

Article

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

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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 Pistilfjörður 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].

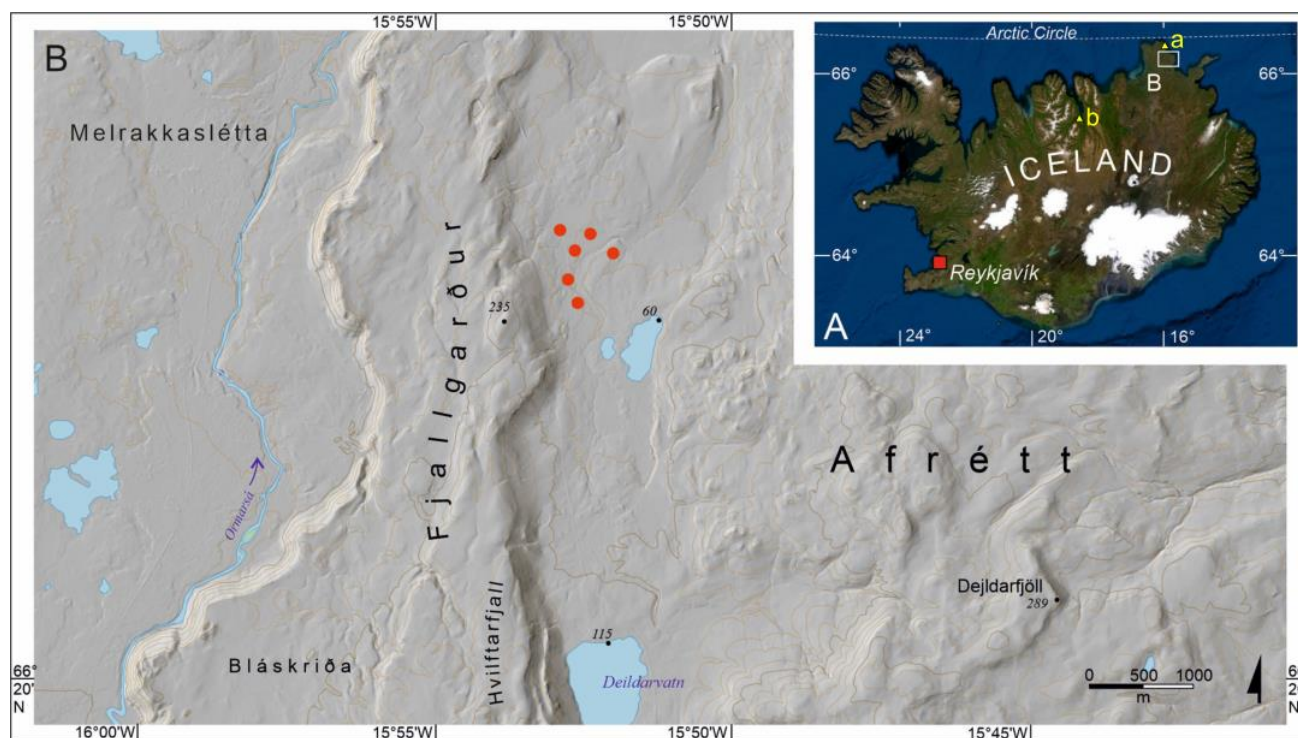


Figure 1. (A) Location of the study area (B) in Northeastern Iceland with an indication of meteorological stations (a) Raufarhöfn and (b) Akureyri, and (B) detailed study area map with locations of the sampling points marked with red color dots (background maps from the National Land Survey of Iceland.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

