I declare that for the following work:
Phulara, M., Balzano, A., Opała-Owczarek, M., Owczarek, P., & Merela, M. (2024). Insights from roots to stems: Comparative wood anatomy and dendroclimatic investigation of two *Salix* species in Iceland. *Forests, 15*(10), 1707.

My participation consisted of planning the methodology for preparing microscopic slides (thin wood slices) according to the established method of our laboratory. I collaborated with advice in analyzing the microscopy results and in writing the methodological part of the article covering the work in our laboratory.

MAKS MERELA
Digitally signed by MAKS MERELA
DN: c=SI, st=Slovenija, o=UL BF, 2.5.4.97=VATSI-94761795, givenName=MAKS, sn=MERELA, cn=MAKS MERELA, serialNumber=2470484416048
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Signature of the co-author of the publication

University of Ljubljana
Biotechnical Faculty
Department of Wood Science and Technology

Angela Balzano

Ljubljana, 03.03.2025

A STATEMENT OF THE APPLICANT'S CO-AUTHOR OF THEIR CONTRIBUTION TO THE WORK

STATEMENT

I declare that for the following work:

Phulara, M., Balzano, A., Opała-Owczarek, M., Owczarek, P., & Merela, M. (2024). Insights from roots to stems: Comparative wood anatomy and dendroclimatic investigation of two Salix species in Iceland. Forests, 15(10), 1707.

My participation consisted of contributing to conceptualization, methodology, resource provision, and involvement in writing and editing the manuscript

Angela Balzano Digitally signed by Angela Balzano
Date: 2025.03.03 10:44:55 +01'00'

....

Signature of the co-author of the publication

* applies to co-authors

University of Ljubljana
Biotechnical Faculty
Department of Wood
Science and Technology
Rožna dolina, C. VIII/34
1000 Ljubljana
Slovenia
T 01 320 3000
F 01 257 2297
www.bf.uni-lj.si

Załacznik nr 10
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OŚWIADCZENIE

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Piotr Owczarek
imię i nazwisko współautora publikacji

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Phulara. M.. Balzano. A., Opała-Owczarek, M., Owczarek, P., & Merela, M. (2024). Insights from roots to stems: Comparative wood anatomy and dendroclimatic investigation of two *Salix* species in Iceland. *Forests. 15*(10). 1707.

(autorzy, rok wydania, tytuł, czasopismo lub wydawca, tom, strony)

Mój udział polegał na: uczestnictwie w pracach terenowych, zebraniu okazów krzewinek do badań laboratoryjnych, przygotowanie części treści manuskryptu (obszar badań), ocenie formalnej i merytorycznej wersji wstępnej manuskryptu.

....
Podpis współautora publikacji

Załacznik nr 10
do pisma okólnego nr 2
Prorektora ds. nauki i finansów
z dnia 19 lutego 2024 r.

OSWIADCZENIE

WSPÓŁAUTORA OSOBY UBIEGAJĄCEJ SIĘ O WŁASNYM WKŁADZIE W POWSTAWANIE PRACY

Katowice . dnia 23.03.2025 r.

Magdalena Opała-Owczarek
imię i nazwisko współautora publikacji

Uniwersytet Śląski w Katowicach
Afiliacja

OŚWIADCZENIE

Oświadczam, że w pracy:

Phulara, M., Balzano, A., Opała-Owczarek, M., Owczarek, P., & Merela, M. (2024). Insights from roots to stems: Comparative wood anatomy and dendroclimatic investigation of two *Salix* species in Iceland. *Forests*, *15*(10), 1707.

(autorzy, rok wydania, tytuł, czasopismo lub wydawca, tom, strony)

Mój udział polegał na: pozyskaniu środków finansowych na badania terenowe, kierowaniu projektami naukowymi częściowo obejmującymi badania opisane w pracy, uczestnictwie w badaniach terenowych, współudziale w wykonaniu analiz dendroklimatycznych i przygotowaniu fragmentów tekstu, ocenie formalnej i merytorycznej wstępnej wersji artykułu.

....
Podpis współautora publikacji

Załącznik nr 10
do pisma okólnego nr 2
Prorektora ds. nauki i finansów
z dnia 19 lutego 2024 r.

