On growth patterns and mechanisms in arctic-alpine shrubs

Dissertation
zur
Erlangung des Doktorgrades (Dr. rer. nat.)
der
Mathematisch-Naturwissenschaftlichen Fakultät
der
Rheinischen Friedrich-Wilhelms-Universität Bonn

vorgelegt von

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aus
Siegen

Bonn 2022

Angefertigt mit Genehmigung der Mathematisch-Naturwissenschaftlichen Fakultät

der Rheinischen Friedrich-Wilhelms-Universität Bonn

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Tag der Promotion: 06.12.2022

Erscheinungsjahr: 2022

Abstract

Arctic-alpine ecosystems are considered hot-spots of environmental change, with rapidly warming conditions causing massive alterations in vegetational structure. These changes and their environmental controls are highly complex and variable across spatial and temporal scales. Yet, despite their numerous implications for the global climate system, the underlying physiological processes and mechanisms at the individual plant scale are still little explored. Using, for the first time systematically and to a greater extent, hourly recordings of shrub stem diameter change provided by dendrometers, paired with on-site environmental conditions, enabled us to shed light on these processes. In this way, growth patterns in three widely distributed shrub species were assessed and linked to thermal and hygric conditions. Starting with a close examination of one evergreen species under extreme environmental conditions, followed by a comparison of evergreen and deciduous species, and, finally, a comparative look at growth patterns across local micro-habitats, our analysis revealed distinct growth strategies, closely linked to species-specific water-use dynamics and cambial rhythms. Within the heterogenous alpine landscape these conditions were mainly attributed to the variation in local micro-habitats, defined by fine-scale topography and consequent variation in snow conditions and exposure. Thus, the overall growth success was mainly controlled by complex seasonal dynamics of soil moisture availability, snow conditions, and associated freeze–thaw cycles and was therefore in many cases decoupled from governing regional climate signals. At the same time, exceedingly high summer temperatures were limiting shrub growth during the main growing season, resulting in more or less pronounced bimodal growth patterns, indicating potential growth limitation with on-going summer warming. While shrubs are currently able to maximize their growth success through a high level of adaptation to local micro-site conditions, their continued growth under rapidly changing conditions is uncertain. However, our results suggest a high level of heterogeneity across spatial and temporal scales. Thus, broad-scale vegetational shifts can not be explained by a singular driver or uniform response pattern. Instead, fine-scale physiological processes and on-site near-ground environmental conditions have to be incorporated into our understanding of these changes.

Zusammenfassung

Die arktisch-alpinen Ökosysteme sind als Hot-spot des Umweltwandels bekannt. Rapide ansteigende Temperaturen haben während den vergangenen Jahrzehnten für massive Veränderungen in der Vegetationsstruktur gesorgt. Dennoch sind diese Veränderungen und ihre Treiber räumlich und zeitlich sehr komplex und trotz ihres starken Einflusses auf das globale Klima sind die zu Grunde liegenden physiologischen Prozesse und Mechanismen auf der Ebene der einzelnen Pflanzen noch immer wenig untersucht. Zum ersten Mal wurden hier deshalb in großem Umfang stündliche Dendrometer-Messungen der Stammdickenveränderungen von Sträuchern, zusammen mit hoch aufgelösten, Standort-spezifischen Umweltdaten genutzt, um diese Prozesse genauer zu beleuchten. Auf diese Weise wurden Wachstumsprozesse dreier Straucharten untersucht und mit den standörtlichen thermischen und hygrischen Bedingungen in Verbindung gebracht. Zunächst wurde dabei das Wachstum einer immergrünen Art unter extremen Umweltbedingungen betrachtet. Es folgte ein Vergleich zwischen immergrünen und laubwerfenden Arten und, abschliessend, eine vergleichende Betrachtung der Wachstumsmuster in unterschiedlichen lokalen Mikrohabitaten. Dadurch konnten ausgeprägte Wachstumsstrategien offengelegt werden, die stark mit dem Wasserhaushalt und Wachstumsrythmus der einzelnen Arten in Verbindung stehen. In heterogener alpiner Topographie sind diese Bedingungen Ausdruck der Variabilität in kleinräumigen Mikrohabitaten, die v.a. durch die Variabilität in Schneeverteilung und Sonneneinstrahlung bedingt wird. Der Wachstumserfolg insgesamt ist hauptsächlich durch saisonale Dynamiken bestimmt, darunter die Verfügbarkeit von Bodenwasser, Schneeverteilung, und damit verbundene Frostwechselzyklen. Übergeordnete, regionale Klimavariabilität spielt eine geringere Rolle. Gleichzeitig wird das Wachstum im Sommer durch außergewöhnlich hohe Temperaturen stark negativ beeinträchtigt, wodurch eine mehr oder weniger stark ausgeprägt Bimodalität in den jährlichen Wachstumsmustern entsteht. Dies deutet auf eine mögliche Wachstumslimitierung unter Sommererwärmung hin. Während Sträucher demnach aktuell in der Lage sind, ihren Wachstumserfolg durch ein hohes Maß an Anpassung an kleinräumige Bedingungen zu maximieren, ist es fraglich, in wie weit dieses Wachstum unter sich schnell ändernden Bedingungen fortgesetzt werden kann. Die Ergebnisse dieser Arbeit deuten darauf hin, dass diese Prozesse stark räumlich und zeitlich variieren werden. Die beobachteten Vegetationsveränderungen in den arktisch-alpinen Ökosystemen können demnach nicht durch einen einzelnen Treiber oder allgemeingültiges Antwortmuster erklärt werden. Stattdessen müssen physiologische Prozesse und standort-spezifische kleinräumige Umweltbedingungen in unser Verständnis dieser Veränderungen einbezogen werden.

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1 Introduction

In alpine ecosystems, where low temperatures prevent tree growth and woody plants reach their upper distribution limit (Körner, 2021), changing vegetation productivity and composition are a highly sensitive indicator of climate and environmental change (Lu et al., 2022). In the arctic-alpine regions, rapid warming is outpacing the global average, turning these high-elevation ecosystems into hotspots of change (IPCC, 2021; Post et al., 2019; AMAP, 2021). Lengthening growing seasons (Epstein et al., 2017), changing snow-cover conditions (Xu et al., 2013), and extreme winter warming events (Bjerke et al., 2017), are strongly enhancing shrub growth and promote shrub encroachment at the uppermost distribution limit, leading to a wide-spread increase in biomass and coverage of dwarf shrubs, as well as profound changes in species composition (Gottfried et al., 2012; Xu et al., 2013; Myers-Smith et al., 2015; Gamm et al., 2018; Zhang et al., 2018). Over the past decades this trend has caused large-scale greening of huge areas of the circumpolar North, confirmed from space with remote sensing methods (Myneni et al., 1997; Jia et al., 2003; Epstein et al., 2012; Berner et al., 2020), as well as through extensive ground observations (Forbes et al., 2010; Elmendorf et al., 2012; Macias-Fauria et al., 2012), and indigenous knowledge (Cuerrier et al., 2015). Consequently, this so-called “Arctic greening,” has been identified as one of the clearest examples of the terrestrial impact of climate change (Forbes et al., 2010; Myers-Smith et al., 2011; Fraser et al., 2014; Carlson et al., 2016; Bjorkman and Gallois, 2020; Collins et al., 2021; IPCC, 2021). Observed and predicted vegetational shifts of this scale are of immense importance to the carbon balance of ecosystems (Joos et al., 2001; Mishra and Riley, 2012; Nauta et al., 2014; Alday et al. 2020), putting a large carbon pool at risk by promoting carbon release from permafrost thaw (Schuur et al., 2013; Schuur et al. 2015). At the same time, they have major impacts on the global water cycle (Zwieback et al. 2019) and lead, due to changes in the surface albedo, to self-amplifying feedbacks regarding the global climate system (Chae et al. 2015; Zhang et al. 2018; Bjorkman and Gallois. 2020).

However, recent observations revealed the complexity and spatial heterogeneity of the greening trend (Macias-Fauria et al., 2020; Myers-Smith et al., 2020), with some areas appearing remarkably stable in the face of rapidly warming conditions (Callaghan et al., 2021), while others even experience a “browning” of vegetation (Bhatt et al., 2013; Phoenix and Bjerke, 2016; Lara et al., 2018; Myers-Smith et al., 2020), caused by physical damage related to extreme events (Bokhorst et al., 2009), as well as reductions in productivity (Myers-Smith et al., 2020). Indeed, when considering the overall trends of greening, browning and stability, the most recent analysis (1985 to 2016) shows that 37.3% of the Arctic has greened, 4.7% has browned, and 58% showed no significant change (Berner et al., 2020).

While this spatial heterogeneity was recognized from space (XU et al, 2013; BERNER et al., 2020), underlying processes and mechanisms of ecological change on the ground are still poorly understood (GAMM et al., 2017; MACIAS-FAURIA et al., 2020; MYERS-SMITH et al., 2020).

Over the past decade, multiple studies explored the complex environmental controls of growth in tundra shrubs and associated shrubification (BLOK et al., 2011; MYERS-SMITH et al., 2015; HOLLESEN et al., 2015; BJORKMAN et al., 2018). Using dendroecological methods, these studies identified temperatures and soil moisture during the main growing season as the most important drivers in controlling cambial activity in shrubs (BLOK et al. 2011, HOLLESEN et al. 2015, ACKERMAN et al., 2017; WEIJERS et al., 2017; FRANCON et al. 2020a). At the same time, plant life, and especially growth processes of low stature shrubs, in arctic and alpine environments is mainly controlled by near-surface climatic conditions, with a strong influence of micro-topography, modifying the general climate conditions (LÖFFLER, 2003; BÄR et al., 2007; KÖRNER, 2012). Therefore, other effects, including small-scale variations in snow protection and snow cover duration caused by winter and spring warming, as well as changes in precipitation, wind exposure and solar insolation might play an additional role in promoting or impeding shrub growth (HOLLESEN et al., 2015; WEIJERS et al., 2018a; FRANCON et al., 2020a). However, since past studies mostly rely on annual measurements of stem or shoot growth, obtained from shrub-ring series (MACIAS-FAURIA et al., 2012; LE MOULLEC et al., 2019), extraction of micro-cores, or wood anatomical analyses (ROSSI et al., 2006; WEIJERS et al., 2010; LIANG et al., 2012; Francon et al., 2020a), the actual, fine-scale physiological processes and mechanisms behind shrub growth remain largely unknown (ACKERMAN et al. 2017). To bridge this knowledge gap, this study presents a novel methodology that aims at the direct exploration of the complex link between environment and stem diameter variation, leading to shrub growth or shrinkage and, ultimately, biomass gain and greening, or biomass loss and decline (Fig. 1).

At the heart of this new methodological approach is the use of fine-scale dendrometers to measure xylem phenology and development at a high temporal resolution. In trees, dendrometers have proven to supply such relevant information with high accuracy, leading to important insights into processes of wood physiology and xylem formation at daily and hourly time scales (DUCHESNE et al. 2012; ROSSI et al. 2016; ZWEIFEL et al. 2021). Previously almost exclusively limited to trees, this tested technology has the potential to provide similarly valuable insigths into growth processes of low stature shrub species, including fine-scale response mechanisms to a changing environment, and information on stem water dynamics and carbon fluxes, with higher quality and resolutions than previously attainable (STEPPE et al., 2015; ZWEIFEL, 2016; GONZÁLEZ-RODRÍGUEZ et al., 2017). Therefore, we here deployed high-precision dendrometers to bridge the gap between classical dendroecology and the underlying growth physiology of several widely distributed shrub species.

Starting at the intra-species level, we focused on one evergreen shrub species (*Empetrum nigrum* ssp. *hermaphroditum*) first, explaining unique growth patterns and adaptation of these patterns under extreme environmental conditions. Here, the application of high-precision dendrometers provided a detailed understanding of the growth processes of this common shrub species and its relation to its immediate environmental surroundings (DOBBERT et al., 2022). Subsequently, we moved to the inter-species level, comparing the highly specialised growth patterns found in *E. hermaphroditum* to a similarly widespread deciduous species (*Betula nana*) at the same sites, revealing highly contrasting growth strategies and environmental controls (DOBBERT et al., 2021a). Finally, a closer look at the spatial variability of these growth strategies within the highly heterogenous alpine landscape gave important insights into the overall plasticity of the examined shrub species and potential range and niche shifts in response to future environmental change. (DOBBERT et al., 2021b). With this project we were thus able to tackle the following questions:

1) How and to what extent are fine-scale physiological mechanisms of common shrub species controlled by the specific conditions of their immediate surroundings?
2) How do these mechanisms and environmental controls vary on an inter-species level?
3) How and to what extent do individual specimens optimize radial growth processes to maximize growth success at contrasting sites within arctic-alpine environemts?
4) How is micro-site environmental change potentially affecting fine-scale physiological mechanisms, driving the observed large-scale vegetational shifts?

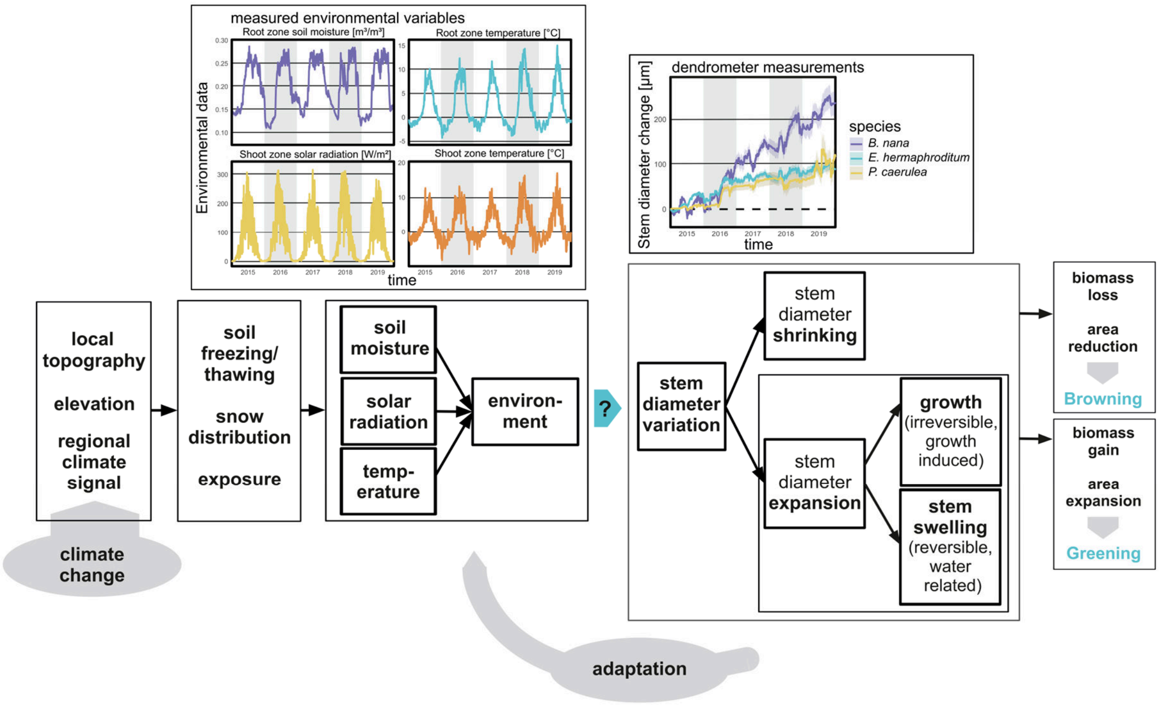

Fig. 1: Stem diameter change can be interpreted as an indicator for shrub growth and consequent shrubification, resulting in biomass gain and greening of the affected areas across tundra ecosystems. Thus, we here explore the important link between on-site environmental conditions and stem diameter measurements provided by fine-scale dendrometers. In turn, these environmental conditions (including near and below ground temperatures, soil moisture and global radiation), are a result of the regional climate signal as well as the heterogenous alpine environment, leading to uneven snow distribution, differences in annual soil freezing and thawing, and exposure to solar radiation.