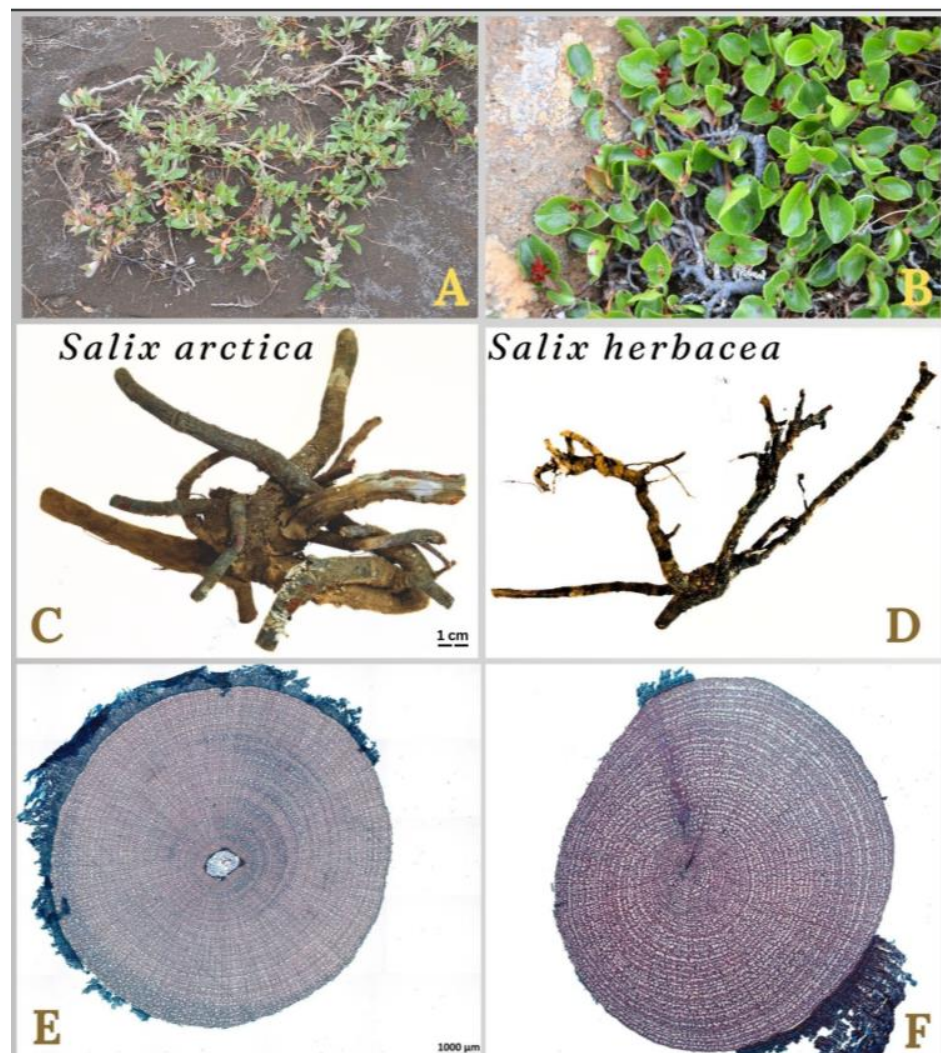


Figure 2. From the field collection to lab examination of the species, highlighting the prepared cross-sections. (A,B) *S. arctica* (SAAR) and *S. herbacea* (SAHE) at the field site, (C,D) collected specimens (whole individuals) for SAAR and SAHE, and (E,F) their prepared micro-sections (E) stem section 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
<i>S. herbacea</i>	3	05	10	15
<i>S. arctica</i>	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.

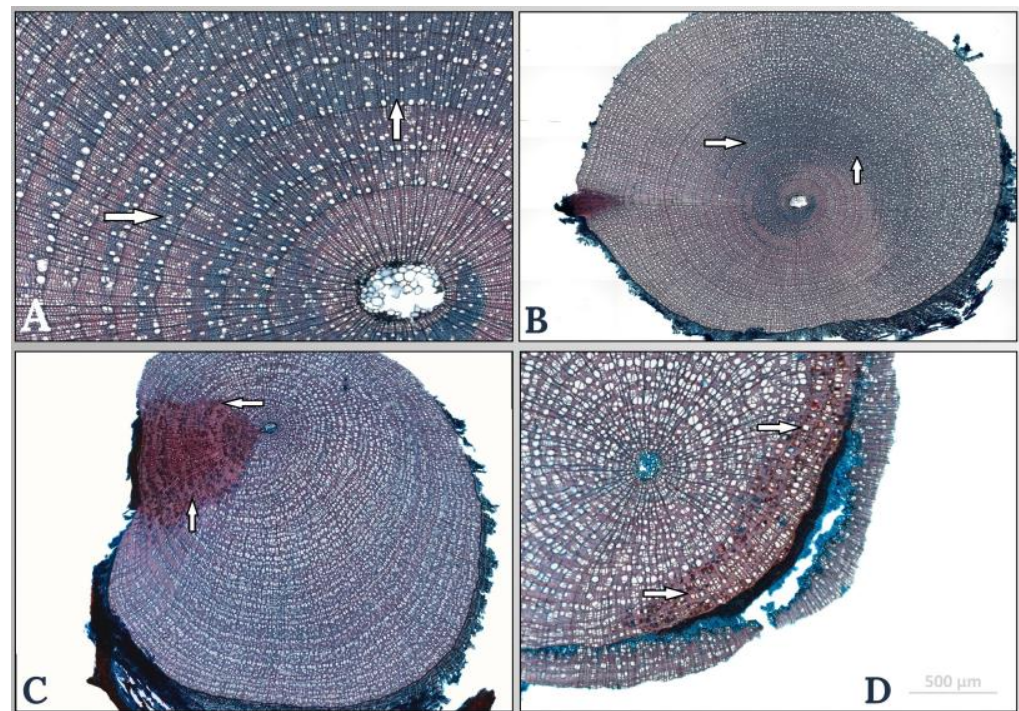


Figure 3. Cross-sections of the stem part of (A,B) *S. arctica* more often show tension wood, (C,D) *S. herbacea* more often shows the presence of gums and phenolic compounds (white arrows) in the reaction zone after an injury (scale—500 μ m).