OŚWIADCZENIE

WSPÓŁAUTORA OSOBY UBIEGAJĄĘJ SIĘ O WŁASNYM WKŁADZIE W POWSTAWANIE PRACY

Miejsce Sosnowiec, dnia 06 marca 2025

Ewa Łupikasza
Imię i nazwisko współautora publikacji

Uniwersytet Śląski,
Wydział Nauk Przyrodniczych
Instytut Nauk o Ziemi
Afiliacja

OŚWIADCZENIE

Oświadczam, że w pracy:

Phulara, M., Opała-Owczarek, M., Szymański, W., Ślopek, J., Węgrzyn, M., Łupikasza, E., Korabiewski, B., & Owczarek, P. (2025). Multiple factors controlling polar willow growth in the High Arctic (Svalbard): Implications for future prediction of tundra productivity. Manuscript under review in *Global Ecology and Conservation.*

(autorzy, rok wydania, tytuł, czasopismo lub wydawca, tom, strony)

Mój udział polegał na wykonaniu analizy statystycznej danych meteorologicznych.

Signed by /
Podpisano przez:

Ewa Bożena
Łupikasza
Uniwersytet Śląski w
Katowicach

Date / Data:
2025-03-06 10:15

Podpis współautora publikacji

Załącznik nr 10
do pisma okólnego nr 2
Prorektora ds. nauki i finansów
z dnia 19 lutego 2024 r.

OŚWIADCZENIE

WSPÓŁAUTORA OSOBY UBIEGAJĄEJ SIĘ O WŁASNYM WKŁADZIE W POWSTAWANIE PRACY

Miejsce Kraków, dnia 03.03.2025

Michał Węgrzyn
Imię i nazwisko współautora publikacji

Instytut Botaniki
Wydział Biologii
Uniwersytet Jagielloński
Afiliacja

OŚWIADCZENIE

Oświadczam, że w pracy:

Phulara, M., Opała-Owczarek, M., Szymański, W., Ślopek, J., Węgrzyn, M., Łupikasza, E., Korabiewski, B., & Owczarek, P. (2025). Multiple factors controlling polar willow growth in the High Arctic (Svalbard): Implications for future prediction of tundra productivity. Manuscript under review in *Global Ecology and Conservation.*

(autorzy, rok wydania, tytuł, czasopismo lub wydawca, tom, strony)

Mój udział polegał na wykonaniu badań terenowych i opracowaniu wyników w zakresie danych botanicznych.

....
Podpis współautora publikacji

Załącznik nr 10
do pisma okólnego nr 2
Prorektora ds. nauki i finansów
z dnia 19 lutego 2024 r.

OŚWIADCZENIE

WSPÓŁAUTORA OSOBY UBIEGAJĄEJ SIĘ O WŁASNYM WKŁADZIE W POWSTAWANIE PRACY

Miejsce Wrocław dnia 5.03.2025

Bartosz Korabiewski
Imię i nazwisko współautora publikacji

Uniwersytet Wrocławski
Instytut Geografii i Rozwoju Regionalnego, Wrocław
Afiliacja

OŚWIADCZENIE

Oświadczam, że w pracy:

Phulara, M., Opała-Owczarek, M., Szymański, W., Ślopek, J., Węgrzyn, M., Łupikasza, E., Korabiewski, B., & Owczarek, P. (2025). Multiple factors controlling polar willow growth in the High Arctic (Svalbard): Implications for future prediction of tundra productivity. Manuscript under review in *Global Ecology and Conservation.*

(autorzy, rok wydania, tytuł, czasopismo lub wydawca, tom, strony)

Mój udział polegał na: pracach terenowych i kameralnych. W terenie konsultowałem i współuczestniczyłem w wyborach stanowisk do szczegółowych badań geomorfologiczno-gleboznawczych, gdzie wykonywane były profile glebowe i zakładałem instrumenty pomiarowe rejestrujące parametry termiczno-wilgotnościowe gleby i powietrza. Dokonywałem również charakterystyki geomorfologicznej terenu. Na etapie prac kameralnych dokonywałem charakterystyki zmiany termiczno-wilgotnościowych zarejestrowanych przez założone wcześniej czujniki, co pozwalało innym co-autorom na wyciąganie wniosków i korelację warunków topoklimatycznych ze wzrostem badanych roślin.

B. Korabiewski
....
Podpis współautora publikacji

Załącznik nr 10
do pisma okólnego nr 2
Prorektora ds. nauki i finansów
z dnia 19 lutego 2024 r.

OŚWIADCZENIE

WSPÓŁAUTORA OSOBY UBIEGAJĄCEJ SIĘ O WŁASNYM WKŁADZIE W POWSTAWANIE PRACY

Wrocław, 8.03.2025 r.