2 Material and Methods

2.1 Focal species

The alpine vegetation of the tundra biome from the treeline upwards is generally sparse and dominated by shrubs, chionophobous lichens and graminoid species (DAHL, 1986), with shrubs close to reaching their elevational limit within our study areas in Central Norway. For this project, we selected three of the most common shrub species found in these areas, two evergreen (*Empetrum nigrum* ssp. *hermaphroditum* (Hagerup), crowberry, hereafter *E. hermaphroditum*, and *Phyllodoce caerulea* (Linnaeus), blue mountain heath, hereafter *P. caerulea*), and one deciduous (*Betula nana* (Linnaeus), dwarf birch, hereafter *B. nana*) (Table 1, Fig. 2). Aside from dominating large parts of the alpine ecosystems of Central Norway, all three species have a near circumpolar distribution (BÜNTGEN et al., 2015; HULTÉN, 1968) and exert considerable effects on tundra communities (BELL and TALLIS, 1973; BRET-HARTE et al., 2001; COKER and COKER, 1973; WAHREN et al., 2005). Thus, they play a key role for the greening and browning trends observed in the area (CRAWFORD, 2008; MYERS-SMITH et al., 2015; HOLLESEN et al., 2015). For this reason, as well as due to their wide availability, especially *B. nana* and

E. hermaphroditum have been excessively studied in recent years (BRET-HARTE et al., 2001; BIENAU et al., 2014; HOLLESEN et al., 2015; CAHOON et al, 2016; LI et al., 2016; HEIN et al., 2020), with *E. hermaphroditum* being the first shrub species for which dendroecological ring-width series were developed (BÄR et al., 2006; BÄR et al., 2007).

B. nana and *E. hermaphroditum* occur across a broad range of micro-habitats and are able to tolerate comparatively low winter temperatures, varying snow cover thickness, and harsh winds to a certain extent (ANDREWS et al., 1980; STUSHNOFF and JUNTTILA, 1986; de GROOT et al., 1997; ÖGREN, 2001; BÄR et al., 2007). However, both species prefer moderate conditions (DIERßEN, 1996), and *B. nana* has been shown to react positively to a warming climate (WAHREN et al., 2005). *P. caerulea*, on the other hand, usually grows best at habitats with prolonged snow cover (more than 100 days annually) and primarily prefers slopes (COKER and COKER, 1973; KAMEYAMA et al., 2008). *B. nana* commonly surpasses both *E. hermaphroditum* and *P. caerulea* in height (COKER and COKER, 1973; DE GROOT et al., 1997), and is thus likely to influence growth of its competitors by restricting their exposure to solar radiation (BRET-HARTE et al., 2001; BÄR et al., 2007).

Table 1: Focal shrub species with sampled specimens: the total number of sampled specimens, positions: the topographical positions at which the respective species was sampled, elevation: the elevational range at which the respective species was sampled, type: evergreen or deciduous species, distribution: the global distribution of the respective species.

Species	**Sampled specimens [n]**	**Positions**	**Elevation [m a.s.l.]**	**Type**	**Distribution**
Betula nana (Linnaeus) dwarf birch	34	ridges/ slopes/depressions	768 – 1510	deciduous	circumpolar (BÜNTGEN et al., 2015)
Empetrum nigrum ssp. *hermaphroditum* (Hagerup) Crowberry	58	ridges/ slopes/depressions	768 – 1565	evergreen	circumpolar (BÜNTGEN et al., 2015)
Phyllodoce caerulea (Linnaeus) blue mountain heath	26	slopes	768 – 1534	eergreen	circumpolar (HULTÉN, 1968)

Fig. 2 Photos of the three focal species *Betula nana*, *Empetrum nigrum* ssp. *hermaphroditum*, and Phyllodoce caerulea (after Löffler et al. 2021).

2.2 Study areas

The study was conducted in two alpine regions of the Tundra biome in Central Norway, representing a steep oceanic-continental gradient (Fig. 3). The Geiranger/Møre og Romsdal region within the inner fjord section of Norway (62°030 N, 7°150 10 E), features well-developed glacial valleys and deeply incised fjords as a result of repeated glaciations during the Quaternary (HOLTEDAHL, 1967). The region is characterized by a mild periglacial climate with slightly to markedly oceanic climatic conditions. The total annual precipitation is 1500 to 2000 mm in the valleys (Aune, 1993) and the mean annual ambient air temperature is 1.9 °C (range −23.2 to 17.2 °C) (LÖFFLER, 2003). To the east, the Vågå/Innlandet region (61°530 N, 9°150 E) is located approximately 150 km from the coast, yet already within the continental climatic section (MOEN and LILLETHUN, 1999). In contrast to the study region to the west, it is characterized by dry conditions, showing the highest aridity found in Norway, with a total annual precipitation of approximately 300 to 500 mm in the valleys (KLEIVEN, 1959). Here, the mean annual ambient air temperature is −1.2 °C (range −29.2 to 16.7 °C) (LÖFFLER, 2003). Both regions are marked by the complex topography typical for alpine environments, where scales of a few tens of metres can give rise to high microclimatic variation (SCHERRER and KÖRNER, 2011; GRAAE et al., 2017; KÖRNER, 2021), with snowdrift leading to an uneven distribution of the snowpack (WUNDRAM and LÖFFLER, 2008), influencing the local species composition (JONASSON, 1981; ODLAND and MUNKEJORD, 2008) (Fig. 4). Consequently, the on-site environmental conditions monitored for this study vary considerably throughout the year, depending on topographical position (Fig. 5c). During winter, north- and south-facing slopes are usually covered by snow, protecting the existing plants till the middle of May and June, respectively. Contrastingly, plants on the wind-blown ridges are exposed the entire year (BÄR et al., 2007), while local depressions are snow filled till well into the summer months. The study sites were chosen to represent this heterogeneity, as well as the steep elevational gradient found in both regions: All sites were located between the treeline (approximately 750 m a.s.l. in the west and approximately 1000 m a.s.l. in the east) and the highest peak in the region (Dalsnibba (1476 m a.s.l.) in the west and Blåhø (1618 m a.s.l.) in the east, Fig. 6). At the lower study sites (low alpine belt), the vegetation is dominated by shrub and heather communities, while the upper sites (middle alpine belt) are characterised by patchy grassy vegetation, with *E. hermaphroditum* eventually remaining the exclusive shrub species within a matrix consisting of debris and graminoids (DAHL, 1986; BÄR et al., 2007). Reindeer and other grazing animals are not present in the study area.

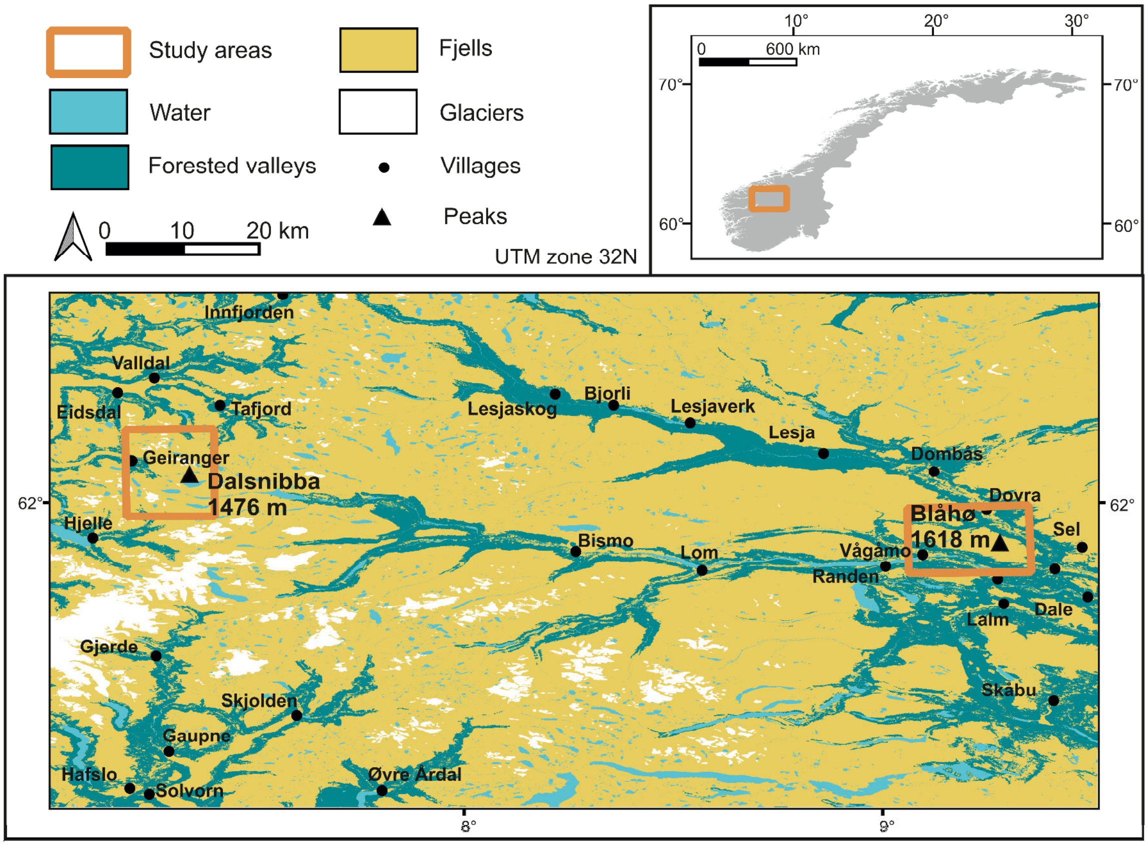

Fig. 3 Study areas in Central Norway with the location the Geiranger/Møre og Romsdal region in the west and Vågå/Innlandet region in the east, marked with orange squares, as well as their location in Norway.

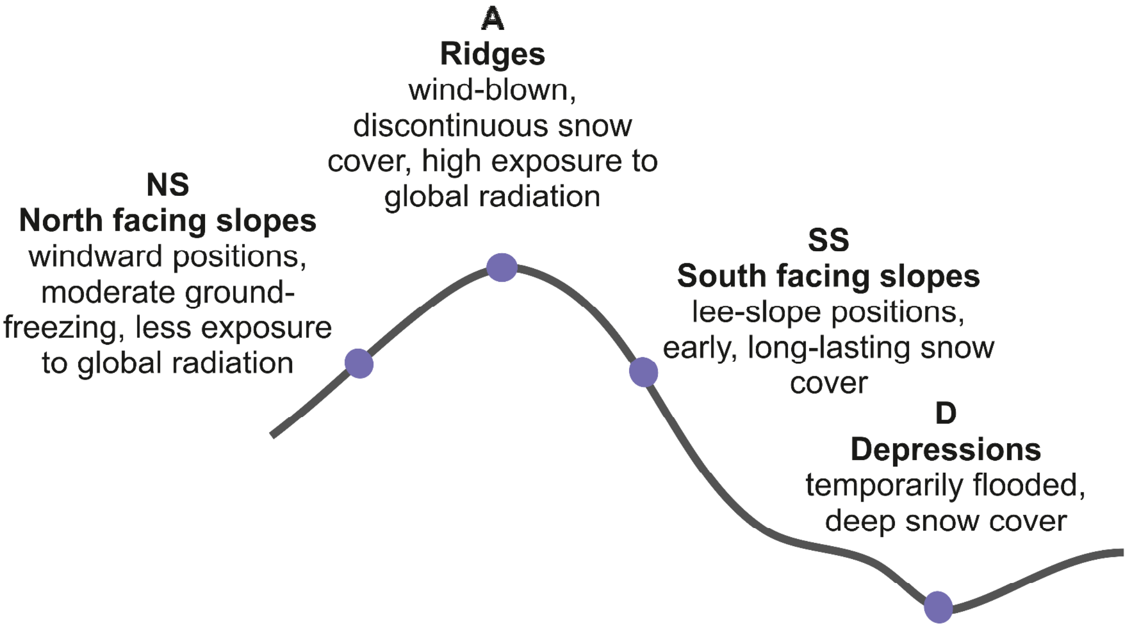

Fig. 4 Micro-topographic gradient and studied topographical positions.

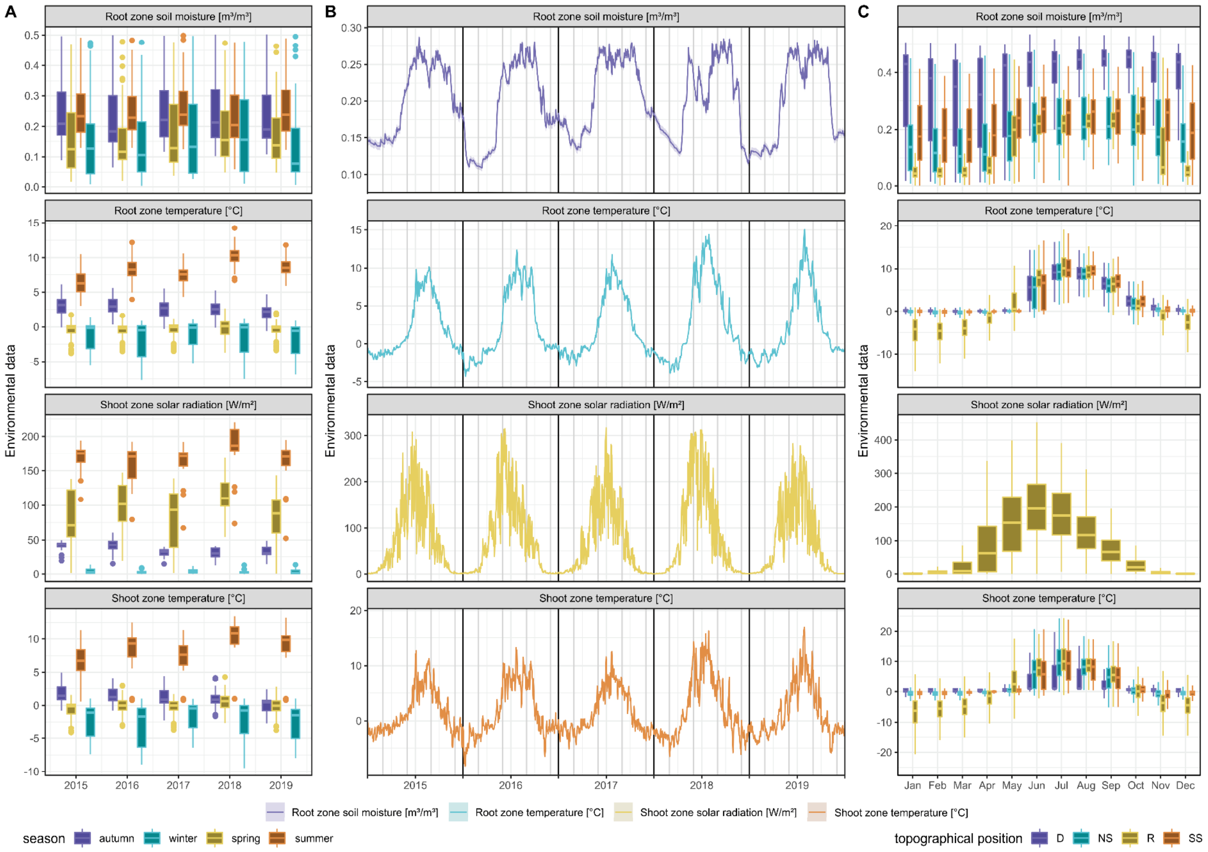

Fig. 5 Measured on-site environmental parameters. Seasonally aggregated data and inter-annual variation (A), and intra-annual regimes throughout the study period with standard deviation indicated by shaded areas (B). Additionally, C shows monthly aggregated variability throughout the year, depending on micro-topographic position.

