

## RESEARCH ARTICLE

# Growth form and leaf habit drive contrasting effects of Arctic amplification in long-lived woody species

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## Abstract

Current global change is inducing heterogeneous warming trends worldwide, with faster rates at higher latitudes in the Northern Hemisphere. Consequently, tundra vegetation is experiencing an increase in growth rate and uneven but expanding distribution. Yet, the drivers of this heterogeneity in woody species responses are still unclear. Here, applying a retrospective approach and focusing on long-term responses, we aim to get insight into growth trends and climate sensitivity of long-lived woody species belonging to different functional types with contrasting growth forms and leaf habits (shrub vs. tree and deciduous vs. evergreen). A total of 530 samples from 7 species (common juniper, dwarf birch, woolly willow, Norway spruce, lodgepole pine, rowan, and downy birch) were collected in 10 sites across Iceland. We modelled growth trends and contrasted yearly ring-width measurements, filtering in high- and low-frequency components, with precipitation, land- and sea-surface temperature records (1967–2018). Shrubs and trees showed divergent growth trends, with shrubs closely tracking the recent warming, whereas trees, especially broadleaved, showed strong fluctuations but no long-term growth trends. Secondary growth, particularly the high-frequency component, was positively correlated with summer temperatures for most of the species. On the contrary, growth responses to sea surface temperature, especially in the low frequency, were highly diverging between growth forms, with a strong positive association for shrubs and a negative for trees. Within comparable vegetation assemblage, long-lived woody species could show contrasting responses to similar climatic conditions. Given the predominant role of oceanic masses in shaping climate patterns in the Arctic and Low Arctic, further investigations are needed to deepen the knowledge on the complex interplay between coastal tundra ecosystems and land-sea surface temperature dynamics.

## KEYWORDS

Arctic amplification, climate-growth association, ring width, tree and shrub, tundra vegetation

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## 1 | INTRODUCTION

Global change is nowadays evident in all the components of the climate system, with remarkable warming across the atmosphere, ocean, and land that led each of the last four decades to be successively warmer than any of the preceding ones since 1850 (IPCC, 2021). The Arctic is warming at a faster rate than lower latitudes; this phenomenon, known as Arctic amplification (AA; Previdi et al., 2021) is still not fully clarified. Yet, it likely involves a spectrum of drivers including enhanced oceanic heating, ice-albedo, and several other positive feedback mechanisms (e.g., ocean heat transport; Chapin et al., 2005; Hinzman et al., 2013; Previdi et al., 2021; Rantanen et al., 2022).

Concurring to this warming pattern, several studies based on repeat photography, vegetation surveys, and retrospective approaches (Elmendorf et al., 2012; Pellizzari et al., 2017; Tape et al., 2006), as well as meta-analysis (Myers-Smith, Elmendorf, et al., 2015; Myers-Smith, Hallinger, et al., 2015; Vowles & Björk, 2019), demonstrated a widespread spatial expansion and increased growth rate of tundra vegetation. This “Arctic greening” (Chae et al., 2015) reflects the observed trends across the region that have been partly attributed to an increase in shrub cover (Myers-Smith et al., 2011; Stow et al., 2007; Sturm, Holmgren, et al., 2001; Sturm, Racine, & Tape, 2001; Tape et al., 2006) and expansion (Vowles & Björk, 2019). Though the main drivers of shrub responses are still under investigation, different leaf habits—deciduous and evergreen—seem to induce slightly different trajectories within the greening process: deciduous species may increase carbon (C) cycling through changes in albedo, while evergreen ones may facilitate C storage decelerating litter decomposition (Vowles & Björk, 2019).

Shrubs lie at the outposts of woody plant living conditions, usually growing beyond the treeline ecotone at high latitudes and altitudes, where trees are less abundant or absent (Körner, 2012a). Therefore, alongside the well-documented shrub expansions (Berner et al., 2020; Elmendorf et al., 2012), trees are expected to undergo similar dynamics tracking AA (Tei et al., 2017; Zhang et al., 2013) with northward and upward treeline shifts, similar to what has already been observed in several boreal forests (Devi et al., 2008; Grace et al., 2002; MacDonald et al., 2008; Soja et al., 2007; Vaganov et al., 1999). However, shrubs and trees usually respond rather differently to environmental factors, with trees showing higher sensitivity to recent climate warming (García-Cervigón Morales et al., 2012; Pellizzari et al., 2017). In fact, shrub species may be more influenced by microclimatic and -topographic conditions, soil temperature (Gazol & Camarero, 2012; Pellizzari et al., 2017), and, regionally, winter precipitations (Carrer et al., 2023; Pellizzari et al., 2014) rather than air temperature. During winter, shrub meristems are often covered by snow which contributes to limiting the risk of drought-induced embolism and mechanical damage compared to trees (Bokhorst et al., 2009; Carrer et al., 2019; Rixen et al., 2010). On the contrary, due to their erect habit and taller stature, trees are usually better coupled to air temperature, with meristems highly sensitive to free atmospheric conditions (Grace, 1989; Grace

et al., 2002; Körner, 2012b). Still, contrasting trends have been observed and predicted in trees according to their leaf habit within the same bioclimatic zone, with deciduous taxa showing an increase in productivity while the evergreen ones showed a significant decline (Miles & Esau, 2016).