Jacek Ślopek
Imię i nazwisko współautora publikacji

Uniwersytet Wrocławski
Afiliacja

OŚWIADCZENIE

Oświadczam, że w pracy:

Phulara, M., Opała-Owczarek, M., Szymański, W., Ślopek, J., Węgrzyn, M., Łupikasza, E., Korabiewski, B., & Owczarek, P. (2025). Multiple factors controlling polar willow growth in the High Arctic (Svalbard): Implications for future prediction of tundra productivity. Manuscript under review in *Global Ecology and Conservation*.

(autorzy, rok wydania, tytuł, czasopismo lub wydawca, tom, strony)

Mój udział polegał na pozyskaniu oraz przetwarzaniu zobrazowań satelitarnych, które posłużyły następnie do wyliczenia rozkładów przestrzennych wskaźnika wegetacyjnego NDVI, dla obszaru badań. Ponadto, brałem udział w przygotowaniu tekstu artykułu, a także przygotowaniu ilustracji (wykresów) związanych z obliczonymi wartościami wskaźnika NDVI dla opisywanych w pracy punktów pomiarowych i w ich bezpośrednim otoczeniu.

J. Ślopek

Podpis współautora publikacji

Załącznik nr 10
do pisma okólnego nr 2
Prorektora ds. nauki i finansów
z dnia 19 lutego 2024 r.

OŚWIADCZENIE

WSPOŁAUTORA OSOBY UBIEGAJĄEJ SIĘ O WŁASNYM WKŁADZIE W POWSTAWANIE PRACY

Miejsce Wrocław, dnia 23.03.2025

Piotr Owczarek
imię i nazwisko współautora publikacji

Instytut Geografii i Rozwoju Regionalnego, Uniwersytet Wrocławski
Afiliacja

OŚWIADCZENIE

Oświadczam, że w pracy:

Phulara, M., Opała-Owczarek, M., Szymański, W., Ślopek, J., Węgrzyn, M., Łupikasza, E., Korabiewski, B., & Owczarek, P. (2025). Multiple factors controlling polar willow growth in the High Arctic (Svalbard): Implications for future prediction of tundra productivity. Manuscript under review in *Global Ecology and Conservation*.

(autorzy, rok wydania, tytuł, czasopismo lub wydawca, tom, strony)

Mój udział polegał na: pozyskaniu finansowania badań, przygotowaniu koncepcji publikacji, uczestnictwie w badaniach terenowych, zebraniu materiału badawczego w terenie, przygotowaniu treści artykułu (obszar badań, część wprowadzenia i dyskusji wyników), przygotowaniu rycin.

....

Podpis współautora publikacji

Załącznik nr 10
do pisma okólnego nr 2
Prorektora ds. nauki i finansów
z dnia 19 lutego 2024 r.

OŚWIADCZENIE

WSPÓŁAUTORA OSOBY UBIEGAJĄEJ SIĘ O WŁASNYM WKŁADZIE W POWSTAWANIE PRACY

Miejsce Kraków, dnia 28.02.2025

Wojciech Szymański
Imię i nazwisko współautora publikacji

Uniwersytet Jagielloński
Instytut Geografii i Gospodarki Przestrzennej
Pracownia Gleboznawstwa i Geografii Gleb
Afiliacja

OŚWIADCZENIE

Oświadczam, że w pracy:

Phulara, M., Opała-Owczarek, M., Szymański, W., Ślopek, J., Węgrzyn, M., Łupikasza, E., Korabiewski, B., & Owczarek, P. (2025). Multiple factors controlling polar willow growth in the High Arctic (Svalbard): Implications for future prediction of tundra productivity. Manuscript under review in *Global Ecology and Conservation.*

Mój udział polegał na przeprowadzeniu terenowych badań gleboznawczych, pobraniu próbek glebowych do analiz laboratoryjnych, oznaczeniu fizycznych i chemicznych właściwości gleb w laboratorium, opisaniu uzyskanych wyników właściwości gleb.

W. Szymański
....
Podpis współautora publikacji

Załącznik nr 10
do pisma okólnego nr 2
Prorektora ds. nauki i finansów
z dnia 19 lutego 2024 r.

OSWIADCZENIE

WSPÓŁAUTORA OSOBY UBIEGAJĄCEJ SIĘ O WŁASNYM WKŁADZIE W POWSTAWANIE PRACY

Katowice . dnia 23.03.2025 r.