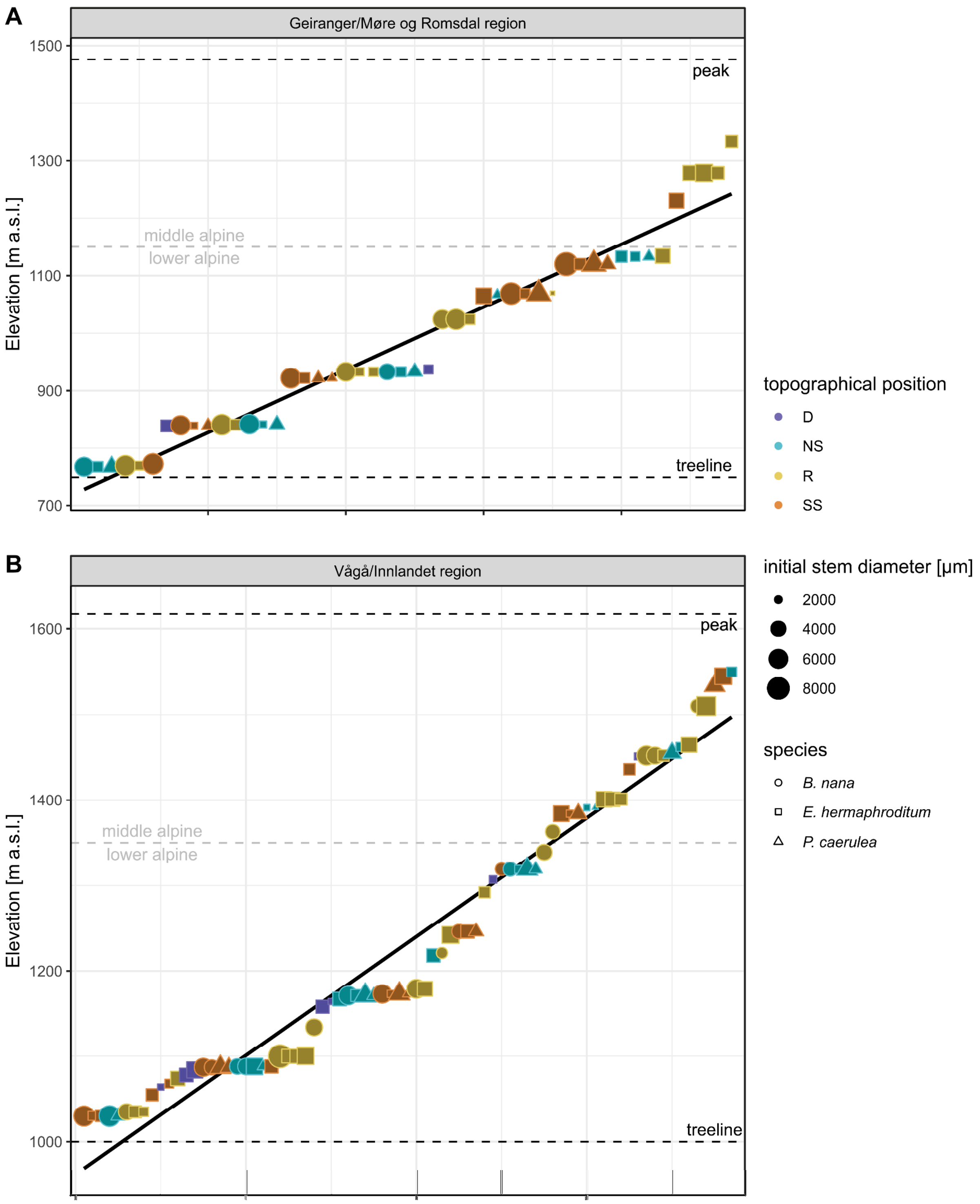

Fig. 6 Location of studied specimens along the elevational gradient in the Geiranger/Møre og Romsdal region (A) and the Vågå/Innlandet region (B). If possible, at each elevational band a broad variation of micro-topographic positions and existent species was sampled. The size of the data points gives the respective stem diameter at the start of the study period in 2015. Additionally, for reasons of readability the data points are shifted along the x-axis, here. However, this shift does not represent any spatial pattern in the study sites.

2.3 Study design and data collection

This study was designed to represent the full complexity of arctic-alpine shrub life from the treeline to the highest local peak. Individual specimens were thus monitored along a regional climate gradient (oceanic-continental), the alpine elevation gradient, and along the micro-topographic gradient (Fig. 6). The result was a five-year dataset containing continuous, hourly measurements of shrub stem diameter variation from 2015/01/01 till 2019/12/31, with some additional data from 2014 and 2020, as well as on-site environmental measurements for the same time period. This dataset gave rise to numerous opportunities for exploring climate-growth relations across scales within these highly relevant ecosystems (Fig. 7), with the focus on multi-scale modelling of complex patterns of stem diameter change from microsite environmental conditions, shedding light on the physiological mechanisms behind radial stem growth.

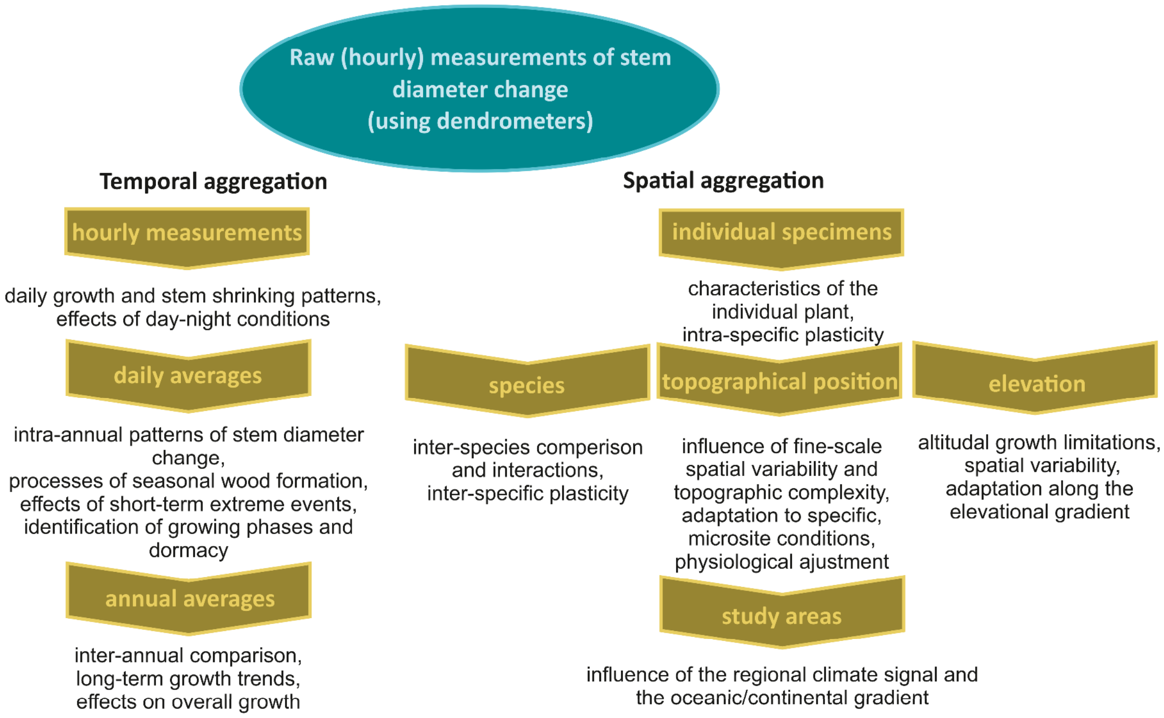

Fig. 7 Temporal and spatial aggregation of the measured data and the information potentially derived from each grouping step.

2.3.1 Dendrometer measurements

Given the current environmental change and uncertain climate prognoses (IPCC, 2021), monitoring forest and tree growth dynamics in a changing environment has become an important field of research and a strong focus of dendroecological studies (Breitsprecher and Bethel, 1990; Duchesne et al., 2012; Ježík et al., 2016; van der Maaten et al., 2018; Smiljanić and Wilmking, 2018; Cruz-García et al., 2019).

The first designs for dendrometers to monitor continuous radial stem change in trees were described in the 1930s and the 1940s (REINEKE, 1932; DAUBENMIRE, 1945). Since then, dendrometers have been widely used in tree physiology and forest sciences, mainly to monitor secondary growth responses to environmental fluctuations (BREITSPRECHER and BETHEL, 1990; DUCHESNE et al., 2012; JEŽÍK et al., 2016; VAN DER MAATEN et al., 2018; SMILJANIĆ and WILMKING, 2018). The stem diameter variability measured by dendrometers is a result of cambial activity and underlying fine-scale, eco-physiological mechanisms, including water-driven turgor pressure changes in the xylem (STEPPE et al., 2015; DREW and DOWNES, 2009; CUNY et al., 2015; CHAN et al., 2016; ZWEIFEL, 2016; PETERS et al., 2021; KÖRNER, 2021). These processes usually occur at timescales ranging from hours to days (DESLAURIERS et al., 2007; KÖCHER et al., 2012; LIU et al., 2018), which is why the fine temporal resolution gained by dendrometers provides valuable additional insights compared to traditional methods. Modern dendrometers developed in recent decades are able to detect radial stem dimensions at hourly or even shorter intervals (DREW and DOWNES, 2009; LIU et al., 2018) and are thus an effective technique for recording intra-annual tree growth variability. Furthermore, because these dendrometers are designed to measure at a micrometer scale, they have the potential to be used on shrubs to provide fine-scale, intra-annual, continuous, and highly comparable information. Consequently, the first study using band dendrometers to monitor radial stem growth of tree-like shrubs was presented recently (GONZÁLEZ-RODRÍGUEZ et al., 2017).

Here, dendrometer measurements were taken using high-precision dendrometers (type DRO; Ecomatik, Dachau/Germany), with a temperature coefficient of <0.2 µm K^{-1}, mounted on one major above-ground stem horizontal to the ground surface for each specimen, as close to the assumed root collar as possible (approximately 1–5 cm above the ground). When choosing the individual specimens, positions near stones and small depressions, inside the radius of other larger shrub species, and near patches of wind erosion were avoided to ensure accurate measurements.

However, with this monitoring design two main concerns arose and were addressed during the installation process of the dendrometers: 1) Given the multi-stemmed nature of the monitored species, the question arises to what extent the measured singular stem represents the whole plant. This issue was addressed by BÄR et al. (2006, 2007) through serial sectioning of *E. hermaphroditum* specimens. They came to the conclusion that the major stem represents the whole plant at least partly, with some amount of variation between the stems of the same plant. Here, this variation was accounted for by sampling a high number of individual specimens, increasing the overall sample size. However, the intra-plant variability of secondary growth processes provides a multitude of opportunities for future research and might be specifically addressed through wood anatomical analyses. 2) Furthermore, dendrometer measurements on trees have been influenced by changing bark water content causing hygroscopic shrinkage and swelling of dead tissues and consequent uncertainties in stem diameter measurements (ZWEIFEL and HÄSLER, 2000; GALL et al., 2002; ILEK et al., 2016). Here, comparative studies revealed a complex interplay of xylem as well as phloem growth and pressure-induced size changes, which simultaneously affect radial stem change and are thus captured by the dendrometers (TURCOTTE et al., 2011; ZWEIFEL et al., 2014; OBERHUBER et al., 2020; KNÜSEL et al., 2021). Following a common practice for dendrometer measurements of trees (e.g., GRAMS et al., 2021; OBERHUBER et al., 2020; WANG et al., 2020), the dead outer bark was therefore removed to place the sensor as close to the living tissue as possible and to eliminate the effects of such processes.

2.3.2 Radial stem changes - Growth or water induced swelling?

Dendrometers produce time series of stem diameter variability with exceptionally high resolution, providing important information on cambial activity, including cell formation and cell enlargement, thus presenting an alternative to time-consuming traditional dendroecological methods (DESLAURIERS et al., 2007; DREW and DOWNES, 2009; MILLER et al., 2022). At the same time, the raw measurements provided by dendrometers contain stem swelling and shrinking resulting from water-driven turgor pressure changes in the xylem. The radial stem variation measured by dendrometers might therefore be higher than the actual stem growth in terms of wood production (STEPPE et al. 2006; ZWEIFEL et al. 2006; STEPPE et al., 2015; ZWEIFEL et al., 2016). Separating these co-occurring processes is therefore highly important for mechanistically interpreting radial stem variations. In trees, this issue has been addressed in recent years and two main approaches have emerged (ZWEIFEL and HÄSLER, 2000; DESLAURIERS et al., 2007; ZWEIFEL et al., 2016):

The use of sigmoid growth models (e.g., Gompertz, Weibull) to infer growth rates as well as critical dates of stem growth phenology (i.e., timings of onset, peak and offset) has proven successful for a number of species and is especially used to explore climatic controls of total annual growth and timing of the growing phase (ROSSI et al., 2003; DUCHESNE et al., 2012; VAN DER MAATEN et al., 2018; LIU et al., 2019) (Fig. 8). With this approach, the estimates produced by the models are considered proxies of seasonal stem growth dynamics. The growing season is then inferred from the model by defining a threshold, i.e. a growth rate larger than 5 µm per day (DUCHESNE et al., 2012), or 5% of the total annual increment (VAN DER MAATEN et al., 2018) for growth start, and 95% or 97.5% of the total annual increment for growth cessation (ZWEIFEL et al., 2016; VAN DER MAATEN et al., 2018). However, a comparison of different thresholds is not included in most studies using this approach (MILLER et al., 2022). Furthermore, potential water deficits and rehydration of the tree stems are not considered, which is why it is especially useful in regions with a longer growing season and no pronounced winter shrinkage (VAN DER MAATEN et al., 2018; LIU et al., 2019). Using this modelling approach to identify intra-annual growth dynamic in shrubs proved to some extend successful for our focal species (DOBBERT et al., 2022). However, it also provided a challenge since the monitored shrub specimens usually showed a higher variability in stem diameter and a less pronounced growing phase with additional stem shrinking during winter and spring (Fig. 8). Here, a more flexible modelling approach (generalized additive models, GAMs) proved more suitable, since additional patterns of stem change, including a pronounced phase of stem shrinking during winter, as well as bimodal growth patterns in some specimens, were captured (Fig. 10a, 11a, 12a).

An alternative to the modelling approach is the so-called zero growth concept, which became increasingly popular in recent years (CUNY et al., 2015; LAMACQUE et al., 2019; PAPPAS et al., 2020; ZWEIFEL et al., 2021). This approach, which was proposed by ZWEIFEL (2016), assumes zero growth during periods of stem shrinkage, providing a concept of how tree growth responds to water shortages. The assumption is based on empirical and theoretical evidence that radial stem growth is suppressed when tree stems are shrinking due to the transpiration-induced lowering of the turgor pressure, meaning that before cell expansion and cell division is promoted, a turgor threshold of the meristem must be crossed (LOCKHART, 1965). Growth is therefore equivalent to an increase in stem radius when the measured radius is larger than it was at any point in the past. Hence, a cumulative maximum curve can be used to describe growth processes, resulting in a stepwise curve (ZWEIFEL et al., 2016; ZWEIFEL et al., 2021; MILLER et al., 2022). Here, growth is understood as irreversible stem increment, including the formation of new wood cells and neglecting any cell maturation processes (CUNY et al., 2015; RATHGEBER et al., 2016) (Fig. 8). This approach was especially useful for shrub growth in ecosystems of the alpine Tundra, where extreme winter conditions and seasonal soil freezing and thawing, as well as irregularly distributed snow cover led to complex hydraulic fluctuations within the stem, resulting in periodic stem shrinking and swelling (DOBBERT et al., 2021a; DOBBERT et al., 2021b).

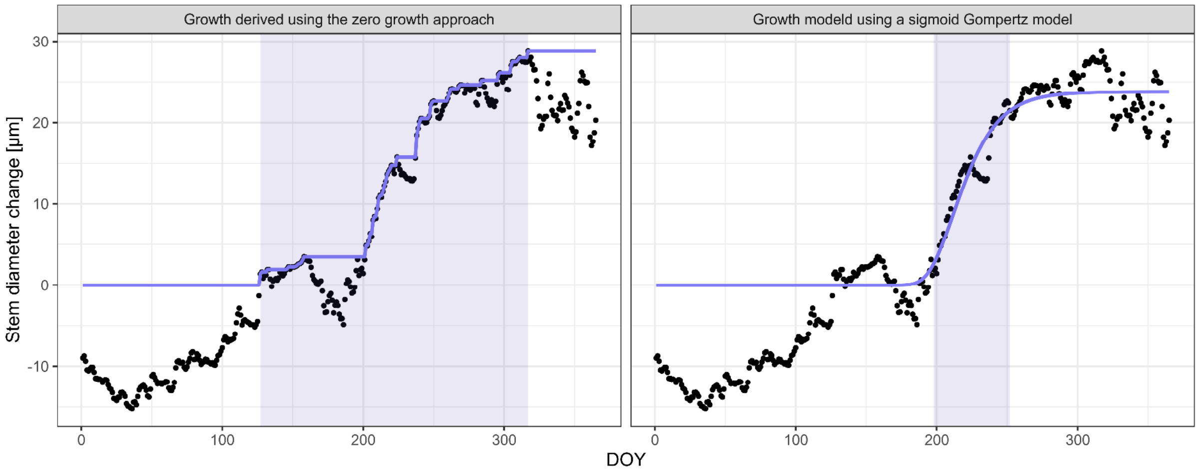

Fig. 8 Approaches to derive timing and magnitude of annual radial stem growth from raw measurements of stem diameter change of *E. hermaphroditum* in 2015. Shaded areas show the respective derived growing season. The threshold for the growing season from the Gompertz-model was defined as 5% and 95% of the total annual increment (e.g. VAN DER MAATEN et al., 2018).