Ongoing and forecasted abrupt changes in the Arctic climate system will therefore interfere not only with long-lived woody species expansion but also with the climate responses of coexisting shrubs and trees—both evergreen and deciduous—causing complex outcomes far from being understood (Chapin et al., 2005; Chapin & Shaver, 1989; MacDonald et al., 2008; Zhang et al., 2013). Moreover, the northward range expansion of the shrubs/trees assemblages could have profound implications for the Arctic biomes (Chae et al., 2015; Chapin et al., 2005; Tape et al., 2006). In fact, modification in long-living woody species composition would deeply alter tundra biome surface energy balance, carbon balance, hydrology, and active layer patterns and features (Chapin et al., 2005; Previdi et al., 2021; Sturm, Holmgren, et al., 2001; Sturm, Racine, & Tape, 2001). Given the direct and indirect changes that the Arctic biome will most likely face in the near future, it is of key importance to further understand the effect of AA on shrub and tree growth dynamics at northern latitudes, together with the role played by different leaf habit on growth responses in such temperature-limited environments (Dobbert et al., 2021; Takahashi & Okuhara, 2012).

Iceland, being located at the polar front astride the Arctic and Atlantic waters and air masses, represents one of the key areas exceptionally susceptible to current Arctic warming (Jónsdóttir et al., 2005). With a mean temperature of the warmest month (July) of around 10°C (Einarsson, 2007; Figure S1), and its vegetation cover, mostly formed by grasslands, tundra, and sparse deciduous woodlands, Iceland belongs to the Sub-Arctic region, with a subpolar climate (Cfc, Köppen; Beck et al., 2018). However, the northernmost part and the highlands could be included in the Arctic region (mean temperature of the warmest month <10°C), with a tundra climate (ET, Köppen; Beck et al., 2018; Einarsson, 2007). As a result, despite native woodlands and shrublands covering roughly 1.4% of the island (Snorrason et al., 2016; Snorrason & Kjartansson, 2017), the Icelandic landscape is characterized by a mixture of growth forms, the most evident one being where the native subarctic birch forest meets the low Arctic tundra (Jónsdóttir et al., 2005). Alongside shrubs, exotic tree species such as Siberian larch, Sitka spruce, lodgepole pine, and Norway spruce have been introduced during the last 70 years and are now established and expanding (Snorrason & Kjartansson, 2017), creating patches of what could be considered as boreal conifer stands (Bonan et al., 1992; Bonan & Shugart, 1989). Across Iceland, it is possible to observe the coexistence of four fundamental functional types, namely evergreen shrubs (EVGS), deciduous shrubs (DECS), evergreen trees (EVGT), and deciduous trees (DECT). For this reason, the area is a crucial spot to investigate AA effects on Arctic long-lived woody species, especially any possible interactions within this shrub/tree and leaf habit dichotomy.

In this study, using a retrospective approach based on ring-width (RW) analysis, we aimed to quantify the long-term growth

responses to rising temperatures of both deciduous and evergreen shrubs and trees across the boreal forests and Arctic tundra biomes in Iceland. Specifically, we aim to answer the following questions:

1. how does secondary growth of long-lived woody species respond to AA in the Sub- and Low-Arctic?
2. are different functional types (shrub vs. tree; evergreen vs. deciduous) and species influenced by similar climatic factors?
3. which functional type benefits the most from current Arctic warming?

We hypothesize that trees, having an erect habit, will be more sensitive to increased temperature compared to shrubs, which should be better coupled to microclimatic and -topographic settings rather than free atmospheric conditions (Carrer et al., 2019; Pellizzari et al., 2017). Given the conspicuous amount of precipitation characterizing Iceland, and hence the virtual absence of any drought stress, we expect to detect a pervasive positive growth trend for each growth form related to the current AA, which provides an overall relaxation of the previous temperature-limiting conditions. Additionally, as already observed within the warming tundra, we expect better growing performance of native deciduous species rather than evergreen ones due to their relatively higher leaf turnover and earlier growth onset (Elmendorf et al., 2012; Prager et al., 2020).

## 2 | MATERIALS AND METHODS

### 2.1 | Targeted species

Within the long-lived woody species growing in Iceland, we selected taxa with both prostrate and erect habit (i.e., shrub and tree species) but also selected for both deciduous and evergreen overwinter strategies. The sampled tundra shrubs are dwarf birch (*Betula nana* L.), woolly willow (*Salix lanata* L.), and common juniper (*Juniperus communis* L.). The two broadleaved shrub species have nearly circumpolar geographic distribution, spreading across the Arctic tundra and cool temperate regions (De Groot et al., 1997; Forbes et al., 2010) that in Iceland occur at higher elevations (200–400 m a.s.l.) and inland. Contrary to dwarf birch, which can grow in drier sites, woolly willow spreads mostly on stream sides, a typical trait of many *Salix* species (De Groot et al., 1997; Forbes et al., 2010). Common juniper, instead, is the most widespread conifer over the Northern Hemisphere and can be found throughout North America, Europe, and Asia (Farjon, 2005; San-Miguel-Ayanz et al., 2016). In Iceland it grows on rocky and south-exposed slopes, from the sea level to 200–400 m in elevation. Its slow growth, known longevity (Carrer et al., 2023) compared to many tree species, and its extremely broad distribution range make it an excellent target for dendroecological analyses. Other dwarf evergreen shrub taxa growing on the island (e.g., *Calluna vulgaris* or *Empetrum nigrum*; Wařowicz, 2020) do not

share all these key features and would likely prevent building robust chronologies length-wise comparable with trees RW series.