Magdalena Opała-Owczarek
imię i nazwisko współautora publikacji

Uniwersytet Śląski w Katowicach
Afiliacja

OŚWIADCZENIE

Oświadczam, ze w pracy:

Phulara, M., Opała-Owczarek, M., Szymański, W., Ślopek, J., Węgrzyn, M., Łupikasza, E., Korabiewski, B., & Owczarek, P. (2025). Multiple factors controlling polar willow growth in the High Arctic (Svalbard): Implications for future prediction of tundra productivity. Manuscript under review in *Global Ecology and Conservation.*

(autorzy, rok wydania, tytuł, czasopismo lub wydawca, tom, strony)

Mój udział polegał na: uczestnictwie w badaniach terenowych, poborze prób do analiz laboratoryjnych, współudziale w opracowaniu statystycznym skal dendrochronologicznych i analizach dendroklimatologicznych, przygotowaniu części tekstu dotyczącego metodyki badań.

....
Podpis współautora publikacji

A STATEMENT OF THE APPLICANT'S CO-AUTHOR OF THEIR CONTRIBUTION TO THE WORK

Location: Sosnowiec, date: 25/03/2025

Statement on Behalf of Pavlo Shuber, Co-Author

I hereby declare on behalf of Dr. Pavlo Shuber, affiliated with the Faculty of Geography, Ivan Franko National University of Lviv, Ukraine, that for the following work:

Owczarek, P., Phulara, M., Shuber, P., Korabiewski, B., Błaś, M., & Opała-Owczarek, M. (2024). Varied growth response of high alpine Rhododendron myrtifolium and forest zone tree species to climate warming in the Eastern Carpathians, Ukraine. Dendrochronologia, 85, 126198.
(authors, year of publication, title, journal or publisher, volume, pages)

Due to the ongoing challenging circumstances in Ukraine related to the war situation, it was not possible to receive a personal statement from Pavlo Shuber. Given the significance of his contributions to this research, I am providing this statement on his behalf. His involvement included facilitating official field permissions for sample collection in the studied region and providing essential long-term meteorological data (1961–2020) from the Pozhyzhevs'ka Meteorological Station.

Signed by /
Podpisano przez:

Mohit Phulara
Uniwersytet Śląski

Date / Data: 2025-03-27 09:16

....

Signature

OŚWIADCZENIE

WSPÓŁAUTORA OSOBY UBIEGAJĄEJ SIĘ O WŁASNYM WKŁADZIE W POWSTAWANIE PRACY

Miejsce Wrocław dnia 5.03.2025

Bartosz Korabiewski
Imię i nazwisko współautora publikacji

Uniwersytet Wrocławski
Instytut Geografii i Rozwoju Regionalnego, Wrocław
Afiliacja

OŚWIADCZENIE

Oświadczam, że w pracy:

Owczarek, P., Phulara, M., Shuber, P., Korabiewski, B., Błaś, M., & Opała-Owczarek, M. (2024). Varied growth response of high alpine *Rhododendron myrtifolium* and forest zone tree species to climate warming in the Eastern Carpathians, Ukraine. *Dendrochronologia, 85*, 126198.

(autorzy, rok wydania, tytuł, czasopismo lub wydawca, tom, strony)

Mój udział polegał głównie na pracach terenowych. W terenie konsultowałem i współuczestniczyłem w wyborach stanowisk pod kątem warunków geomorfologicznych i ich ewentualnego wpływu na wzrost badanych roślin. Pomagałem również w poborze prób i dokumentowaniu stanowisk badawczych

B. Korabiewski
....
Podpis współautora publikacji

OŚWIADCZENIE

WSPOŁAUTORA OSOBY UBIEGAJĄEJ SIĘ O WŁASNYM WKŁADZIE W POWSTAWANIE PRACY

Miejsce Wrocław, dnia 23.03.2025

Piotr Owczarek
Imię i nazwisko współautora publikacji

Instytut Geografii i Rozwoju Regionalnego, Uniwersytet Wrocławski
Afiliacja

OŚWIADCZENIE

Oświadczam, że w pracy:

Owczarek, P., Phulara, M., Shuber, P., Korabiewski, B., Błaś, M., & Opała-Owczarek, M. (2024). Varied growth response of high alpine *Rhododendron myrtifolium* and forest zone tree species to climate warming in the Eastern Carpathians, Ukraine. *Dendrochronologia, 85*, 126198.
(autorzy, rok wydania, tytuł, czasopismo lub wydawca, tom, strony)

Mój udział polegał na: pozyskaniu finansowania badań, przygotowaniu koncepcji publikacji, uczestnictwie w badaniach terenowych, zebraniu materiału badawczego w terenie, przygotowaniu treści artykułu (obszar badań, część wprowadzenia i dyskusji wyników), przygotowaniu rycin, odpowiedzi na recenzje.