2.3.3 Environmental measurements

In the field of alpine ecosystem research, the importance of reliable environmental data with high spatial and temporal resolution is undisputed. However, given the complex alpine topography (BARRY, 2008; KÖRNER, 2021), and the fact that most official meteorological stations are located in valleys (PRICE and BARRY, 1997; WUNDRAM et al., 2010), obtaining such data often provides a challenge in alpine settings. It has therefore become a common practise to use macroclimatic data, such as free atmospheric air temperature (e.g., BÄR et al., 2007; BÄR et al., 2008; HOLLESEN et al., 2015; WEIJERS et al., 2018b) or general climate scenarios derived from global circulation models with coarse resolution (SÆTERSDAL and BIRKS, 1997; ENGLER et al., 2009). However, within the complex alpine terrain with contrasting elevations, high topographic heterogeneity, and consequent microhabitat differentiation (BARRY, 2008; WUNDRAM et al., 2010; KÖRNER, 2021), incorporating fine-scale spatial variability of near-surface conditions is essential. Here, temperatures, moisture and radiation were therefore measured directly at each individual site, within the root- and shoot zone of the monitored specimens.

In general, it is believed that temperatures are the driving force behind alpine plant distribution, with thermal constrains defining the upper range limit, as temperatures are decreasing with increasing elevation (KÖRNER and HILTBRUNNER, 2018; KÖRNER, 2021) (Fig. 9), comparable to range limits at high latitudes (RANDIN et al., 2013). However, evidence of advancing alpine shrublines with warming conditions at high elevations is limited (LU et al. 2021; WANG et al., 2021). At the same time, especially air temperature has been identified as the key driver of shrub growth (ROSSI et al., 2016), linking recent warming to the greening trend observed in high latitude regions (MYERS-SMITH et al., 2015; ELMENDORF et al., 2012; HOLLESEN et al., 2015). While seasonal xylem formation in shrubs is still poorly understood (ROSSI et al., 2016), multiple studies agree upon the negative effects of low air temperatures during the growing season on cambial activity (GRIČAR et al., 2006; BÄR et al., 2008; MYERS-SMITH et al., 2015). At the same time, soil temperatures were found to be similarly important for shrub growth, controlling microbial activity and composition, as well as nutrient and liquid water availability, and soil freezing and thawing processes (BJÖRK and MOLAU, 2007; BÄR et al., 2008). For this project, soil temperatures (°C) were measured at a depth of 15 cm below the ground surface (i.e., within the root zone) and air temperatures at 15 cm above the ground surface (i.e., within the shoot zone), at all sites. Temperatures were measured at 1 min intervals and recorded as hourly means using Onset's HOBO loggers (type H21-002) and type S-TMB-M002 temperature sensors (±0.2 °C accuracy). For the air temperature measurements, the sensors were equipped with passively ventilated radiation shields. As expected, air and soil temperatures followed a similar regime within the studied regions, with temperatures rising in April or May and staying high for a comparatively short period throughout the summer months before falling again in autumn and reaching their lowest values during winter (Fig. 5). Within the studied period, the year 2015 was characterized by a relatively long winter, with lasting low temperatures throughout the meteorological spring and reoccurring soil freezing. In contrast, the years 2019 and 2018 were characterized by relatively short, cold winters with an early rise in spring temperatures and unusually high summer temperatures (Fig. 5).

In recent years, the spatial and temporal heterogeneity of the shrubification trend, often decoupled from warming conditions (MARTIN et al., 2017; BRODIE et al., 2019; MYERS-SMITH et al., 2020), has shifted the focus from thermal conditions during the growing season to consider additional environmental factors controlling growth processes and, consequently, shrubline dynamics and vegetational shifts (MYERS-SMITH et al., 2015; MARTIN et al., 2017; BJORKMAN et al., 2020; WANG et al., 2021). Such conditions include seasonal soil moisture availability and snow cover dynamics (GRYTNES et al. 2014; ACKERMAN et al., 2017; WANG et al., 2021), shaping micro-site conditions within the heterogenous alpine regions (LÖFFLER, 2005). To identify the soil moisture constraints caused by cold and dry conditions and regular soil freezing directly within in the root zone of the observed specimens, the volumetric soil water content (m^3/m^3) 15 cm below the soil surface was measured at all sites. The uncalibrated soil moisture was measured at 1 min intervals and recorded as hourly means using Onset's HOBO type S-SMD-M005 soil moisture sensors (±3 % accuracy). Similar to the temperature regimes, the resulting soil moisture curves followed a distinct annual pattern, rising in spring with thawing soils and sinking in autumn with the winter frosts (Fig. 5). Consequently, fine-scale fluctuations in soil moisture contained important information on freeze-thaw cycles and timing of snowmelt. In

2015, for instance, soil moisture rose gradually, indicating reoccurring freezing conditions. In contrast, the years 2019 and 2018 experienced considerable spring cold snaps (as evident by drops in the soil moisture regimes), indicating renewed soil freezing.

Additionally, the exposed ridge positions provided the opportunity to measure global radiation within the shoot zone (W m^{-2}) at 1 cm above the ground surface in close proximity to each plant using Onset's HOBO type S-LIB-M003 silicon pyranometers (±10 W m^{-2} accuracy). We made sure that those measurements were not affected by the canopy.

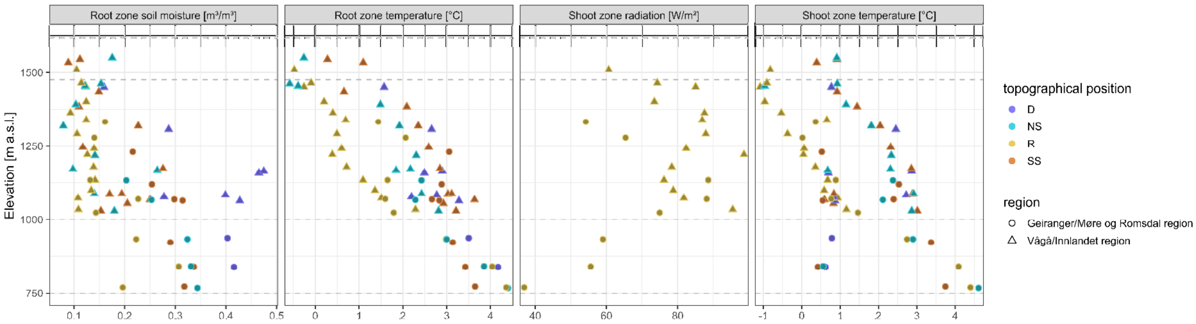

Fig. 9 Observed on-site environmental conditions along the elevational gradient within the two studied regions. Dotted lines represent the treeline and highest peak in each region: Light grey for the Geiranger/Møre og Romsdal region, and dark grey for the Vågå/Innlandet region.

2.4 Statistical analysis and modelling of growth processes

All statistical analysis was carried out using the R statistical software version 4.1.2 (R Core Team, 2021). For practical reasons concerning the processing speed of the mathematical operations performed for the analysis, the hourly measurements were first aggregated to daily mean values. Patterns of stem diameter change were then modelled from the aggregated dendrometer measurements using generalized additive models (GAMs, Wood, 2006) with the mgcv R package (Wood, 2011). Compared to other approaches commonly used to model growth processes, GAMs allow the data to determine the shape of the response curves and make no prior assumption about the functional relationship between the variables (Yee and Mitchell, 1991). They are thus especially suited for modelling flexible data and non-linear patterns. Stem diameter change was modelled with restricted maximum likelihood as a smoothing function of seasonality, expressed as day of the year. The individual specimens and years were included as random effects into the model to account for intra-annual and inter-plant variation.

For inter-annual comparison, total annual growth was then calculated for each individual specimen following the zero growth approach described in chapter 2.3.2. Mathematically, annual growth can therefore be described as the maximum stem diameter measured during one year minus the maximum stem diameter measured during the previous year, thus capturing irreversible stem expansion and excluding reversible stem shrinking and swelling. In turn, these water-related changes in stem diameter were defined as tree water deficit, an indicator of the individual specimen's internal water status and potential drought stress (ZWEIFEL et al., 2005) (Fig. 8).

To relate the on-site environmental conditions to overall growth success of the individual plants, the relationship was modelled with linear mixed effects models, using the lmer function from the lme4 R package (BATES et al., 2015). This widely used modelling approach is highly suitable for grouped data (ALLER et al., 2019; BOLKER et al., 2009; HENN et al., 2018; FIRN et al., 2019) and was therefore chosen to incorporate the complex spatial and temporal variation within the study design. Similarily to the approach presented in DOBBERT et al. (2021b), (log-transformed) total annual growth entered into the analysis as dependent variable, while environmental parameters entered as dependent variables. Species, season, and topographical position were implemented into the models as nested random effects, controlling variation in slope and intercept.

Linear mixed effects models were also used to explore the variation in the stem diameter change patterns captured by the dendrometers, as well as the variability within the micro-site environmental conditions. For this purpose, total annual growth, as well as mean values of each measured environmental variable (including shoot zone temperature, root zone temperature, and root zone soil moisture) were modelled from a set of grouping factors, which entered into the models as random effects. These included spatial factors (study region, elevation, topographical position), as well as temporal factors (Year, Season, Day of the year (DOY)). The percentage of variance explained by each factor was then derived from the models using the VarCorr function (BATES et al., 2015) in R. To represent the study design within the model structure, we nested topographical position within the region and elevation factors, and DOY within the season and year factors. The final models included no fixed effects. All environmental data were standardized (scaled by means and standard deviations) prior to model fitting to make the results comparable (GRACE and BOLLEN, 2005).

3 Results and Discussion

Linking the findings of DOBBERT et al. (2021a, 2021b, 2022) allows for a nuanced, novel perspective on intra-annual growth dynamics, fine-scale physiological mechanisms of stem change, and environmental controls. The detailed data on stem diameter change provided by the dendrometers forms the base of this work. Similar to measurements of radial stem change in trees, the recorded processes can be interpreted as a result of irreversible stem increment, or growth, associated with cambial activity (ROSSI et al., 2008; STEPPE et al., 2015; ZWEIFEL, 2016), as well as reversible expansion or shrinking, related to changes in turgor pressure and xylem water tension (LINTUNEN et al. 2016; LINDFORS et al., 2019) (see chapter 2.3.2). Thus, the information recorded by the dendrometers can be directly linked to the overall physiology and biological mechanism of the individual plant (MARTIN et al., 2017). In turn, this physiology and growth mechanism at each micro-site is a result of regional genotypic variation (CHEVIN et al., 2010; HOFFMANN and SGRÒ, 2011; EIDESEN et al., 2013) and physiological plasticity within the shrub species, a remodelling of the plant's physiology to meet local environmental conditions (CALLAWAY et al., 2003; SEEBACHER et al., 2015). The data presented here therefore contains detailed information on adaptive strategies, resilience, and vulnerabilities of the three focal shrub species in a rapidly changing ecosystem (DUPUTIÉ et al., 2015; ZWEIFEL, 2016; MARTIN et al., 2017).

For the first time, this data allowed for a detailed look at the physiology and growth mechanism of *E. hermaphroditum* at the exposed ridge positions, revealing high intra-species variability in radial stem growth but strong synchrony in response patterns to the local environment, with unique adaptive strategies reflected in highly specialized patterns of stem increment and shrinking (DOBBERT et al., 2022). Subsequently, our comparative analysis showed how these strategies and patterns are highly species-specific, potentially altering species composition with changing environmental conditions (DOBBERT et al., 2021a). At the same time, the heterogenous alpine topography found in the studied regions added to the overall complexity, with growth processes strongly related to fine-scale snow-cover variation and associated freezing and thawing (DOBBERT et al., 2021b). Coming from a nuanced, fine-scale understanding of the individual species' growth processes on an intra-annual scale (with *E. hermaphroditum* being the main focus here), we were thus able to infere important general knowledge on shrub growth and community structure, and the observed large-scale vegetational shifts.

3.1 *Empetrum nigrum* ssp. *hermaphroditum*

As it was the first shrub species for which dendroecologically meaningful ring width chronologies were created (BÄR et al., 2007), the evergreen shrub *E. hermaphroditum*, or crowberry, has become one of the most extensively studied species in high-latitude shrub communities (BÄR et al., 2008; BIENAU et al., 2014; ANGERS-BLONDIN and BOUDREAU, 2017; HEIN et al., 2020). In accordance with previous findings defining a wide thermal niche for *E. hermaphroditum* (LÖFFLER and PAPE, 2020), the species showed the widest range across the studied regions (Fig. 6) and was present at all topographical positions, from the snow-filled depressions to the exposed ridges. Consequently, spatial variation in annual growth processes at these diverse sites was mainly controlled by topographically driven variability in soil moisture conditions, caused by the heterogenous snow distribution within the studied regions. *E. hermaphroditum* also had the highest upper distribution limit, remaining the exclusive shrub species at high elevations, with changing environmental conditions with elevation showing little effects on growth success (Fig. 10e). Overall, these findings suggest a high plasticity and capacity to adapt to extreme conditions in diverse environments (BIENAU et al., 2014; DOBBERT et al., 2021b), with little impact of larger-scale, regional climate signals. Accordingly, modelling stem diameter change dynamics on an intra-annual scale revealed complex patters of stem change, highly adapted to the specific conditions at the respective micro-topographical positions (Fig. 10a). At the exposed, windblown ridges, for instance, *E. hermaphroditum* showed a distinct and strongly pronounced phase of stem shrinkage during the winter months (Fig, 10a, 10g), which can be interpreted as a form of active cell dehydration in the stem to protect the cells from frost damage (FONTI et al., 2010; SCHOTT and ROTH-NEBELSICK 2018). It is thus a direct physiological adaptation to the temperature extremes experienced at these sites, where protective snow cover is missing during most of the year (Fig. 5) (DOBBERT et al., 2021a). Additionally, *E. hermaphroditum* proved not only able to survive at these extreme positions but might profit from photosynthetic opportunities provided by the high global radiation, directly reaching the individual plants (KÖRNER, 2015; SACCONE et al., 2017, DOBBERT et al., 2021a), thus allowing them to benefit from prolonged snow-free periods during the winter months (SPERRY, 2003; FONTI et al., 2010; BOWLING et al. 2018). In order to continue photosynthetic activity in this way, and remain energetically effective in synthesizing carbohydrates despite limited nutrition and soil moisture availability, the evergreen species has to sustain water transport to the canopy to some extent (FONTI et al., 2010; GIMENO et al., 2012; WYKA and OLEKSYN, 2014; LÖFFLER and PAPE, 2020; DOBBERT et al., 2021a). These processes are reflected in the high synchrony between short periods of soil thawing in winter and stem diameter fluctuations (Fig. 10f), exposing the plants to a high risk of frost damage, while allowing for resource acquisition early in the season (DOBBERT et al., 2021a). In accordance with past studies, this phase of early season stem expansion in spring proved especially complex, yet crucial for the individual specimen's growth success during the following years (FONTI et al., 2010; KRAB et al., 2017; VENN and GREEN, 2018; WEIJERS et al., 2018a; DESCALS et al., 2020). Especially at the north-facing slopes, which were usually protected from extreme soil temperatures and soil freezing by an isolating snow cover lasting till well into the spring months, *E. hermaphroditum* proved vulnerable to spring cold-snaps after an early growth start. In most cases, the individual specimens were able to start stem increment and growth directly after snowmelt, utilizing the liquid water in the root zone available after soil thawing to replenish stem water and start growth processes (BRÅTHEN et al., 2018; WEIJERS et al., 2018a; CABON et al., 2020; DESCALS et al., 2020; ZWEIFEL et al., 2021). However, an early growth start left these specimens vulnerable to low temperatures and soil freezing in spring leading to reduced growth and stem shrinking during the following years, indicating cell damage (DOBBERT et al., 2021b) (Fig. 10b). Thus, *E. hermaphroditum* showed the overall least growth success at the slopes and thrived in the depressions, where freezing events in spring were usually absent. Here, the species showed a surprisingly bimodal growth curve, with a short phase of growth cessation or shrinkage in early summer, which was to some extent present at all topographical positions, implying a clear limitation of summer growth (Fig. 10a). This limitation was closely linked to exceptionally high summer temperatures (Fig. 10h), and can thus be interpreted as a reaction to a temperature-induced increase in transpiration after depletion of snowmelt water in spring, interrupting growth processes (SABATER et al., 2019; ZWEIFEL et al., 2021). *E. hermaphroditum* is therefore highly sensitive to changing thermal conditions and the rapidly warming summers observed across the tundra biome (IPCC, 2021). With the cambial rhythm strongly controlled by thermal conditions and snow cover influencing soil freezing and thawing and associated soil moisture availability, as well as exposure to global radiation and associated photosynthetic opportunities, the highly cold-adapted species might struggle to adapt to warming summer conditions and altering snow distribution. Thus, *E. hermaphroditum* will most likely show negative growth responses in a warming environment, with prolonged phases of summer dormancy. At the same time, the species' high physiological plasticity, enabling the individual plants to match their growth mechanism to fine-scale microsite conditions, might similarly allow for the development of coping strategies resulting in a highly complex, non-uniform response to warming conditions across *E. hermaphroditum* populations.