Regarding trees, we selected Norway spruce (*Picea abies* (L.) H. Karst.) and lodgepole pine (*Pinus contorta* Douglas) as evergreen and non-native tree species introduced respectively from northern Europe and the Pacific coast of North America. They have been both extensively planted, after long seed provenance trials, during the first half of the last century and now most of the newly established stands in Iceland are composed by these conifers together with Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and Siberian larch (*Larix sibirica* Ledeb.; Blondal, 1987; Snorrason & Kjartansson, 2017). Downy birch (*Betula pubescens* Ehrh.) and rowan (*Sorbus aucuparia* L.), which constitute the vast majority of native forest species in Iceland, were selected as deciduous broadleaf trees. Birch woodlands account for 43% of current total forest area on the island, while rowan occurs as isolated individuals or small patches within birch woodlands (Blondal, 1987; Snorrason et al., 2016; Snorrason & Kjartansson, 2017). Their growth habit, especially for birch, is usually twisted and stunted, reaching an average height of 5 m as a result of the harsh environmental conditions.

### 2.2 | Study sites and sample processing

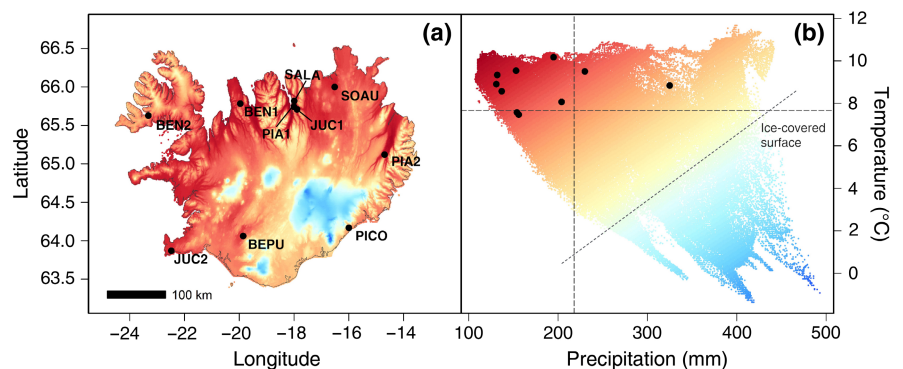
We selected 10 sites located across Iceland, two for evergreen shrubs (hereafter EVGS, common juniper), three for DECS (DCDS, two for dwarf birch and one for woolly willow), three for evergreen trees (EVGT, two for Norway spruce, one for lodgepole pine), and two for DECT (DCDT, downy birch and rowan; Table 1). Site locations were chosen according to the presence of the species and to span most of the Iceland forest area, which is concentrated in a belt around the coastline (Figure 1). The sites' elevations vary from 40 to 540 m a.s.l. (Table 1). Within the sites, mean annual temperature ranges from 1.02 to 4.15°C (Figure S1) while mean annual precipitation spans from 734 to 1468 mm year<sup>-1</sup>. Wettest sites are in the southern and eastern parts of the island, while the driest sites lie in peninsulas and promontories in northern Iceland (Figure 1). Natural woodlands and forest plantations occur in lowlands and on the foothills. Shrubs were mostly found at higher elevations and in more inland sites, where vegetation turns to a mixture of dwarf shrubs, mosses and graminoid tundra. Bedrock and soil types are quite similar throughout the island with predominantly volcanic rocks, where basaltic tephra giving rise to andic soils (Arnalds, 2015). Samples were randomly selected, and two increment cores were collected from each dominant or codominant tree 50 cm above the ground. For shrubs, stem discs were collected as close as possible to the ground, choosing the largest branch of each individual. At the lab, increment cores and disks were sanded with progressively finer sandpaper to get a clear visualization of the annual rings. RWs of each sample were measured to the nearest 0.01 mm using TSAP package and Lintab system (RinnTech, 2010). In tundra environments, prostrate shrubs often present irregular growth forming typical lobate stems, due to microclimatic conditions, disturbances, or, as in junipers, irregular strip-bark growth.

**TABLE 1** Description of the study sites. Mean annual temperature and precipitation sum for the period 1967–2018 are based on 0.5° CRU gridded dataset.

Site	Species	Functional type	Lat (N)	Long (W)	Elevation (ma.s.l.)	Temperature (mean, °C)	Precipitation (sum, mm)
JUC1	<i>Juniperus communis</i>	EVGS	65°49'	17°59'	370	1.02	745
JUC2	<i>Juniperus communis</i>	EVGS	63°52'	22°29'	40	4.15	816
SALA	<i>Salix lanata</i>	DCDS	65°45'	18°01'	540	1.06	734
BEN1	<i>Betula nana</i>	DCDS	65°47'	20°00'	480	1.02	745
BEN2	<i>Betula nana</i>	DCDS	65°38'	23°19'	300	1.63	479
PICO	<i>Pinus contorta</i>	EVGT	64°10'	16°00'	100	2.84	1468
PIA1	<i>Picea abies</i>	EVGT	65°42'	17°53'	170	1.02	745
PIA2	<i>Picea abies</i>	EVGT	65°07'	14°41'	120	1.40	1282
SOAU	<i>Sorbus aucuparia</i>	DCDT	65°60'	16°31'	150	1.57	901
BEPU	<i>Betula pubescens</i>	DCDT	64°04'	19°52'	180	3.04	1250

Abbreviations: BEN; *Betula nana*; BEPU, *Betula pubescens*; DCDS, deciduous shrub; DCDT, deciduous trees; EVGS, evergreen shrub; EVGT, evergreen tree; JUC, *Juniperus communis*; PIA, *Picea abies*; PICO, *Pinus contorta*; SALA, *Salix lanata*; SOAU, *Sorbus aucuparia*.

**FIGURE 1** (a) Locations of shrub and trees sampling sites in Iceland (black dots). (b) Location of study sites in the climatic space. Colour gradients describe the interaction of two climate variables (June to August mean temperature and total precipitation for the 1967–2018 period), from red (warm, dry) to blue (cold, wet). Perpendicular dashed lines indicate the median values of the observations.