....
Podpis współautora publikacji

Załącznik nr 10
do pisma okólnego nr 2
Prorektora ds. nauki i finansów
z dnia 19 lutego 2024 r.

OŚWIADCZENIE

WSPÓŁAUTORA OSOBY UBIEGAJĄEJ SIĘ O WŁASNYM WKŁADZIE W POWSTAWANIE PRACY

Miejsce ...Wrocław...., dnia ...04.03.2025...

Marek Błaś.......
Imię i nazwisko współautora publikacji

...University of Wrocław.......................................
Afiliacja

OŚWIADCZENIE

Oświadczam, że w pracy:

Owczarek, P., Phulara, M., Shuber, P., Korabiewski, B., Błaś, M., & Opała-Owczarek, M. (2024). Varied growth response of high alpine *Rhododendron myrtifolium* and forest zone tree species to climate warming in the Eastern Carpathians, Ukraine. *Dendrochronologia, 85*, 126198.
(autorzy, rok wydania, tytuł, czasopismo lub wydawca, tom, strony)

Mój udział polegał na przygotowaniu rdzeni do analizy z wykorzystaniem komputerowego oprogramowania WinDendro i następnie wyznaczeniu sekwencji szerokości przyrostów rocznych drzew.

opisać szczegółowo swój własny – (a nie osoby ubiegającej się) – udział w powstaniu pracy, (np. mój udział w powstanie tej publikacji polegał na wykonaniu doświadczeń techniką ....., analizie statystycznej wyników eksperymentów zilustrowanych na ryc. ...., przygotowaniu tekstu manuskryptu zamieszczonego w rozdziale......, kierowaniu projektem naukowym obejmującym badania opisane w tej pracy, itp.).*

Marek Błaś
....
Podpis współautora publikacji

Załacznik nr 10
do pisma okólnego nr 2
Prorektora ds. nauki i finansów
z dnia 19 lutego 2024 r.

OSWIADCZENIE
WSPÓŁAUTORA OSOBY UBIEGAJĄCEJ SIĘ O WŁASNYM WKŁADZIE W POWSTAWANIE PRACY

Katowice . dnia 23.03.2025 r.

Magdalena Opała-Owczarek
Imię i nazwisko współautora publikacji

Uniwersytet Śląski w Katowicach
Afiliacja

OŚWIADCZENIE

Oświadczam, że w pracy:

Owczarek. P.. Phulara. M.. Shuber. P., Korabiewski, B., Błaś, M., & Opała-Owczarek, M. (2024). Varied growth response of high alpine *Rhododendron myrtifolium* and forest zone tree species to climate warming in the Eastern Carpathians, Ukraine. *Dendrochronologia*, *85*. 126198.

(autorzy, rok wydania, tytuł, czasopismo lub wydawca, tom, strony)

Mój udział polegał na: współudziale w opracowaniu koncepcji artykułu, współudziale w opracowaniu statystycznym skal dendrochronologicznych i analizach dendroklimatologicznych, przygotowaniu fragmentów tekstu, współudziale przy odpowiedzi na recenzje, ocenie formalnej i merytorycznej artykułu.

Opała- Owcz

....
Podpis współautora publikacji

Swiss Federal Research Institute WSL
Eidg. Forschungsanstalt WSL
Institut fédéral de recherches WSL
Istituto federale di ricerca WSL

Davos, March 6, 2025

WSL Institute for Snow and Avalanche Research SLF
Alpine Environment and Natural Hazards
Dr Alexander Bast
alexander.bast@slf.ch

Statement of the applicant's co-author of their contribution to the work

To Whom It May Concern

I hereby declare that for the following work:

Phulara, M., Opała-Owczarek, M., Owczarek, P., Bast, A., Bhatt, I. D., & Gärtner, H. (2025). Tracing aphid infestations through wood anatomical markers: Insights from *Rhododendron campanulatum* D. Don of the Himalayan region. Manuscript under review in *Dendrochronologia.*

My contribution to this work primarily involved conducting statistical analyses and creating figures, specifically for the segmented regression analysis. Additionally, I wrote a significant portion of the statistical methods section. I also contributed to the overall writing and editing of the paper based on the suggestions and work of Mr. Mohit Phulara.