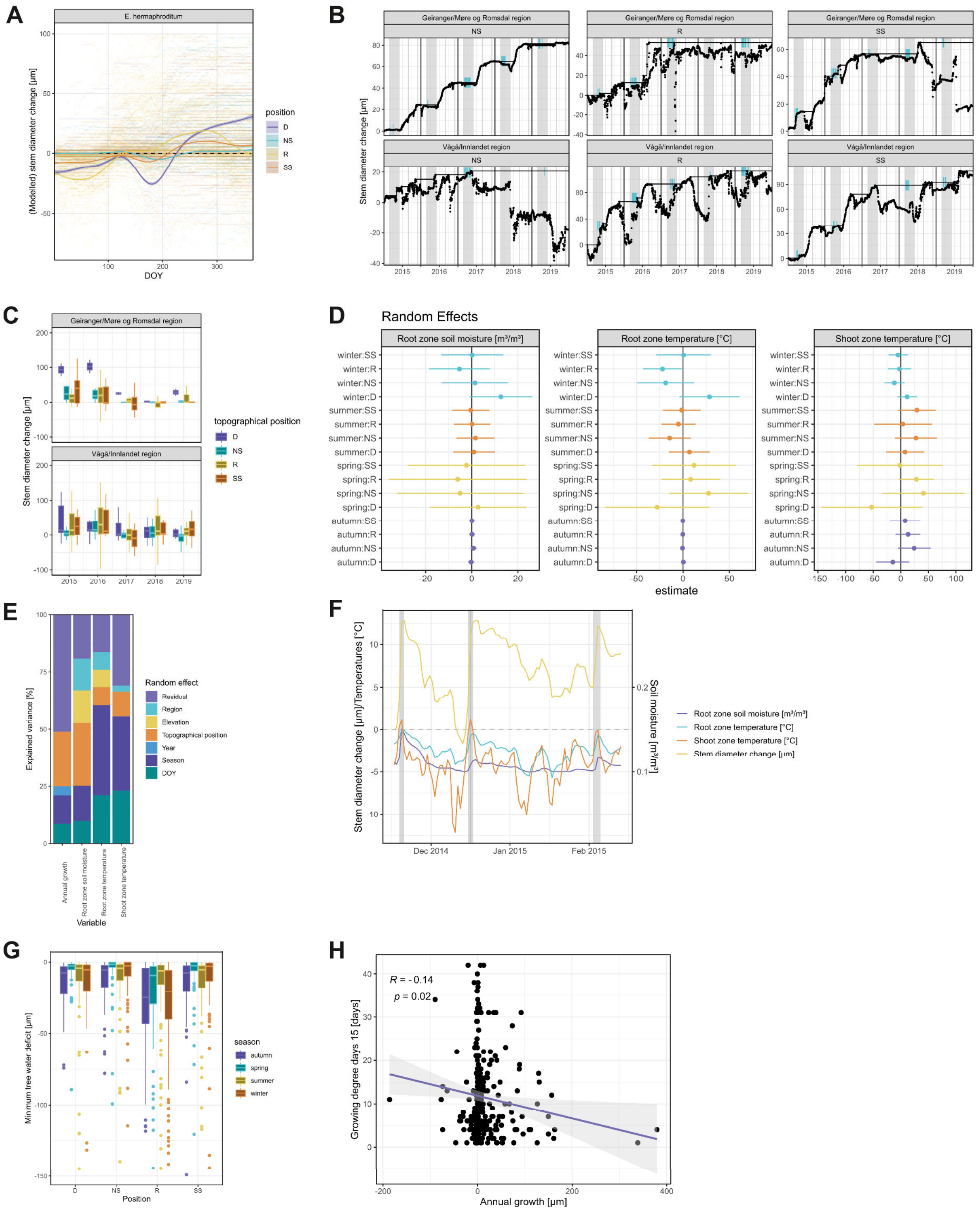

Fig. 10 Growth patterns and climate-growth relations of *E. hermaphroditum*. (A) Intra-annual stem diameter change predicted by generalized additive models (GAMs). Transparent, dotted curves show daily means of measured stem diameter change in relation to the start of the year for all individual dendrometers. Coloured lines show modelled stem diameter change from these raw data for the three focal species and topographical positions. Sampling site and year were included as random effects into the model. (B) Average daily stem diameter change at each topographical position (dotted lines) and cumulative maxima (solid lines) with spring cold spells marked in blue. Cold spells were defined as frost periods (shoot zone temperatures < 0 °C) after the first temperature rise (shoot zone temperatures > 0 °C) in spring. Depressions were not included here, since they did not experience any cold spells in spring. (C) Total annual stem diameter change at each

topographical position. (D) Random effects derived from linear mixed effects models for each season and topographical position. Total annual growth entered into the analysis as dependent variable, and environmental parameters entered as dependant variables. Season and topographical position entered as nested random effects. The error bars represent the 95% confidence intervals. (E) Partitioned variance in total annual growth and environmental parameters, explained by variation in spatial and temporal grouping variables from linear mixed effects models with the grouping variables entering as random effects. (H) Averaged daily stem diameter change and environmental conditions during the winter 2014/2015 with short phases of soil thawing marked in grey. (G) Minimum tree water deficit during each season, representing the maximum stem shrinkage experienced during this season. The values were obtained by calculating the minimum value from the tree water deficit curves, derived by subtracting the measured daily stem diameter change from the cumulative maximum curves (Zero growth curves). (H) Linear regression for total annual growth and the number of days with shoot zone temperatures > 15 °C (GDD15).

3.2 *Betula nana*

Similar to *E. hermaphroditum*, the widespread dwarf shrub *B. nana*, or dwarf birch, has become a focus species for exploring climate-growth relations across the arctic and tundra biome in recent decades (Bret-Harte et al., 2001; Hollesen et al., 2015; Cahoon et al., 2016; Li et al., 2016; Nielsen et al., 2017). Most of these studies highlight the deciduous species positive growth response to warming conditions and lengthening growing seasons, making it a key contributor to the observed greening trend (Deslippe et al., 2011; Hollesen et al., 2015; Nielsen et al., 2017). Within the regions studied here, temperatures proved indeed crucial in promoting secondary growth processes, especially at the south-facing slopes (Dobbert et al., 2021b) (Fig. 11d). Here, *B. nana* was highly adapted to the isolating snow and might benefit from warmer winters with pronounced snow cover and early snowmelt, providing increased nutrition availability (Sturm et al. 2005, Hagedorn et al. 2014) and high soil moisture content. The early flowering species is then able to start budburst and leaf-forming processes early in the season (Morgner et al., 2010; Hallinger et al. 2010, Blok et al. 2015) and can thus profit from the predicted lengthening of the growing season (Fig. 11g). At the same time, the observed *B. nana* specimens at the mostly snow free ridge positions, showed a high level of frost resistance through active stem shrinking during the winter months (Dobbert et al., 2021a). While *E. hermaphroditum* profited from generally narrow vessels here, which embolize less readily than wide ones and can thus be interpreted as an adaptation to extreme conditions (Carlquist and Zona, 1988; Gorsuch et al., 2001), *B. nana* usually has a wider mean vessel diameter. However, recent studies suggest that *B. nana* specimens are able to actively adapt vessel lumen to environmental conditions, thus altering a key anatomical trait in order to increase frost resistance (Nielsen et al., 2017). Like *E. hermaphroditum*, the species is thus able to grow at extreme positions and occupy a wide thermal niche (Löffler and Pape, 2020). Yet, in contrast to the evergreen species, spatial growth variability of *B. nana* was to some extent influenced by the regional climate signal, with higher soil moisture availability promoting shrub growth in the eastern study region (Fig. 11c, 11e). At the same time, falling temperatures with increasing elevation limited the species' range at the highest study sites (Fig. 11e). This is in accordance with general assumptions made for alpine regions, naming declining temperatures with elevation and latitude the main constraining factor for plant growth in these ecosystems (KÖRNER, 2021). However, similar to *E. hermaphroditum*, cambial activity in *B. nana* showed no clearly defined thermal thresholds (ROSSI et al., 2006; GRAAE et al., 2018; KÖRNER, 2021; RAUNKIÆR, 2015). Instead, modelling the intra-annual growth pattern of *B. nana* also revealed a bimodal growth curve, with rapid stem expansion in spring, linked to snowmelt and soil thawing (DOBBERT et al., 2021b), followed by a short phase of stem contraction before a main growing phase in summer (Fig. 11a, 11f). This indicates a clear limitation of summer growth, as well as possible difficulties of the species to adapt to rapidly warming conditions (FRANCON et al., 2020b; DOBBERT et al., 2021b). Hence, deciduous species like *B. nana* might profit from lengthening growing seasons, experience an upward range expansion with warming conditions, and gain a competitive advantage over evergreen species like *E. hermaphroditum* at exposed positions, where these species currently rely on their ability to benefit from cold, snow-free winters by continued photosynthetic activity. Yet, an increase in summer heat waves and associated drought might mitigate these effects, potentially altering species composition and reversing the greening trend (DOBBERT et al., 2021a; DOBBERT et al., 2021b).

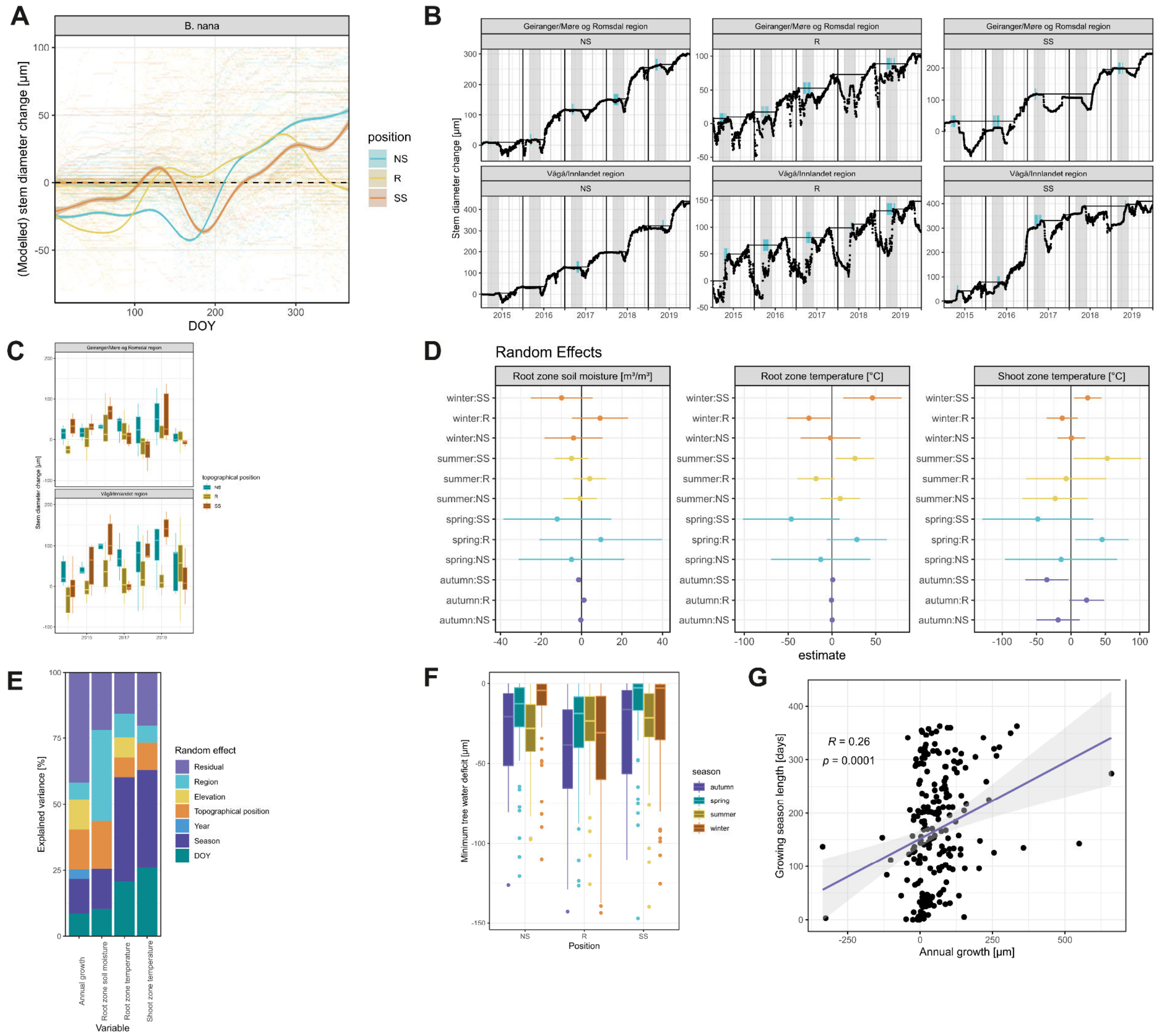

Fig. 11 Growth patterns and climate-growth relations of *B. nana*. (A) Intra-annual stem diameter change predicted by generalized additive models (GAMs). Transparent, dotted curves show daily means of measured stem diameter change in relation to the start of the year for all individual dendrometers. Coloured lines show modelled stem diameter change from these raw data for the three focal species and topographical positions. Sampling site and year were included as random effects into the model. (B) Average daily stem diameter change at each topographical position (dotted lines) and cumulative maxima (solid lines) with spring cold spells marked in blue. Cold spells were defined as frost periods (shoot zone temperatures < 0 °C) after the first temperature rise (shoot zone temperatures > 0 °C) in spring. (C) Total annual stem diameter change at each topographical position. (D) Random effects derived from linear mixed effects models for each season and topographical position. Total annual growth entered into the analysis as dependent variable, and environmental parameters entered as dependant variables. Season and topographical position entered as nested random effects. The error bars represent the 95% confidence intervals. (E) Partitioned variance in total annual growth and environmental parameters, explained by variation in spatial and temporal grouping variables from linear mixed effects models with the grouping variables entering as random effects. (F) Minimum tree water deficit during each season, representing the maximum stem shrinkage experienced during this season. The values were obtained by calculating the minimum value from the tree water deficit curves, derived by subtracting the measured daily stem diameter change from the cumulative maximum curves (Zero growth curves). (G) Linear regression for total annual growth and growing season length.

3.3 *Phyllodoce caerulea*

In contrast to both *E. hermaphroditum* and *B. nana*, the dendroecological potential of the evergreen species *P. caerulea*, or blue mountain heath, has not yet been explored, with very little studies focusing on the physiology of the species. However, it has been noted that *P. caerulea* is usually able to tolerate very short growing seasons and prolonged snow cover (COKER and COKER, 1973; KUDO, 1991). Accordingly, the species was mostly confined to the north- and south-facing slopes within our studied regions, indicating a high adaptation to those positions where snow cover provided protection from extreme temperatures until well into spring, when growth processes begun. Consequently, the species' growth success was mostly influenced by soil moisture conditions in spring and its growth pattern closely linked to seasonal fluctuations in soil moisture availability (Fig.12d, 12e), linked to soil freezing and thawing, as well as snow cover and snowmelt. Thus, *P. caerulea* growth was also to some extend influenced by the regional climate signal, mostly due to differences in precipitation (Fig. 12e). The individual specimens are most likely not able to adjust their growth patterns and physiological processes to extreme environmental conditions, including the low winter temperatures found at the exposed ridges and high soil moisture levels within the depressions. This suggests a comparatively low plasticity, indicating a low adaptive capacity. Thus, *P. caerulea* will most likely not be able to cope with the profound changes in winter snow conditions predicted for the region (CALLAGHAN et al. 2011; BIENAU et al., 2014; IPCC, 2021). With the species' growth mechanism highly adapted to prolonged snow cover, an earlier onset of snowmelt (CALLAGHAN et al. 2011) might leave the specimens vulnerable to spring soil freezing, exposing them to unexpected frost-stress. This will most likely impede *P. caerulea*'s growth success closely linked to changes in snow conditions.