For this reason, within each shrub, we measured two to four radii per disk to account for the high RW variability. Subsequently, we compared each radius per individual and, when matching, averaged them to obtain the individual mean growth curve. This drawback never occurred with trees, where for each sample we averaged the RW series obtained from the two increment cores. Each individual growth curve was then crossdated following the standard dendrochronological procedures (Stokes & Smiley, 1968). First, we visually compared and matched each individual series within each site, with the software CDendro (CDendro 9.0.1; Cybis Elektronik & Data AB). Subsequently, dating and measurement errors were checked using the COFECHA program (Holmes, 1983). At this stage, we discarded roughly 40% of the samples, mostly shrub species due to crossdating issues (Table 2). The frequent anomalies in shrub growth prevented us from adopting the basal area increment (BAI) as a metric of growth performance, which, although appropriate in trees, could introduce some biases in the analysis when applied to the irregular stem shape typical of dwarf arctic shrubs. Therefore, we decided to perform all the analyses investigating the different growth forms and leaf habits using the RW measurements. To compare RW variability with climate variables, we first standardized each individual series to remove trends in mean RW that typically occur with ontogenesis or other disturbance pulses, using the ARSTAN program

(Cook & Holmes, 1986). We applied a single-step detrending using a cubic spline function (frequency response of 50% at a wavelength of 100 years) to maintain mid-frequency (decadal to multi-decadal) growth variability (Figure S2). Finally, a mean chronology using the biweight robust mean (Cook et al., 1990) was computed for each site together with the respective descriptive statistics, such as mean RW, standard deviation, and mean inter-series correlation ( $R_{bar}$ ), which expresses the average correlation between all series throughout the entire chronology (Fritts, 1976; Speer, 2010).

### 2.3 | Climate data

Although automatic weather stations are now often in use in Iceland, many of them, for both temperature and precipitation, have short and fragmentary records, preventing sound and reliable climate-growth correlation analysis. We, therefore, opted for the 0.5° CRU gridded dataset of monthly mean land temperatures and precipitation sums (1901–2020; Harris et al., 2020). Since the Icelandic vegetation occurs mainly on a belt around the coastline, we also considered the sea surface temperature as a potential driver of plant growth. To this end, we used the 0.1 HadISST gridded sea surface temperature (SST) dataset (1870–2020; Rayner et al., 2003).

Site	Functional type	Individuals sampled/analysed	Age (years) mean/max	Mean RW $\pm$ SD (mm)	Mean Rbar
JUC1	EVGS	113/45	77/155	0.14 $\pm$ 0.05	0.18
JUC2	EVGS	76/54	100/162	0.10 $\pm$ 0.05	0.15
SALA	DECS	64/34	51/84	0.09 $\pm$ 0.05	0.20
BEN1	DCDS	67/37	45/95	0.14 $\pm$ 0.05	0.26
BEN2	DCDS	80/40	47/87	0.12 $\pm$ 0.05	0.27
PICO	EVGT	15/15	45/53	3.54 $\pm$ 0.88	0.47
PIA1	EVGT	22/22	45/56	1.73 $\pm$ 0.4	0.52
PIA2	EVGT	24/24	46/56	2.32 $\pm$ 0.73	0.48
SOAU	DCDT	25/22	58/81	1.01 $\pm$ 0.34	0.57
BEPU	DCDT	44/31	60/111	0.70 $\pm$ 0.26	0.41

**TABLE 2** Metadata for the different functional type with some descriptive statistics: Mean ring width and standard deviation (RW  $\pm$  SD) computed on the whole chronology length and the mean inter-series correlation (Rbar) computed over the common 1967–2018 period.

All the statistical analyses were computed over the 1967–2018 period, which is the longest common period for all the series.

## 2.4 | Statistical analysis

Principal component analysis (PCA) based on the correlation matrices computed with the raw chronologies was used as a clustering technique to identify common modes of growth variability among the different growth forms and leaf habits. We also performed an ANOVA test (Girden, 1992) followed by a Tukey multiple comparison test (Haynes, 2013), to assess the differences among RW values of each functional group.

Then the spatiotemporal growth patterns for each growth form (broadleaved shrubs and trees, conifer shrubs and trees) were assessed by applying the generalized additive mixed models (GAMMs; Wood, 2006). GAMM is a flexible semiparametric method used to model the nonlinear patterns existing between a response variable as a function of some explanatory variables (Wood, 2006) that allows the treatment of autocorrelation and repeated measures (Wood, 2006). The variables included in the model were the following:

$$RW_i = s[\text{year}_i \times (\text{growth form}_i \times \text{winter habit}_i)] + (\text{growth form}_i \times \text{winter habit}_i) + s(\text{age}_i) + Z_i B_i + \epsilon$$

In the model, the RWs of a theoretical shrub or tree  $i$  were modelled as a function of calendar year, age, and the interaction of different functional types, such as growth form (shrub, tree) and winter habit (evergreen, deciduous). We also included a further interaction term between calendar year and each different functional type to account for different growth trends between each growth form and winter habit. The tree/shrub identity ( $Z_i B_i$ ) was considered as a random factor to account for multiple RW measurements performed on different individuals, growth- and site-wise. Thin plate regression splines ( $s$ ) were used to represent all the smooth terms, with a degree of smoothing determined by internal cross-validation (Wood, 2006).

We ranked all the potential models that could be generated using different explanatory variables and different levels of smoothing according to the Akaike information criterion (AIC) and finally chose the model with the lowest AIC (Table S1). GAMMs were fitted using the *mgcv* package (Wood, 2006). All analyses were run with R (v4.1.3, R Core Team, 2022).