Yours sincerely

Alexander Bast

Eidg. Forschungsanstalt WSL
Institut fédéral de recherches WSL
Istituto federale di ricerca WSL
Swiss Federal Research Institute WSL

Ein Institut des ETH-Bereichs

To whom it may concern

Birmensdorf, 03.03.2025

Dr. Holger Gärtner

A STATEMENT OF THE APPLICANT'S CO-AUTHOR OF THEIR CONTRIBUTION TO THE WORK

Holger Gärtner
(First and last name of co-author of the publication)

Swiss Federal Research Institute WSL, Dendrosciences, Zürcherstrasse 111, CH-8903 Birmensdorf
(Affiliation)

STATEMENT

I declare that for the following work:

Phulara, M., Opała-Owczarek, M., Owczarek, P., Bast, A., Bhatt, I. D., & Gärtner, H. (2025). Tracing aphid infestations through wood anatomical markers: Insights from Rhododendron campanulatum D. Don of the Himalayan region. Manuscript under review in Dendrochronologia.
(authors, year of publication, title, journal or publisher, volume, pages)

My participation consisted of contributing to the analyses of aphid traces, the anatomical comparison to other anatomical markers and to the overall writing and editing of the paper.

Holger Gärtner
……………………………………………………………
Signature of the co-author of the publication

गोविन्द बल्लभ पन्त राष्ट्रीय हिमालयी पर्यावरण संस्थान
G.B. Pant National Institute of Himalayan Environment (NIHE)
कोसी–कटारमल, अल्मोड़ा– 263643, उत्तराखण्ड
Kosi-Katarmal, Almora- 263 643, Uttarakhand

A STATEMENT OF THE APPLICANT'S CO-AUTHOR OF THEIR CONTRIBUTION TO THE WORK

Location: Kosi, Almora; date 10.03.2025

Dr. Indra D. Bhatt
First and last name of co-author of the publication

Center for Biodiversity Conservation and Management, G.B. Pant National Institute of Himalayan Environment, Almora, Uttarakhand, India
Affiliation

STATEMENT

I declare that for the following work:

Phulara, M., Opała-Owczarek, M., Owczarek, P., Bast, A., Bhatt, I. D., & Gärtner, H. (2025). Tracing aphid infestations through wood anatomical markers: Insights from *Rhododendron campanulatum* D. Don of the Himalayan region. Manuscript under review in *Dendrochronologia.*
(authors, year of publication, title, journal or publisher, volume, pages)

My participation included securing field permissions for sample collection from the study regions, as well as contributing to the final review and editing of the draft.

Signature of the co-author of the publication

(पर्यावरण, वन एवं जलवायु परिवर्तन मंत्रालय, भारत सरकार का स्वायत्तशासी संस्थान)
(An Autonomous Institute of Ministry of Environment, Forest & Climate Change, Government of India)
दूरभाष : (05962) - 241150, 241041 फैक्स : (05962) - 241150
Phone: (05962) - 241150, 241041 Fax: (05962) - 241150
E-mail: ao@gbpihed.nic.in

Załącznik nr 10
do pisma okólnego nr 2
Prorektora ds. nauki i finansów
z dnia 19 lutego 2024 r.

OŚWIADCZENIE

WSPÓŁAUTORA OSOBY UBIEGAJĄEJ SIĘ O WŁASNYM WKŁADZIE W POWSTAWANIE PRACY

Miejsce Wrocław, dnia 23.03.2025

Piotr Owczarek
imię i nazwisko współautora publikacji

Instytut Geografii i Rozwoju Regionalnego, Uniwersytet Wrocławski
Afiliacja

OŚWIADCZENIE

Oświadczam, że w pracy:

Phulara, M., Opała-Owczarek, M., Owczarek, P., Bast, A., Bhatt, I. D., & Gärtner, H. (2025). Tracing aphid infestations through wood anatomical markers: Insights from *Rhododendron campanulatum* D. Don of the Himalayan region. Manuscript under review in *Dendrochronologia*.

(autorzy, rok wydania, tytuł, czasopismo lub wydawca, tom, strony)

Mój udział polegał na dyskusji wyników oraz ocenie formalnej i merytorycznej wersji wstępnej manuskryptu.

POwczarek
....
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Mój udział polegał na ocenie formalnej i merytorycznej wstępnej wersji artykułu, współpracy w przygotowaniu i dyskusji finalnej wersji artykułu.

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