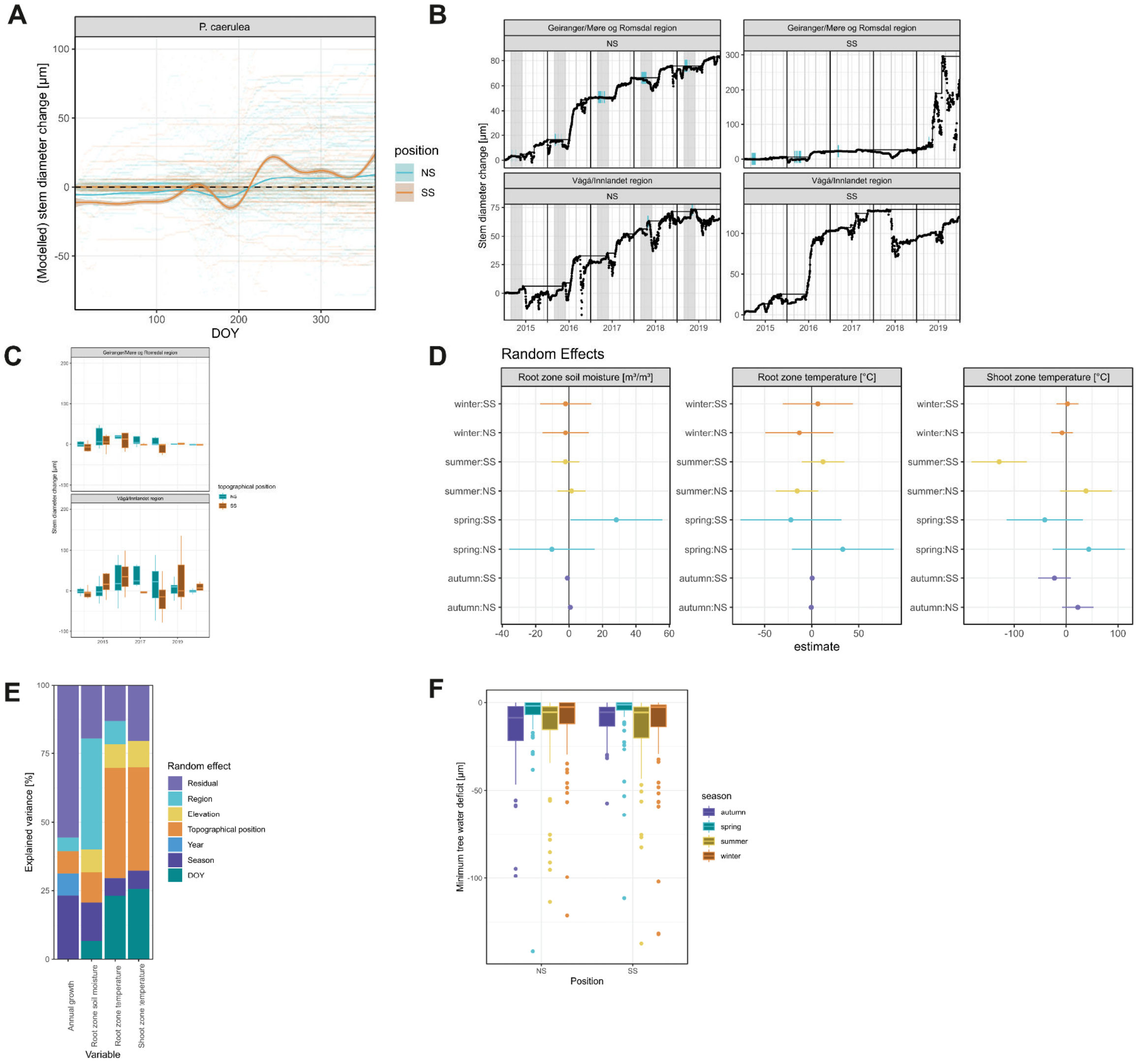

Fig. 12 Growth patterns and climate-growth relations of *P. caerulea*. (A) Intra-annual stem diameter change predicted by generalized additive models (GAMs). Transparent, dotted curves show daily means of measured stem diameter change in relation to the start of the year for all individual dendrometers. Coloured lines show modelled stem diameter change from these raw data for the three focal species and topographical positions. Sampling site and year were included as random effects into the model. (B) Average daily stem diameter change at each topographical position (dotted lines) and cumulative maxima (solid lines) with spring cold spells marked in blue. Cold spells were defined as frost periods (shoot zone temperatures < 0 °C) after the first temperature rise (shoot zone temperatures > 0 °C) in spring. (C) Total annual stem diameter change at each topographical position. (D) Random effects derived from linear mixed effects models for each season and topographical position. Total annual growth entered into the analysis as dependent variable, and environmental parameters entered as dependant variables. Season and topographical position entered as nested random effects. The error bars represent the 95% confidence intervals. (E) Partitioned variance in total annual growth and environmental parameters, explained by variation in spatial and temporal grouping variables from linear mixed effects models with the grouping variables entering as random effects. (F) Minimum tree water deficit during each season, representing the maximum stem shrinkage experienced during this season. The values were obtained by calculating the minimum value from the tree water deficit curves, derived by subtracting the measured daily stem diameter change from the cumulative maximum curves (Zero growth curves).

3.4 General conclusions and synthesis

This study provides new insights into the environmental controls and physiological mechanisms behind secondary growth processes of alpine shrubs. These processes, visible in distinct intra-annual patterns of stem diameter change, were closely linked to species-specific water-use dynamics and cambial rhythm. Especially soil moisture availability and snow conditions at the specific sites proved key drivers of radial stem growth in arctic and alpine regions (DOBBERT et al., 2022), and our analysis revealed contrasting and inter-annually nuanced response patterns for evergreen and deciduous species (DOBBERT et al., 2021a). On an intra-species level, the individual plant's fine scale physiolgical growth mechanism was highly adjusted to its immediate, near- and below-ground surroundings and therefore strongly controlled by the variation in local micro-habitats, which is mainly defined by fine-scale topography and snow distribution within the heterogenous alpine setting (ROPARS et al., 2015, Ropars et al., 2017; YOUNG et al., 2016, NIELSEN et al., 2017; DOBBERT et al., 2021b). How and to what extent the species were able to adjust to this variation, including specific coping strategies under extreme conditions, varied between the three focal species. How do these mechanisms and environmental controls vary on an inter-species level While stem diameter change in all three species followed clear periodic annual cycles of cambial activity and dormancy, closely linked to the climatic regime of the tundra biome, the overall growth success was controlled by fine-scale micro-climatic conditions and therefore in many cases decoupled from governing regional climate signals (PAPE and LÖFFLER 2016; PAPE and LÖFFLER 2017), resulting in a high level of variation in total annual growth between individual sites, specimens and years (DOBBERT et al., 2021a; DOBBERT et al., 2021b; DOBBERT et al., 2022). Conversely, the main drivers of this variation were to a lesser extent atmospheric temperatures and growing season length (ROSSI et al., 2008; ROSSI et al., 2016), but rather complex seasonal dynamics of soil moisture availability, snow conditions, and associated freeze–thaw cycles (DOBBERT et al., 2021b; DOBBERT et al., 2022).

Overall, we can confirm that shrubs, similar to trees (GRIČAR et al., 2015) develop distinct, species-specific strategies of wood formation to function optimally in local conditions and maximize growth success. However, in a rapidly changing environment, this adaptation becomes critically challenged. Species already occupying a wide range of micro-habitats are usually able to closely match their growth mechanism to a variety of differing environmental conditions through physiological adjustment, resulting in growth success at most topographical positions (CRAWFORD, 2008; WIPF, 2010; BIENAU et al., 2014). Given their high phenotypic plasticity, these species (here *E. hermaphroditum* and *B. nana*) have a higher ability to adapt and are thus more likely to persist locally under rapidly changing conditions (JONASSON, 1981; TURCOTTE and LEVINE, 2016, PFENNIGWERTH et al., 2017, GRAAE et al., 2018).

Physiological plasticity can, thus, be directly linked to a species ability to cope with change (e.g., PÉREZ-RAMOS et al., 2019; SEEBACHER et al., 2015). At the same time, species with low phenotypic plasticity, currently relying on highly specific environmental conditions (here *P. caerulea*), might not be able to adjust. While already altering species composition, the observed and predicted changes in the tundra biome (POST, 2019; IPCC, 2021), might therefore potentially reduce species richness in these ecosystems by promoting growth in already dominant species with wide ecological niches and high adaptive capacity. At the same, all three focal species proved sensitive to exceedingly high summer temperatures (DOBBERT et al., 2021a; DOBBERT et al., 2022) with summer temperatures clearly limiting cambial activity during the main growing season (FRANCON et al., 2020b), resulting in a bimodal growth curve and potentially negative growth responses with on-going summer warming. If the species' adaptive capacity is sufficient to match the rapidly rising temperatures predicted for these highly relevant regions therefore remains to be explored in future studies. In general, the findings presented here confirm that there is a strong link between secondary growth of shrubs and changing environmental conditions, including summer and winter warming, as well as altered snow regimes and consequent changes in soil moisture. This link, however, is not uniform and highly variable over spatial and temporal scales (ELMENDORF et al., 2012; MYERS-SMITH et al., 2015), which is why generalizing assumptions across large parts of the arctic and alpine regions might be misleading. Here, a detailed perspective on fine-scale physiological processes and species-specific response patterns to on-site near-ground environmental conditions is key for a profound understanding of broad-scale vegetational changes, including the observed greening and browning trends.

4 References

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5 The application of dendrometers to alpine dwarf shrubs – a case study to investigate stem growth responses to environmental conditions

DOBBERT, S.; PAPE, R.; LÖFFLER, J. (2022): The application of dendrometers to alpine dwarf shrubs – a case study to investigate stem growth responses to environmental conditions. *Biogeosciences* 19 (7), pp. 1933–1958. DOI: 10.5194/bg-19-1933-2022.

Abstract

Considering the recent widespread greening and browning trends associated with shrubs in arctic–alpine ecosystems, further understanding of how these shrubs respond in a rapidly changing environment is of crucial importance.

We here monitor shrub growth, using high-precision dendrometers to produce fine-scale intra-annual growth patterns from hourly stem diameter variability in a widespread evergreen species (*Empetrum nigrum* ssp. *hermaphroditum*). Measurements were taken at a micrometer scale for the period 2015 till 2018 on exposed and mostly snow-free ridge positions. With the same temporal resolution, we collected near-ground environmental data and identified on-site controls of growth behavior.

We found high inter-plant variability in radial stem growth but strong similarities in response patterns to the local environment. Our results suggest that the evergreen species is highly adapted to the specific local conditions, remaining partly photosynthetically active during the snow-free winter, which facilitates carbohydrate accumulation for early-season physiological activities. Additionally, we discovered a phase of radial stem shrinkage during the winter months, which can be attributed to an active cell water reduction to protect the plant from frost damage.

We conclude that soil moisture availability and winter snow conditions are the main drivers of radial stem growth of *E. hermaphroditum* in arctic and alpine regions and could negatively affect the species' distribution in a warming climate.

Biogeosciences, 19, 1933–1958, 2022
https://doi.org/10.5194/bg-19-1933-2022

Biogeosciences Open Access

The application of dendrometers to alpine dwarf shrubs – a case study to investigate stem growth responses to environmental conditions

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Received: 15 April 2021 – Discussion started: 10 May 2021
Revised: 14 February 2022 – Accepted: 15 February 2022 – Published: 5 April 2022

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1 Introduction

Arctic and alpine ecosystems are especially sensitive to recent climate variability, with temperatures increasing thrice as much as the global average in the past decades, caused by a rising concentration of atmospheric CO_2 and accompanied by a substantial lengthening of the growing period (e.g., IPCC, 2014; Post et al., 2019; AMAP, 2021). This trend has favored growth, abundance, and biomass production of numerous shrub species, resulting in a widespread, yet spatially heterogenic, greening of the affected areas – with potentially global effects (Myers-Smith et al., 2011; Gough et al., 2015; Brodie et al., 2019; Myers-Smith et al., 2020). The observed greening has been verified using remote sensing techniques (e.g., Carlson et al., 2017) and is caused by both evergreen and broadleaved species, although in different ways (Vowles and Björk, 2019; Weijers and Löffler, 2020). Relations between carbon assimilation through photosynthesis, environmentally controlled wood formation, and associated plant growth were shown to be complex, complicating the understanding of underlying processes, as well as predictions of future trends (Fatichi et al., 2019; Peters et al., 2021). In general, shrubs are considered one of the most responsive plant functional groups to climate variability (Elmendorf et al., 2012). Their expanding trend, in turn, has been associated with climatic feedbacks, such as influence on surface albedo and frozen-ground processes (Sturm et al., 2001; Chapin et al., 2005; Blok et al., 2011; Aartsma et al., 2021). Therefore, an understanding of shrub growth physiology and its environmental controls is of crucial importance.

Over the past decade, dendroecological studies have identified temperatures and soil moisture as the most important drivers in controlling cambial activity in shrubs, potentially independent of carbon assimilation (Van der Wal and Stien, 2014; Cabon et al., 2020). Here, conditions during the main growing season have proven especially important (Elmendorf et al., 2012; Hollesen et al., 2015; Ackerman et al., 2017; Weijers et al., 2017). Additionally, most recent studies have suggested that snow cover and winter warming may play an important role in promoting shrub growth (Hollesen et al., 2015; Weijers et al., 2018a; Francon et al., 2020), as well as spring warming (Weijers et al., 2018a). Yet, an increased frequency of spring freezing events might counteract these positive effects (Choler, 2018). Collectively, these studies agree on the fine-scale complexity of growth behavior, niche shifts, and local adaptation of shrubs in arctic and alpine regions, with a multitude of still little understood, site-related environmental drivers (Graae et al., 2018; Pape and Löffler, 2017; Löffler and Pape, 2020). Such studies, however, mostly rely on measurements of stem or shoot growth, obtained from shrub-ring series (Macias-Fauria et al., 2012; Shetti, 2018; Le Moullec et al., 2019), extraction of micro-cores, or wood anatomical analyses (Rossi et al., 2006; Weijers et al., 2010; Liang et al., 2012; Francon et al., 2020) – all of which are conducted at an inter-annual timescale, which might not be sufficient in explaining the observed complexity due to a too coarse temporal resolution.

High-resolution data, as provided by dendrometer measurements, have the potential to bridge this knowledge gap. They are likely to provide valuable insights into fine-scale response mechanisms to a changing environment, including information on stem water dynamics and carbon fluxes, with higher quality and resolutions than previously attainable (Fritts, 1976; De Schepper and Steppe, 2010; Steppe et al., 2015; Zweifel, 2016; González-Rodríguez et al., 2017). In general, stem diameter increase can be described as a result of cambial division and cell enlargement, which are in turn closely linked to temperature and water potential and therefore strongly affected by environmental stressors. Thus, stem diameter variability is closely related to cambial activity and underlying fine-scale, eco-physiological mechanisms, including water-driven turgor pressure changes in the xylem (Steppe et al., 2015; Drew and Downes, 2009; Cuny et al., 2015; Chan et al., 2016; Zweifel, 2016; Peters et al., 2021; Körner, 2021). Because cambial activity occurs at timescales ranging from hours to days (Deslauriers et al., 2007; Köcher et al., 2012; Liu et al., 2018), the fine temporal resolution that is gained by dendrometers provides valuable additional insights compared to traditional methods. These include intra-annual and seasonal growth behavior of shrubs in alpine environments, thereby bridging existing knowledge gaps regarding plant productivity in remote ecosystems (Le Moullec et al., 2019).