Finally, climate-growth relationships, referring to a time window from June of the previous year to September of the current year, were defined through the bootstrap Pearson correlation coefficients (Guiot, 1991) computed between indexed (RWI) site chronologies and monthly and seasonal climate variables. To assess the contribution of temperature and precipitation in different time domains, climate-growth correlations were also computed on both the low- and high-pass filtered chronologies. High- and low-frequency components were obtained by filtering the indexed chronologies through the Fast Fourier Transform (FFT; Brigham, 1988) above and below the cut-off frequency of 10 years.

## 3 | RESULTS

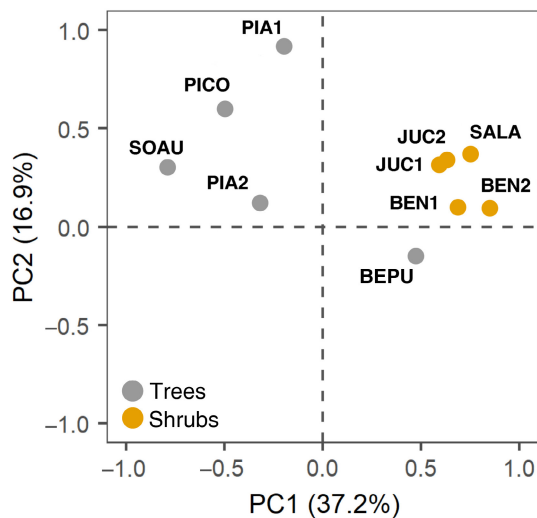
A total of 530 samples, 400 shrubs, and 130 trees, were collected and measured. After crossdating, we discarded half of the shrub samples and just a few trees, the latter mostly related to cores' faults. Therefore, in the final shrub chronologies, we included 189 common junipers (two sites), 64 woolly willows, and 137 dwarf birches (two sites). In the final tree chronologies, we included 15 lodgepole pine, 46 Norway spruce (two sites), 25 rowan and 44 downy birch individuals (Table 2).

Mean RW resulted lower for shrubs than trees, ranging from 0.09 (woolly willow) to 0.14 (common juniper, dwarf birch) mm. EVGT had the widest RW with 3.54 mm for lodgepole pine and 2.32 and 1.73 mm for the two Norway spruce sites, respectively (Table 2). The oldest sampled individual was a 162-year-old common juniper (at JUC2 site). EVGS and EVGT resulted in the oldest and youngest functional type, respectively. Mean inter-series correlation (Rbar) computed for standardized chronologies shows lower values for

shrubs, spanning from 0.14–0.15 (common juniper) to 0.27 (dwarf birch), while it is higher than 0.4 for trees. PCA computed over raw chronologies further highlights a clear separation between shrubs and trees (Figure 2) except for downy birch (BEPU) which does not clearly belong to any specific type. ANOVA and Tukey multiple comparisons highlighted significant ( $p < .001$ ) differences in the RW of each functional group, apart from EVGS and DECS, which showed no statistical difference (Table S2).

### 3.1 | Growth trends and patterns

When discriminating between growth forms, the results of GAMM models highlighted quite different growth patterns (Figure 3a). Shrubs showed a monotonic increasing growth trend, with just a recent slight decline, whereas trees demonstrated strong fluctuations but no substantial increase nor decrease over time. In parallel, when

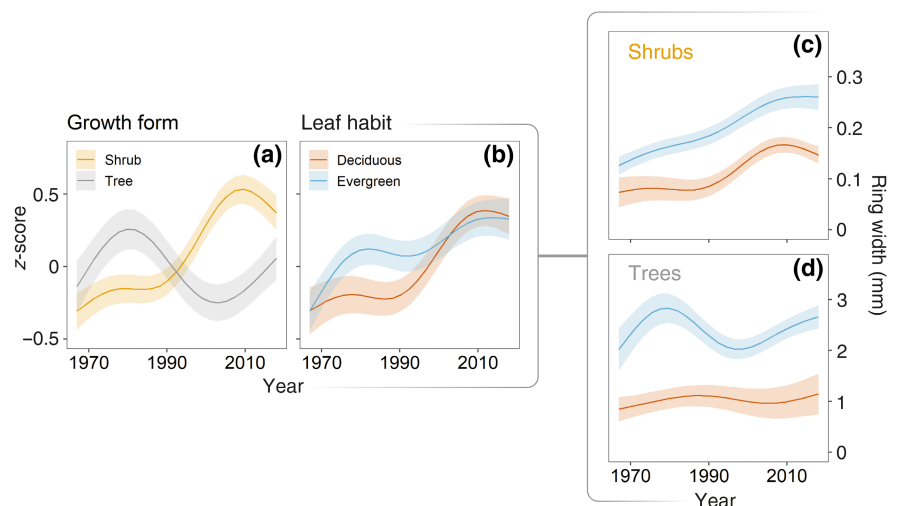


**FIGURE 2** Scatter plots of weighting coefficients for PC1 and PC2 calculated with the raw chronologies. Axis labels report the percentage of variance expressed by each component.