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.

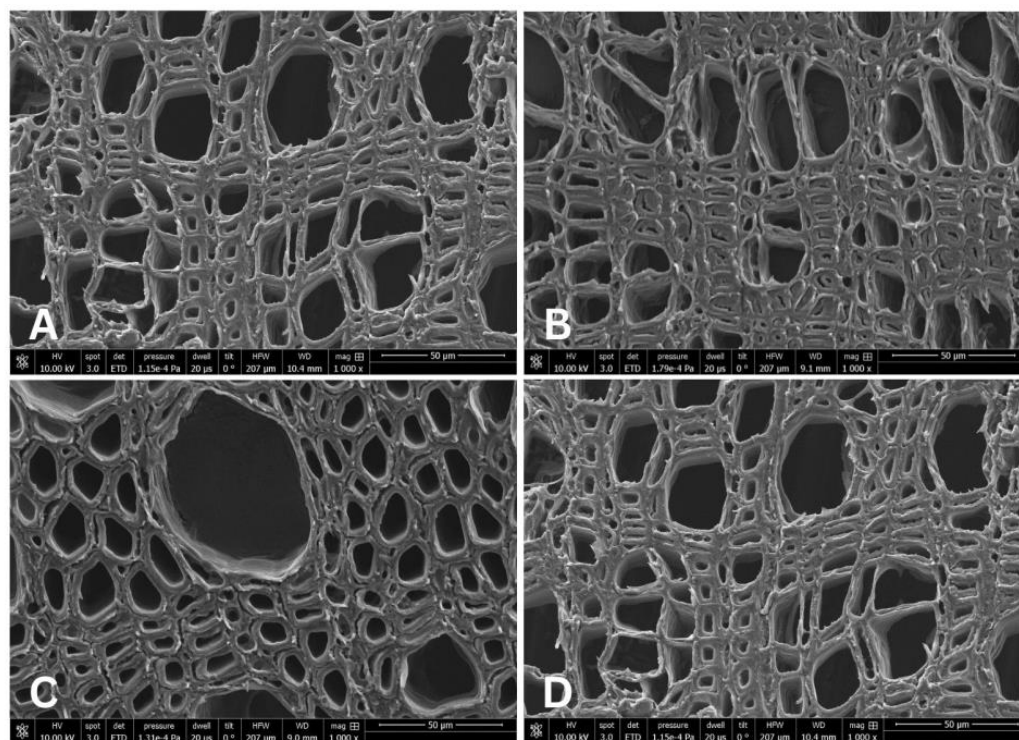


Figure 4. SEM photographs showing cross-sections of the root (A–C) and stem (B–D) of *S. herbacea* (A,B) and *S. arctica* (C,D), respectively. In the photographs, the conductive elements in normal wood are shown.

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/mm².

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/mm². 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	<i>Salix herbacea</i> (SAHE)				<i>Salix arctica</i> (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/mm ²		359/mm ²	50	232/mm ²		130/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	