In tree physiology and forest sciences, dendrometers have already proven useful for monitoring tree responses to environmental fluctuations (Breitsprecher and Bethel, 1990; Duchesne et al., 2012; Ježík et al., 2016; Van der Maaten et al., 2018; Smiljanić and Wilmking, 2018), as recent dendrometers can detect radial stem dimensions at hourly or even shorter intervals (Drew and Downes, 2009; Liu et al., 2018). Starting with the early designs, first described in the 1930s and the 1940s (Reineke, 1932; Daubenmire, 1945), dendrometers have been widely used, focusing on long-term monitoring of growth responses to environmental variables (e.g., Duchesne et al., 2012; Liu et al., 2018; Van der Maaten et al., 2018). Recently, a first study using band dendrometers to monitor radial stem growth of tree-like shrubs was presented (González-Rodríguez et al., 2017). Because current dendrometers are designed to measure at a micrometer scale, they have the potential to be used on shrubs to provide fine-scale, intra-annual, continuous, and highly comparable information (Dobbert et al., 2021a, b).

In this context, we monitored intra- and inter-annual stem diameter variability at alpine ridge positions, testing this novel approach using high-precision dendrometer data derived from individual specimens of the shrub species *Empetrum nigrum* ssp. *hermaphroditum* (hereafter *E. hermaphroditum*), an evergreen shrub that is almost circumpolar in distribution (Bell and Tallis, 1973) and abundant in the Scandes mountain chain. *E. hermaphroditum* has been identified as a niche constructor species with strong direct effects on tundra communities, including a potential slowing of process rates and lowering of biodiversity with *E. hermaphroditum* encroachment (Bråthen et al., 2018). Because of its complex response to variation in snow cover, it is most common at positions with either shallow or relatively deep snow cover (Bienau et al., 2014, 2016). Additionally, *E. hermaphroditum* has been described as comparatively resistant to low winter temperatures (Stushnoff and Junttila, 1986; Ögren, 2001) and is usually not affected by grazing (Weijers and Löffler, 2020). The species' stem anatomy was described by Carlquist (1989) and is characterized by a narrow vessel diameter, which can be interpreted as a form of adaptation to drought or physiological drought due to cold as it impedes embolism formation (Fig. A1 in Appendix A). In general, the family of heath-like shrubs is known to match extreme environments by adapting stem anatomy (Carlquist, 1989) and generally occurs in a wide phytogeographic range at various sites along the alpine elevational gradient. We therefore expect to find the monitored specimens highly adapted to their local environment at the exposed ridge positions, possibly independent from larger-scale environmental variability associated with the elevational gradient. Thus, we aim to (1) explain major growth patterns and their variation between years and specimens, (2) identify the most important environmental drivers controlling these patterns across sites, and (3) gain insights into potential response to environmental change. The main objective of our work is thus to gain detailed understanding of the growth patterns of one common arctic–alpine dwarf shrub (*Empetrum nigrum* ssp. *hermaphroditum*) and its relation to its immediate environmental surroundings. With this, we hope to bridge the gap between observed large-scale vegetational shifts and the fine-scale physiological mechanisms driving these complex changes within the highly relevant arctic–alpine ecosystems.

2 Material and methods

2.1 Study sites

We conducted our study in two alpine mountain regions of central Norway. To the west, the Geiranger, Møre og Romsdal, region (62°03′ N, 7°15′ E) is located within the slightly to markedly oceanic climatic section (O1–O2; Moen, 1999) of the inner fjords. It is characterized by humid conditions, with total annual precipitation of 1500–2000 mm in the valleys (Aune, 1993) and a mean annual ambient air temperature of 1.9 °C (range −23.2 to 17.2 °C) (Löffler, 2003). To the east, the Vågåmo, Innlandet, region (61°53′ N, 9°15′ E) is located within the continental climatic section (C1; Moen, 1999). The total annual precipitation is low, approximately 300–500 mm in the valleys (Kleiven, 1959), and the mean annual ambient air temperature is −1.2 °C (range −29.2 to 16.7 °C) (Löffler, 2003). Our own measurements in the alpine parts of the studied regions indicated that the annual liquid precipitation was 900 mm in the west and 375 mm in the east. The additional amount of snow and its water equivalent remains unknown, but snowdrift leads to an uneven distribution of the snowpack within the complex alpine topography (Löffler, 2007).

Across both regions, we chose micro-topographical positions at exposed, wind-blown ridges as study sites. These positions likely represent the most extreme thermal regimes, with discontinuous snow cover and deeply frozen ground during winter. Within the framework of our long-term alpine ecosystem research project (LTAER; e.g., Löffler and Finch, 2005; Hein et al., 2014; Frindte et al., 2019; Löffler et al., 2021), sites were stratified randomly chosen along the elevational gradient to represent the full elevational range of the focal species within our sampled sites. The elevational gradient was stratified into six elevational bands from the treeline upwards, shifted by 100 m between regions to account for slightly different conditions and a diverging position of the treeline. In the oceanic region, we used 900, 1000, 1100, 1200, 1300, and 1400 m a.s.l. (above sea level), in accordance with the treeline in this region, which is located at about 750 to 800 m a.s.l. In the continental region, we used 1000, 1100, 1200, 1300, 1400, and 1500 m a.s.l. Here, the treeline is situated slightly higher, at about 1000 m a.s.l. (Rößler et al., 2008; Rößler and Löffler, 2007). Thus, all of our studied sites were located above the treeline. Our study design resulted in a total of 12 sites, i.e., 2 regions × 6 elevational bands, with one specimen monitored per site ($N = 12$), resulting in 48 annual dendrometer curves, i.e., 12 × 4 years. A summary of the total stem diameter variation and environmental conditions measured at each site is presented in Fig. A2.

2.2 Dendrometric data and monitoring setup

Here, we applied a technological approach, commonly used for trees, to our multi-stemmed specimens of *E. hermaphroditum*, taking radial stem measurements using dendrometers. The general idea was to apply well-established methods from dendroecology and tree growth analysis within a novel setting to assess intra- and inter-annual variation in growth patterns and environmental factors controlling this variation. We mounted our dendrometers on one major aboveground stem of a randomly chosen specimen per site, horizontally to the ground surface and as close to the assumed root collar as possible. During this process, we removed the dead outer bark (periderm) to place the sensor as close to the living tissue as possible, following a common practice for dendrometer measurements of trees (Oberhuber et al., 2020; Wang et al., 2020; Grams et al., 2021). This ensures that hygroscopic shrinkage and swelling of dead tissues from the outer bark do not influence the diameter measurements. Such processes have been previously addressed in trees (Zweifel and Häsler, 2000; Gall et al., 2002; Ilek et al., 2016), and comparative studies revealed a complex interplay of xylem as well as phloem growth and pressure-induced size changes, which simultaneously affect radial stem change and are thus captured by the dendrometers (Turcotte et al., 2011; Zweifel et al., 2014b; Oberhuber et al., 2020; Knüsel et al., 2021) (Fig. A1). Additionally, we avoided specific micro-positions near stones and depressions, inside the radius of other larger shrub species, and near patches of wind erosion (Fig. A3). Stem diameter data were measured at 1 min intervals using dendrometers (type DRO; Ecomatik, Dachau, Germany). The sensor has a temperature coefficient of $< 0.2\,\mu\mathrm{m\,K^{-1}}$. To ensure that the dendrometers produce meaningful data, unaffected by the mounting process and bark removal, we tested the study design for several years before presenting the final study period here. In order to facilitate the following analysis, we aggregated the measured hourly values to obtain daily stem diameter variability, defined as the maximum stem diameter measured each day, following the “daily maximum approach” (Deslauriers et al., 2007). This approach assumes suppressed radial growth during times of stem shrinking, in accordance with Zweifel (2016). All calculations were made using R statistical software (R Development Core Team, 2020).

2.3 Analysis of seasonal growth patterns

To assess major growth patterns and growth variation between years, we first defined specific parameters and dates of annual stem growth for each year, resulting in a set of growth-defining parameters for each individual dendrometer curve. This included (a) total growth, defined as growth-induced stem expansion. To separate this expansion from reversible shrinking and swelling associated with stem water fluctuations, we chose the approach proposed by Zweifel (2016), which assumes radial stem growth to be suppressed during times of stem shrinking due to the transpiration-induced lowering of the turgor pressure, preventing cell expansion and cell division. Growth is thus defined as an increase in stem radius when the measured radius is larger than it was at any point in the past. Consequently, total growth realized throughout the year can be derived from the original measured data by calculating the sum of the cumulative maxima (Zweifel et al., 2014a; Zweifel, 2016; Zweifel et al., 2021). Following this approach, we were able to extract the growth-induced stem increment during the main growing season, as well as patterns of radial stem shrinkage (expressed as stem water deficit and derived by subtracting daily stem diameter values from the previously obtained cumulative growth curves; Zweifel, 2016). From these patterns we derived (b) peak shrinking, which we defined as the maximum stem water deficit and which usually occurred during the winter months. Subsequently, we aimed to further define the timing of the main growing season, calculating accurate dates for the parameter (c) peak growth (maximum daily growth rate), as well as (d) growth initiation (start of the growing season) and (e) growth cessation (end of the growing season). Here, we found sigmoid Gompertz models to be the best fit for our growth curves. Although multiple models have been used to describe growth, the Gompertz equation is the most widely used in dendrochronological studies and has been proven to explain the variations in dendrometer measurements (for trees) well (e.g., Rossi et al., 2003, 2006; Duchesne et al., 2012; Van der Maaten et al., 2018; Liu et al., 2019). The equation used for the model was Eq. (1):

$$y(t) = \alpha \times \exp(-\beta \times \exp(-k \times t)), \tag{1}$$

where α is the upper asymptote, β is the x-axis placement parameter, and k is the growth rate. We calculated these input parameters from our original data using the equations defined by Fekedulegn et al. (1999). To assess how well the models fit our data, we calculated a goodness-of-fit (GoF) measure using the least-squares method with the formula Eq. (2):

$$\mathrm{GoF} = 1 - (\Sigma(f - f^2)^2 / \Sigma f^2), \tag{2}$$

where f is the original and f^2 is the modeled stem diameter.

We determined growth initiation (onset) and cessation (offset) from this modeled curve. Since raw dendrometer data are known to deliver rough estimates of cambial activity and less reliable critical dates (Deslauriers et al., 2007; van der Maaten et al., 2018; Cruz-García et al., 2019), this modeling approach allowed us to clearly define the main growth phase and ensure high comparability between years and specimens. Growth initiation and cessation were defined as the time when 10 % and 90 %, respectively, of the total annual modeled growth occurred. We chose these thresholds in accordance with our data, and they were slightly higher than the thresholds used in similar studies for trees (e.g., Van der Maaten-Theunissen et al., 2013; Van der Maaten et al., 2018; Drew and Downes, 2009). This is a result of the unique growth patterns of the sampled shrubs.

Some of our specimens did not experience any growth in specific years. Years with no or little growth have been detected in other shrubs, for example, in *Salix arctica* by Polunin (1955). Buchwal et al. (2013) assumed such mechanisms to be related to carbon allocation and to occur irregularly along the stem because growth is not homogeneously allocated within the different plant segments. In accordance with their findings for *Salix polaris*, the specimens might preferentially allocate resources to less exposed parts (e.g., roots) in these years. In general, such partial dormancy (Preece et al., 2012) might reflect insufficient resources for homogenous growth across the entire plant. We did not calculate a growing season for these years, and the analyses proceeded separately, excluding them from most of our calculations.

2.4 Environmental data collection

To identify the thermal constraints of our species at both the critical location and the timescale of action (cf. Körner and Hiltbrunner, 2018), we measured soil temperatures (°C) at a depth of 15 cm below the ground surface (i.e., within the root zone, hereafter T_{RZ}) and air temperatures 15 cm above the ground surface (i.e., within the shoot zone, hereafter T_{SZ}), at all sites. Temperatures were measured at 1 min intervals and recorded as hourly means using Onset's HOBO loggers (type H21-002) and type S-TMB-M002 temperature sensors ($\pm 0.2\,^{\circ}\mathrm{C}$ accuracy). For the T_{SZ} measurements, the sensors were equipped with passively ventilated radiation shields. Moreover, to identify the soil moisture constraints in the root zone of our specimens, we measured the volumetric soil water content ($\mathrm{m}^3\,\mathrm{m}^{-3}$) 15 cm below the soil surface (hereafter $\mathrm{SM}_{\mathrm{RZ}}$) at all sites. The uncalibrated $\mathrm{SM}_{\mathrm{RZ}}$ was measured at 1 min intervals and recorded as hourly means using Onset's HOBO type S-SMD-M005 soil moisture sensors ($\pm 3\,\%$ accuracy). Additionally, we measured the shoot zone global radiation ($\mathrm{W\,m^{-2}}$) at 1 cm above the ground surface in close proximity to the plant (hereafter $\mathrm{GR}_{\mathrm{SZ}}$) using Onset's HOBO type S-LIB-M003 silicon pyranometers ($\pm 10\,\mathrm{W\,m^{-2}}$ accuracy). We made sure that those measurements were not affected by the canopy. Our data covered a period of 4 full calendar years from 1 January 2015 to 31 December 2018. Missing data did not occur at the chosen sites.

We did not explicitly measure data regarding snow cover but calculated snow cover from the daily shoot zone temperature amplitude and validated those calculations using radiation sensor measurements. We assumed that a daily amplitude of less than 5 % of the maximum amplitude reached throughout the year indicated that a layer of snow restricted daily air temperature fluctuations at the measured height of 15 cm. The respective periods were therefore defined as snow-covered. However, because of the chosen positions on wind-blown ridges, most of our monitored sites did not experience long periods of snow cover. Nonetheless, snow and its presumed effects, such as mitigating extreme negative temperatures by acting as an isolating barrier and, hence, reducing the effects of frost (Körner, 2021; Bienau et al., 2014), might play a role in influencing the growth response and were therefore included in our analysis.

For further analysis and to assess inter-annual variability, we calculated a set of 25 annual parameters from the collected raw data (Table 1), defining the near-ground environmental conditions experienced by each specimen for each year, based on the expected effects on different growth mechanisms.

2.5 Statistical analysis of climate–growth relations and potential drivers of radial stem change

To analyze the effect of the on-site environmental conditions on the observed growth patterns and to identify the most important environmental drivers controlling these patterns across sites, we utilized linear mixed-effect models, alongside correlation analyses. All statistical analyses were carried out in R (R Development Core Team, 2020), and site-specific values of the previously defined growth-defining and environmental parameters for each sampled specimen and year were entered into each analysis to overcome common misconceptions regarding the averaging of environmental data (cf. Körner and Hiltbrunner, 2018; Löffler and Pape, 2020).

First, we were interested in how the timing and duration of the growing season are linked to total realized growth and the observed shrinking phase during the winter months. Therefore, we tested relations among our previously defined parameters (cf. Sect. 2.3) by modeling total annual growth and peak shrinking (dependent variables) from growth initiation, cessation, and peak growth (independent variables), using linear mixed-effect models with the study sites included as a random effect to account for inter-site variability (Table 2).

Having thus identified the role of these parameters in determining overall growth, we then analyzed the environment–growth relationship by modeling the parameters (total annual growth, peak shrinking, growth initiation, peak growth, and growth cessation) from the potential microenvironmental drivers presented in Table 1, similarly using linear mixed-effect models with the study sites included as a random effect. Since we observed a prominent period of radial stem shrinking during the winter months, we additionally included two parameters defining the timing of this period here (start of the shrinking period and day of year (DOY) on which peak shrinking occurred).

In addition to these inter-annual assessments of growth patterns and environmental controls, we subsequently analyzed the fine-scale, intra-annual seasonality in stem diameter variability to gain insight into seasonal response patterns of stem shrinking and swelling to local environmental surroundings. We performed a moving-window correlation, correlating daily rates of stem diameter variability (compared to the previous day) with measured daily environmental values for each of our four environmental parameters (i.e., T_{RZ}, T_{SZ}, $\mathrm{GR}_{\mathrm{SZ}}$, and $\mathrm{SM}_{\mathrm{RZ}}$). Coefficients are calculated over lagged time windows of 3 and 30 d, after testing window widths of up to 6 months. Overall, window width showed surprisingly little effect on the results.

3 Results

3.1 Intra-annual stem diameter variability and growth patterns

In general, the seasonal variability in stem diameter was well explained by non-linear, sigmoid regressions (Gompertz curves) with a GoF between 0.90 and 0.94 (Fig. 1), and all specimens experienced distinct growing seasons starting in May or June, with little variation between the two study regions (Fig. A4). Moreover, our data revealed a distinct phase of radial stem shrinking following the growing phase towards the end of the year, starting in October, with remarkably little variation in timing between years (on average starting between the 287th and the 311th Julian day). In most cases, the stem radius remained below the previously achieved maximum for the entire winter and started to increase again with the following year's growing season (Fig. 1). The start of this shrinking period was significantly linked to the day when peak growth occurred ($R = 0.50$; $p = 0.004$), as well as to growth initiation ($R = 0.40$; $p = 0.023$) and cessation ($R = 0.52$; $p = 0.0023$).