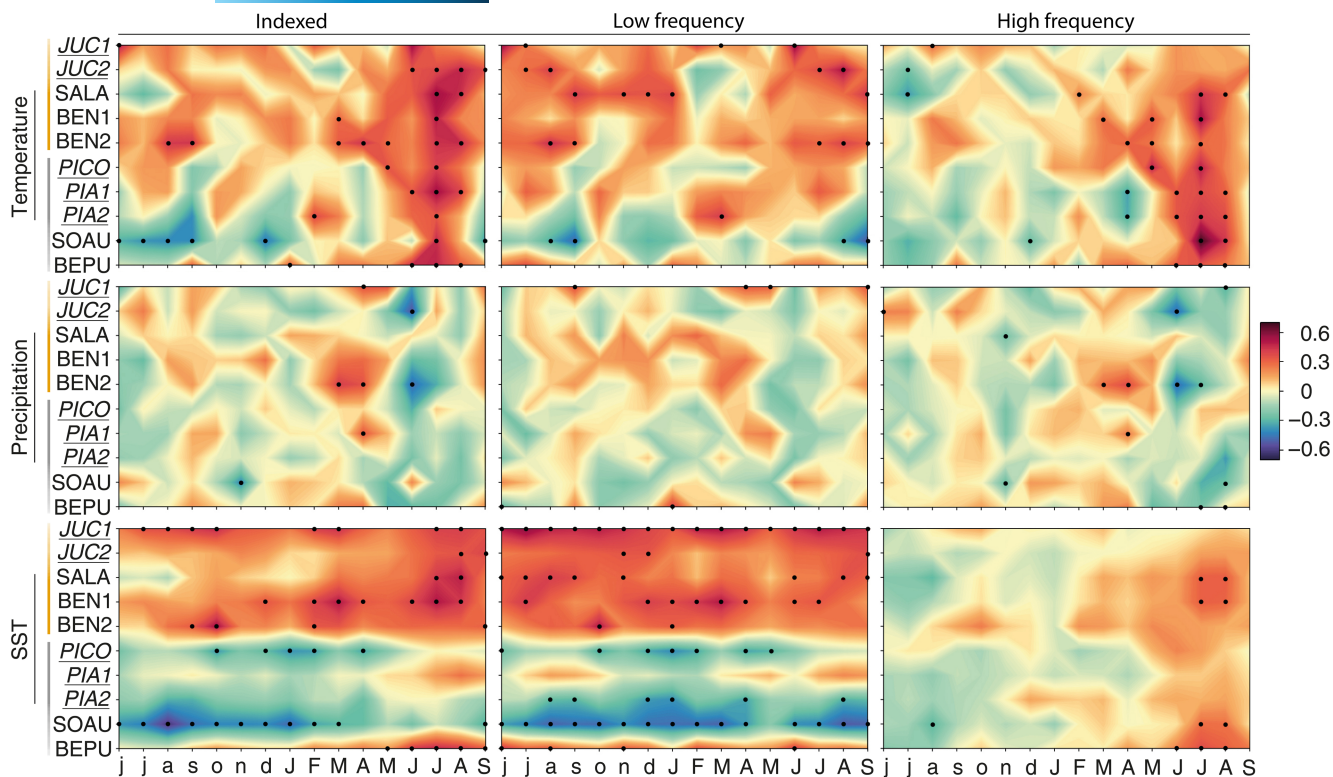
considering different leaf habits, no relevant difference emerged between evergreen and deciduous species (Figure 3b). When intersecting growth form with leaf habit (Figure 3c,d), growth trends increase similarly over time for both EVGS and DECS. Nevertheless, while EVGS showed a steady increase in RW, the growth of DECS boosted only after 1990 (Figure 3c). In trees, deciduous taxa showed the most uniform growth rate with just a weak variability (Figure 3d), while evergreen ones featured strong fluctuations with an initial steep increase until 1980, then a growth decline until the mid-1990s and a more recent boost until present.

### 3.2 | Climate-growth responses

All functional types seem particularly sensitive to growing season temperatures (Figure 4). Specifically, July temperatures had the strongest (positive) effect on RW in all the sites except JUC1. A positive influence of spring temperatures (March to May) on growth is also evident, especially in deciduous species (Figure 4). Previous year temperatures, from June to October, seem to promote only shrub growth while weakly influencing EVGT (positively) and DECT (negatively). However, a significant relationship emerged for rowan. Specifically, a positive association of late growing season and early autumn temperatures (August to October) on growth is evident in all shrub species except woolly willow (SALA), reaching the significance threshold only for BEN2. Such responses are largely mirrored in the high-frequency domain (Figure 4). On the contrary, the low-frequency component provided a different representation, with shrubs better coupled to the long-term increase in temperature even during the previous year of growth, while trees showed almost no significant relationships, aside for SOAU (Figure 4). Rowan, in fact, resulted negatively associated with previous and current growing seasons. Precipitation showed a much lower impact on growth compared to temperature (Figure 4), with no clear pattern among growth form or leaf habit in all time domains. Nonetheless, precipitation from May to July seemed to influence growth slightly negatively in all species. RW growth associations with SSTs revealed



**FIGURE 3** Growth trends for different growth forms (a) and leaf habit (b–d) based on the generalized additive mixed models (GAMM). Trends are expressed as z-score values (a, b) and as mean RW (mm) (c, d)  $\pm$ SE.



**FIGURE 4** Climate-growth associations between monthly climate parameters (precipitation, mean land temperature and sea surface temperature) and ring-width indexed chronologies split in their related low- and high-frequency components. Climate variables (1967–2018) were considered from June of the previous year to September of the growth year. Lowercase letters refer to previous years' months. Correlation values are coded according to the colour scale on the right. Significant values at  $p < .05$  are highlighted by black dots. Evergreen species are identified by underlined and italic fonts.

remarkable differences with respect to the previous climate factors (Figure 3). Correlation profiles, especially those computed on the low-frequency RW chronologies component, clearly discriminated between growth habits, with a positive significant association for both deciduous and evergreen shrubs, and a negative one for all the tree species apart from BEPU. The distinct dual pattern highlighted with low frequency disappeared when considering the high frequency. Here the representation closely resembled that computed with air temperature and the unfiltered chronologies, albeit with lower correlation values during the warm season.