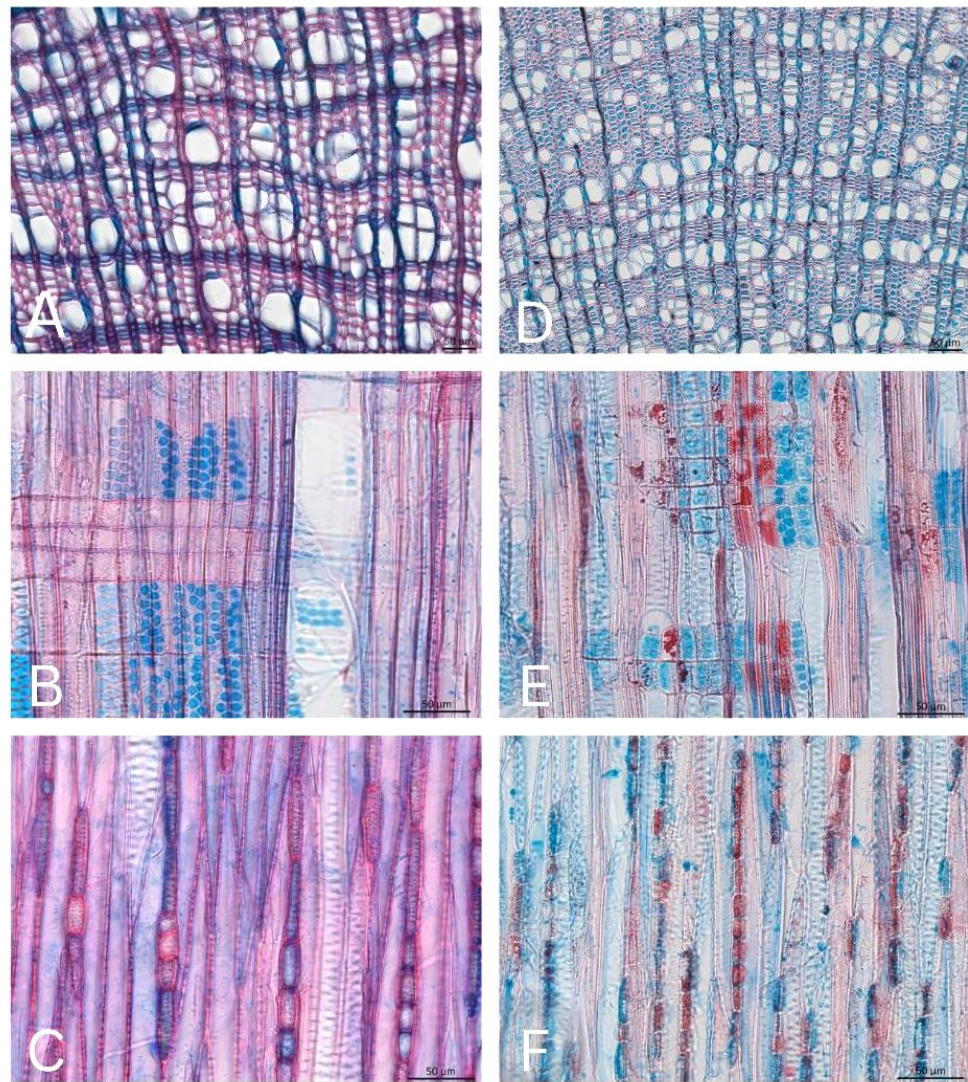


Figure 5. Photomicrographs showing three sections: cross (A,D), radial (B,E), and tangential (C,F) for roots (A–C) and stems (D–F) of *Salix herbacea* (cross—20 $\times$ and radial and tangential—40 $\times$, scale: 50 μ m).

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 μ m, which lies in the range of 17.83–36.52 μ m, smaller than *S. herbacea*,

so, overall, $<50\ \mu\text{m}$, whereas the vessel's frequency per square millimeter is $232/\text{mm}^2$, 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.