## 4 | DISCUSSION

Arctic and Sub-Arctic regions are warming at an unparalleled rate compared to any other region of the globe. As a consequence, we observed a widespread increase in productivity and growth of woody plants, especially toward the limits of their distribution (Masek, 2002; Myers-Smith et al., 2011; Normand et al., 2013; Zhu et al., 2016). However, previous investigations mostly paid attention to the dynamics of the overall vegetation assemblage rather than to the role of different growth forms (shrub vs. erect tree) and leaf habits (evergreen vs. deciduous; Chapin et al., 2005; Macias-Fauria et al., 2012; Myers-Smith et al., 2011). In this study, we show that the

secondary growth of each functional type features diverging patterns only when sorting shrubs and trees. In fact, both evergreen and deciduous shrub species show an overall increasing trend in RW, which is not mirrored by trees in the last decades (Figure 3c,d). Shrubs, despite having an average secondary growth rate an order of magnitude lower, seem to take more advantage of the improved growing condition compared to trees (Figure 3c,d). At the same time trees, without showing the typical and consistent age/size-related decline in RW, did not perform that negatively over the last half-century.

Our results aligned well with previous investigations in Arctic tundra ecosystems that found widespread shrub expansion and increased growth rate (Chapin et al., 2005; Elmendorf et al., 2012; Myers-Smith et al., 2011; Myers-Smith, Elmendorf, et al., 2015; Myers-Smith, Hallinger, et al., 2015). Recent warming at higher latitudes seems to promote growth and productivity with shrub species showing higher sensitivity to climate and the ability to anticipate and accelerate their growth dynamics and expansion respect trees (Forbes et al., 2010; Francon et al., 2023; Pellizzari et al., 2017). Trees, being much more coupled to air temperature and related atmospheric patterns, might still be affected by cool summer conditions and short growing seasons (Carrer et al., 2019; Pellizzari et al., 2017). This could explain why, contrary to our assumptions, recent trends in growth rate in trees showed less steep increase

compared to shrubs despite the recent warming. Yet, evergreen and deciduous species showed high similarity in the growth trend, with an overall increase in RW over time independent of growth form (Figure 3). Thus, growth form (but not leaf habits) appears to be crucial in influencing long-lived woody species at high latitudes. That is, having an erect rather than a shrubby-prostrate life form is still the main structural feature driving growth in these environmental conditions (Normand et al., 2013; Sturm, Holmgren, et al., 2001; Sturm, Racine, & Tape, 2001; Tape et al., 2006).

The dichotomic growth patterns highlighted by GAMM models are also supported within the climate-growth correlation profiles, though it is possible to appreciate some weak site-specific similarities crossing growth forms, as in JUC1 and PIA1 when considering monthly precipitation (Babst et al., 2013; Fritts, 1976). Generally, all the functional types are positively associated with growing season temperature conditions. This confirms the persistent limiting role of this factor in heat-limited environments (Callaghan et al., 1989; Forbes et al., 2010; Havstrom et al., 1993; Pellizzari et al., 2017; Power et al., 2022 and references therein) and aligns with previous investigations on climate sensitivity of Icelandic woody species (Hannak & Eggertsson, 2020; Levanič & Eggertsson, 2008). Juniper is an exception with less strong temperature associations. In fact, this species was found to be particularly sensitive to other drivers, such as the amount and duration of snow cover, microclimatic conditions, biotic interactions, or disturbance regime (Carrer et al., 2019, 2023; Pellizzari et al., 2014). These results were echoed in the high-frequency domain, highlighting the role of summer year-to-year temperature variability in driving yearly RW for all long-lived woody species. On the contrary, the low-frequency component showed a clear divergent response to temperature, with shrubs positively and trees negatively associated with temperature. An analogous, highly significant, divergent response occurred when analysing the SST-growth relationship. While shrubs seem to positively track the long-term increase in SST, trees showed almost the opposite tendency.

Such pervasive response to SST from Arctic shrub species have never been reported except for a study by Beil et al. (2015), though performed over a much shorter period, on *Calluna vulgaris* in the Faroe Islands; crossdating issues, a focus on the year-to-year variability, and the lack of long enough chronologies, likely prevented the detection of a similar outcome (Myers-Smith, Elmendorf, et al., 2015; Myers-Smith, Hallinger, et al., 2015). Nonetheless, in Iceland, we highlighted a substantial difference between growth form adaptation strategies in coping with the increasing temperature pattern. Such a tendency might account for the recorded increase in shrub growth in the Arctic and Low Arctic under the recent AA phenomenon (Gamm et al., 2018; Myers-Smith et al., 2011; Myers-Smith, Elmendorf, et al., 2015; Myers-Smith, Hallinger, et al., 2015). We can consider a spectrum of hypotheses to justify this pattern: (i) trees, due to their typical erect growth form, are usually tightly coupled to prevailing free atmospheric conditions, while shrubs, due to their lower stature, are partially decoupled and benefit from higher heat accumulation in the leaf canopy (Körner, 2012b). For this reason, trees should be more sensitive to high-frequency (daily, yearly)

climate variability than shrubs and, considering that SST can highly affect coastline areas, this could explain the higher shrub association with low-frequency SST; (ii) management practices on tree stands could induce disturbance pulses that can conceal any potential long-term fluctuation and response to climate (Fritts, 1976). The sharp increase in competition at the pole stage at the end of the last century, combined with its sudden release after the first thinning operations, especially in coniferous stands, is likely one of the key factors for the uneven growth trends recorded in trees (Figure 3c) and (iii) endemic tree species (e.g. birch) are usually particularly sensitive to biotic and abiotic disturbances such as grazing, insect outbreaks, and wind gusts that have caused severe reductions in vegetation productivity over time (Babst et al., 2010; Levanič & Eggertsson, 2008; Marteinsdóttir et al., 2017).