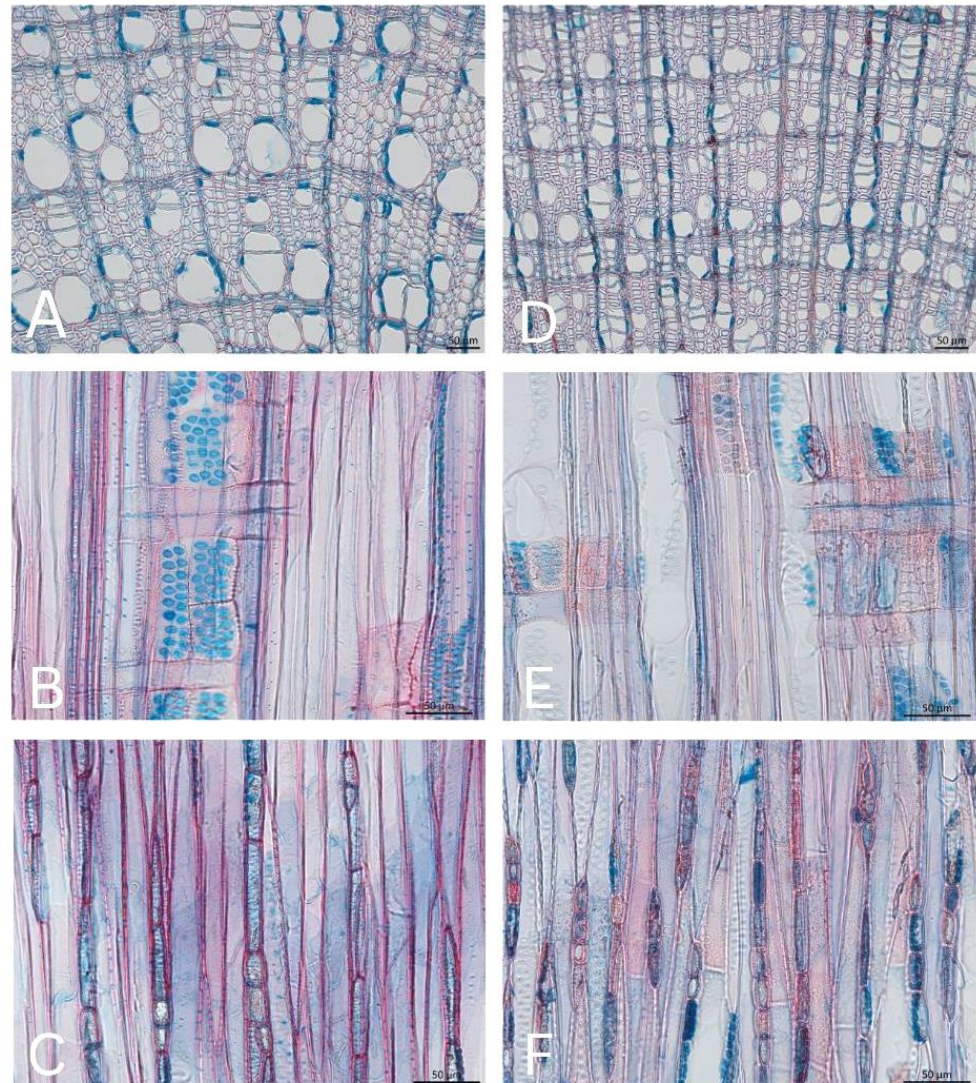


Figure 6. Photomicrographs showing three sections: cross (A,D), radial (B,E), and tangential (C,F), for roots (A–C) and stems (D–F) of *Salix arctica* (cross— $20\times$ and radial and tangential— $40\times$, scale: $50\ \mu\text{m}$).

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 $46.97\ \mu\text{m}$, which lies in the range of $45.45\text{--}50.59\ \mu\text{m}$, so, overall, $<50\ \mu\text{m}$, whereas the vessels per square millimeter are $130/\text{mm}^2$. 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
<i>t</i> -statistic	0.362		9.299		−4.523		−9.587	
<i>p</i> -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

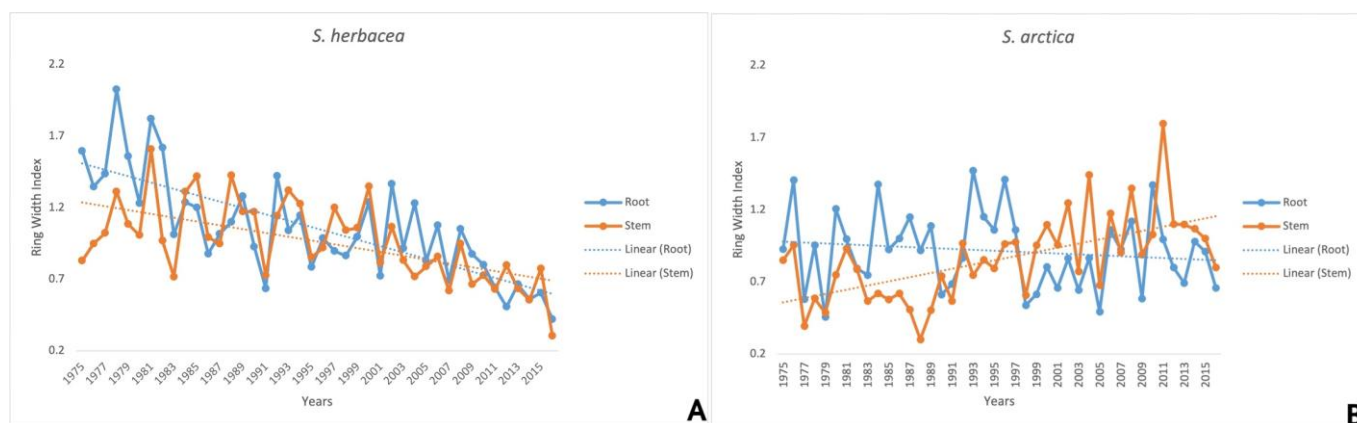


Figure 7. Standardized chronologies of stem and root parts for the *Salix* species in a time span of 1975–2016. (A) *Salix herbacea* and (B) *Salix arctica*.

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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