RW in each functional type was only slightly affected by precipitation, even in juniper, which has been previously shown to be highly sensitive to snow cover duration in cold environments (Carrer et al., 2019, 2023). This result suggests that, given the strong oceanic imprint of Iceland climate (Einarsson, 2007), soil moisture should not be considered as a limiting factor in the area (Ackerman et al., 2017; Babst et al., 2010; Gamm et al., 2018). Moisture sensitivity of shrub species in the Arctic seems highly dependent on microclimatic and -topographic factors and this could be the reason why very often contrasting results are found (Myers-Smith, Elmendorf, et al., 2015; Myers-Smith, Hallinger, et al., 2015; Weijers, 2022). Therefore, further research is needed to disentangle the role and interactions of different drivers.

Contrary to our hypotheses and as previously highlighted by GAMMs, correlation profiles within each growth form did not highlight any substantial difference between different leaf habits, showing that this trait has little relevance in conditioning growth responses to climate at high latitudes (Normand et al., 2013; Sturm, Holmgren, et al., 2001; Sturm, Racine, & Tape, 2001; Tape et al., 2006). Many investigations identify deciduous species as the favoured group under warming tundra due to the more rapid resource acquisition from faster leaf turnover (Elmendorf et al., 2012; Prager et al., 2020). However, evergreen shrubs could also be highly responsive to warming as they are not restricted by spring leaf-forming processes and can invest in radial stem growth earlier than deciduous taxa (García Criado et al., 2022; Hudson et al., 2011; Vowles & Björk, 2019; Vuorinen et al., 2017). Moreover, the very high individualistic and idiosyncratic responses to environmental variability (e.g., microsite conditions, water, and nutrient availability, herbivory, pathogen outbreaks) stems from a rather weak relationship between leaf habit and climate sensitivity, as we found across Iceland but also in other studies with different species and regions (Bjorkman et al., 2020; Myers-Smith, Elmendorf, et al., 2015; Myers-Smith, Hallinger, et al., 2015; Wipf et al., 2009). In fact, our results suggest a growth form and a species-specific, rather than a leaf habitus-specific, climate sensitivity (Myers-Smith, Elmendorf, et al., 2015; Myers-Smith, Hallinger, et al., 2015; Wipf et al., 2009).

Under the ongoing Arctic and low-Arctic warming trends and future projections (IPCC, 2021), tundra shrub will also likely become



less temperature-limited and more moisture limited, especially if the warming is coupled with insufficient water availability (Weijers, 2022; Weijers et al., 2017). Recent investigations performed through direct growth measurements with dendrometers, highlighting a bimodal response to climate (Dobbert, Albrecht, et al., 2022; Dobbert, Pape, & Löffler, 2022), or adopting satellite-derived vegetation indices (Myers-Smith et al., 2020; Phoenix & Bjerke, 2016), seem to confirm this scenario. However, our results suggest that Icelandic long-lived woody species are currently experiencing a pervasive boost in secondary growth, with tundra shrub rapidly growing and most likely expanding its distribution. In fact, the typical age-related trend in RW for most shrub species living in heat-limited environments should be almost flat (Carrer et al., 2023; Lehejček et al., 2023) rather than monotonically increasing (Figure 3). The majority of evergreen trees, especially lodgepole pine, will likely track shrub behaviour (Figure 3; Jónsdóttir et al., 2005; Myers-Smith et al., 2011; Myers-Smith, Elmendorf, et al., 2015; Normand et al., 2013; Zhang et al., 2013). In fact, recent warming is already enhancing exotic tree species regeneration and accelerating encroachment dynamics in the area (Eggertsson et al., 2022). Nevertheless, further research is essential to understand the complex interplay and dynamics between trees and shrubs in such a rapidly warming scenario and to extend our inferences to other taxa over the broad tundra biome. We also highlighted a strong influence of SST on shrub growth, showing the crucial importance of this climatic variable in coastal tundra shrub ecosystems. Ocean masses make up roughly 85% of total Arctic surface, with a predominant role in influencing atmosphere and land climate conditions within the region. Given the recent abrupt Arctic warming trend, our results suggest to further explore the role of SST in shaping long-lived woody species growth responses. This is of key importance to deepen the understanding of vegetation dynamics within Arctic and Low Arctic coastal regions, shedding light on the future of these extremely sensitive ecosystems.

#### AUTHOR CONTRIBUTIONS

Davide Frigo and Marco Carrer designed the study. Field work was carried out by Marco Carrer, Angela Luisa Prendin, Lucrezia Unterholzner, Davide Frigo and Ólafur Eggertsson. Samples were measured and crossdated by Marco Carrer, Raffaella Dibona, Davide Frigo and Ólafur Eggertsson, Davide Frigo and Marco Carrer carried out the analysis and wrote the first draft of the manuscript with inputs from Angela Luisa Prendin. All authors contributed to the discussion, interpretation of the results and critically revised the final version of manuscript.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

#### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Zenodo at <http://doi.org/10.5281/zenodo.8163977>, reference number [10.5281/zenodo.8163977](https://doi.org/10.5281/zenodo.8163977).

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## SUPPORTING INFORMATION

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