The observed total annual growth ranged from 11 µm in 2017 to 65 µm in 2016, on average (Table 3), with high variation between specimens and sites. Some specimens (31 % of the dendrometer curves) experienced zero growth in one or more years, and these dormant years were linked to comparatively long periods of snow cover during the previous winter, with a highly negative correlation between stem diameter change and the number of snow-free days ($R = -0.60$; $p = 0.024$; Fig. A5) during these years. Interestingly, patterns of stem diameter variability and timing of the growing season were similar in the two studied regions (Fig. A4). Furthermore, while our data showed slight differences in total annual growth between the two regions (Fig. A6), there were no clear overall patterns in our data related to the elevational gradient or study regions, beyond the high inter-specimen variability observed in the whole dataset (Fig. A2c). Our chosen growth parameters – growth initiation, peak growth, and growth cessation – together explained 88 % of the variance in total annual growth, with peak growth (the maximum daily growth rate) having by far the greatest influence, indicating

Table 1. Summary of calculated environmental parameters (means) for each year. Numbers in parentheses represent inter-site variability (coefficient of variation, CV).

Parameter	2015	2016	2017	2018
Shoot zone temperature (T_{SZ})				
Day when maximum T_{SZ} is reached [DOY]	183 (0.1)	203 (0.14)	203 (0.01)	208 (0)
First day on which $T_{\mathrm{SZ}} > 0$ °C [DOY]	100 (0.37)	74 (0.47)	25 (0.80)	104 (0.02)
Annual T_{SZ} sum [°C]	37.28 (11.65)	47.96 (7.91)	16.21 (28.54)	199.96 (1.78)
T_{SZ} sum at growth initiation [°C]	−291.87 (0.74)	−421.91 (1.95)	−189.45 (1.86)	−384.76 (2.13)
Number of days with $T_{\mathrm{SZ}} > 0$ °C (growing degree days, GDD0) [days]	175 (0.14)	169 (0.09)	165 (0.11)	173 (0.11)
Number of days with $T_{\mathrm{SZ}} > 5$ °C (growing degree days, GDD5) [days]	82 (0.23)	117 (0.12)	100 (0.24)	121 (0.11)
Number of days with $T_{\mathrm{SZ}} > 10$ °C (growing degree days, GDD10) [days]	21 (0.37)	32 (0.44)	12 (0.65)	57 (0.19)
Root zone temperature (T_{RZ})				
Day when maximum T_{RZ} is reached [DOY]	186 (0)	206 (0)	204 (0)	197 (0.03)
First day on which $T_{\mathrm{RZ}} > 1$ °C [DOY]	146 (0.09)	140 (0.04)	139 (0.04)	127 (0.03)
Annual T_{RZ} sum [°C]	358.52 (1.17)	351.23 (1.03)	339.15 (1.19)	477.58 (0.65)
T_{RZ} sum at growth initiation [°C]	−127.05 (2.93)	−326.05 (4.74)	−116.97 (2.25)	−303.43 (3.64)
Number of days with $T_{\mathrm{RZ}} > 0$ °C (growing degree days, GDD0) [days]	182 (0.16)	170 (0.09)	176 (0.11)	196 (0.11)
Number of days with $T_{\mathrm{RZ}} > 5$ °C (growing degree days, GDD5) [days]	96 (0.21)	124 (0.06)	117 (0.17)	119 (0.08)
Number of days with $T_{\mathrm{RZ}} > 10$ °C (growing degree days, GDD10) [days]	7 (1.01)	14 (0.99)	10 (1.04)	57 (0.25)
Soil moisture ($\mathrm{SM}_{\mathrm{RZ}}$)				
Day when maximum soil moisture is reached [DOY]	197 (0.37)	219 (0.36)	193 (0.36)	222 (0.43)
Day when minimum soil moisture is reached in autumn [DOY]	351 (0.32)	342 (0.03)	351 (0.02)	353 (0.03)
Annual soil moisture sum [$\mathrm{m}^3\,\mathrm{m}^{-3}$]	54.65 (0.26)	52.78 (0.23)	55.52 (0.22)	54.51 (0.22)
First day on which soil moisture > $0.15\,\mathrm{m}^3\,\mathrm{m}^{-3}$ [DOY]	135 (0.05)	128 (0.07)	126 (0.08)	110 (0.04)
Global radiation ($\mathrm{GR}_{\mathrm{SZ}}$)				
Day when maximum global radiation is reached [DOY]	171 (0.09)	156 (0.02)	181 (0.06)	177 (0.1)
First day when global radiation > $50\,\mathrm{W\,m}^{-2}$ [DOY]	74 (0.38)	75 (0.31)	85 (0.27)	76 (0.27)
Annual global radiation sum [$\mathrm{W\,m}^{-2}$]	26 686.66 (0.18)	27 742.87 (0.14)	25 863.3 (0.21)	31 229 (0.15)
Global radiation sum at growth initiation [$\mathrm{W\,m}^{-2}$]	16 342.47 (0.22)	15 435.76 (0.32)	16 197.58 (0.38)	15 928.75 (0.55)
Snow				
Number of snow-free days [days]	361 (0.05)	361 (0.23)	358 (0.22)	356 (0.05)
First autumn frost ($T_{\mathrm{RZ}} < 0$ °C) [DOY]	320 (0.04)	296 (0.03)	310 (0.05)	301 (0.05)

Table 2. Results of linear mixed-effect modeling of total annual growth (measured cumulative stem diameter increment in comparison to the previous year's maximum stem diameter) and annual peak shrinking (maximum stem water deficit), modeled from growth parameters (growth initiation, growth cessation, and peak growth). Sites (including study region and elevation) entered into the models as random effects. R^2 for the models was calculated using the r.squaredGLMM function from the MuMIn package (Barton, 2020).

Dependent variable	Independent variable (fixed effect)	Estimate	Standard error	T statistic	p value
Total annual growth	Growth initiation	−0.285	0.177	−1.615	0.117
	Growth cessation	0.383	0.161	2.377	0.025*
	Peak growth	25.103	2.02	12.433	< 0.001***
Model R^2 (conditional)	0.876				
Partial R^2 (marginal)	0.83				
Annual peak shrinking	Growth initiation	0.071	0.23	0.307	0.761
	Growth cessation	0.040	0.252	0.157	0.877
	Peak growth	0.540	0.119	4.518	< 0.001***
Model R^2 (conditional)	0.745				
Partial R^2 (marginal)	0.309				

Asterisks indicate the significance based on the p value: * is significant (p value < 0.1); *** is strongly significant (p value < 0.01).

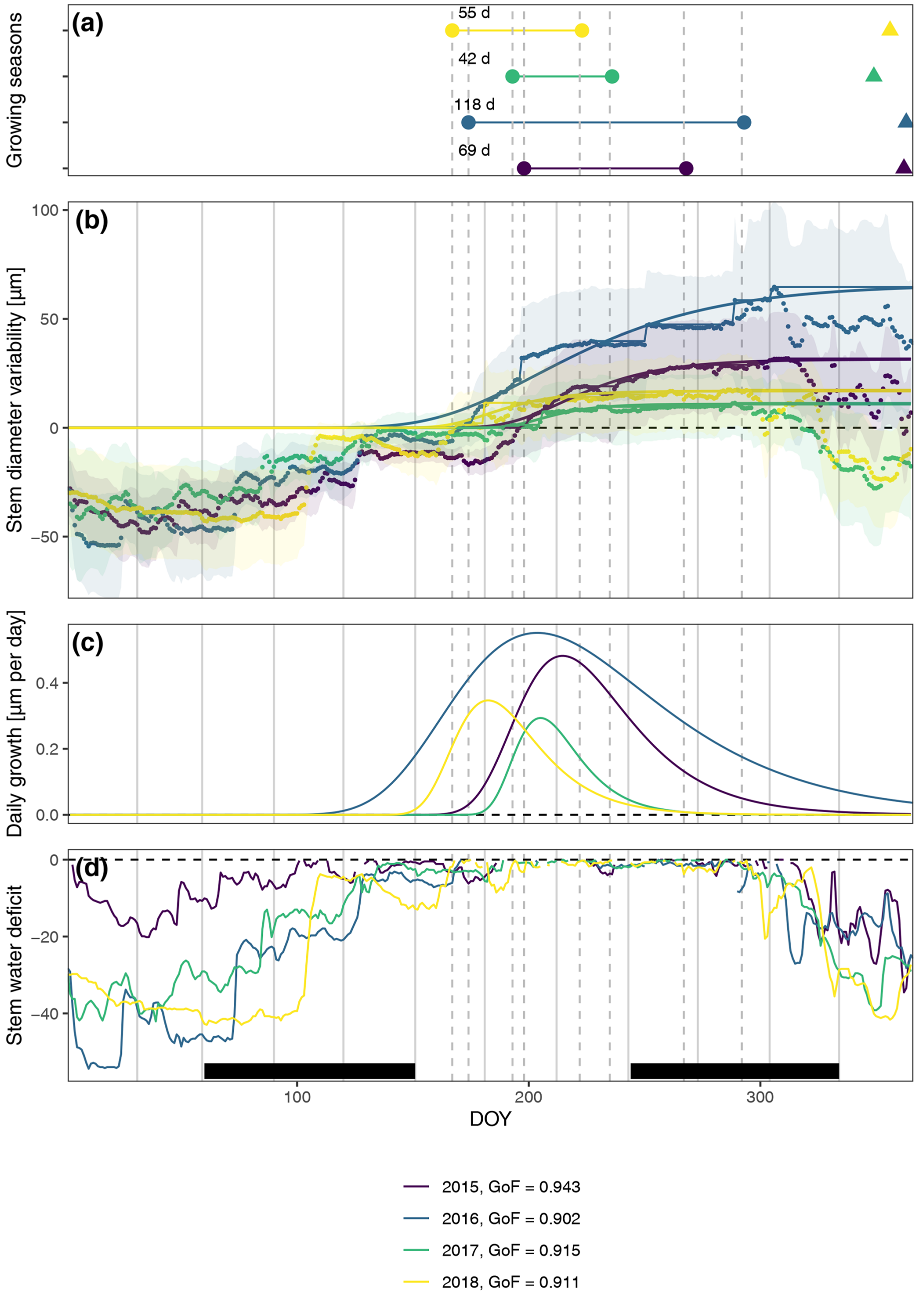


Figure 1. Observed and modeled variability in stem diameter. **(a)** Growing seasons derived from fitted Gompertz models and timing of peak shrinking defined as the maximum stem water deficit (triangles). **(b)** Averaged measured daily stem diameter variability and fitted Gompertz models (a goodness-of-fit (GoF) measure was calculated using the least-squares method). Models were fitted to zero growth curves derived from the original measurements as cumulative maxima (thin lines), assuming zero growth during phases of prolonged stem shrinkage. In this way, annual growth and, consequently, growth start are directly linked to growth during the previous year, and additional rehydrating processes before the start of the main growing season are excluded. Shaded areas indicate standard deviation, showing the variability among the specimens. **(c)** Daily growth rates derived from Gompertz models. **(d)** Stem water deficit defined as reversible radial stem variability at times when no growth-induced irreversible stem expansion was measured. Black bars indicate meteorological seasons, while dashed lines show timing of the respective growing seasons to aid visual interpretation.

Table 3. Parameters of stem change (means). Numbers in parentheses represent variability between specimens (coefficient of variation, CV).

Year	2015	2016	2017	2018
Stem diameter change (measured variation between start and end of the year) [µm]	31.74 (1.4)	63.86 (0.63)	11.35 (6.35)	19.91 (1.93)
Stem radial growth (growth-induced, irreversible stem increment compared to the previous year) [µm]	31.81 (1.17)	64.66 (1.06)	11.38 (2.01)	17.45 (1.38)
Stem radial shrinking (stem shrinking during the winter months, after the end of the main growing season) [µm]	34.52 (0.83)	28.19 (0.9)	39.16 (0.81)	41.62 (0.79)
Day peak shrinking occurs [DOY]	362 (0.18)	363 (0.06)	349 (0.23)	356 (0.3)
Day shrinking starts [DOY]	311 (0.49)	306 (0.2)	289 (0.14)	287 (0.18)
Growth initiation [DOY]	198 (0.3)	174 (0.33)	193 (0.28)	167 (0.38)
Growth cessation [DOY]	267 (0.22)	292 (0.26)	235 (0.17)	222 (0.26)
Growth duration [days]	69 (0.84)	118 (0.73)	42 (1.69)	55 (0.88)
Peak growth (maximum daily growth rate) [µm]	0.48 (1.39)	0.55 (1.34)	0.29 (2.25)	0.35 (1.95)
Day peak growth occurs [DOY]	215 (0.21)	204 (0.28)	205 (0.13)	182 (0.23)
Mean daily growth [µm]	0.11 (1.19)	0.22 (1.26)	0.05 (2)	0.08 (1.38)

that the overall duration of the growth phase was less important for overall growth than the daily growth rate. For stem contraction (shrinking), the same parameters explained 75 % of the variance (Table 2 and Fig. A7), suggesting that the observed winter shrinking in *E. hermaphroditum* might be linked to growth during the growing season.

3.2 On-site environmental conditions

The different near-surface regimes of T_{RZ}, T_{SZ}, $\mathrm{SM}_{\mathrm{RZ}}$, and $\mathrm{GR}_{\mathrm{SZ}}$ at our monitored sites are illustrated in Fig. 2. Averaged values for all sites ($N = 12$) are summarized in Table 4. In all four monitored years, our sampled specimens experienced the highest temperatures during summer and, due to the exposed, wind-blown nature of the studied sites, only short periods of shallow snow cover during winter (Fig. 3). The period in which our specimens were snow-covered varied considerably between the monitored winters and between sites. The winter of 2015/16 had comparatively little snow, whereas 2017/18 was snow-covered for the longest period. In 2018, the highest mean temperatures were expressed because of exceptionally high summer temperatures (number of days with $T_{\mathrm{SZ}} > 10\,^{\circ}\mathrm{C}$ – i.e., GDD10 – is 57), whereas 2015 and 2017 both experienced shorter periods of high temperatures. Temperatures varied slightly among sites (Table 4 and Fig. A2), with a noticeable but not linear temperature decline with elevation. As expected, the shoot and root zone temperature curves were well coupled. Additionally, we detected slight variability between the two studied regions but overall similar seasonal temperature patterns on the measured microscale (Figs. 3 and A1), which differs from the regional climate signal. Global radiation showed similar patterns at all sites as well, following the course of the astronomic sun angle, with a mid-summer maximum; however, there were large variations according to cloud coverage. As such, 2018 experienced a short period of temperature and radiation decrease during summer (Fig. 2).

3.3 Environmental controls of stem diameter variability

We investigated how the specific on-site environmental conditions were linked to the parameters described above. Moving-window correlations revealed a high seasonal variation in the relation of stem diameter variability and environmental conditions, with additional high variation across years. Overall, on-site environmental conditions had comparatively strong explanatory power during spring, when many of the specimens started stem increment. This spring stem increment was positively linked to radiation during cold spring conditions in 2015 and 2017 and showed no clear relation to spring temperatures (Figs. 2 and 4).

The linear mixed models (Fig. 5) confirmed the lack of uniformity, indicating that a multitude of environmental drivers influenced growth, albeit to a very low degree and with high inter-annual variation. During 2016, the year with the highest radial stem growth, we also measured the highest number of days with soil temperatures above 5 °C, with temperatures rising quickly and steadily to 5 °C without reaching continuously higher values during the summer (Fig. 2). This indicates that optimum growth conditions lie within a soil temperature span of 5 to 10 °C. At the same time, maximum soil moisture had a strong positive influence on total annual growth, and growth was also linked to the timing of soil moisture rise in spring, resulting from thawing soils. Overall, our results indicate a strong influence of soil moisture on growth processes, with especially winter stem diameter variability closely linked to soil moisture availability and singular thawing events (Fig. A8). Growth initiation, on the other hand, was closely linked to radiation and winter temperatures. Here, our results show no clear influence of ris-

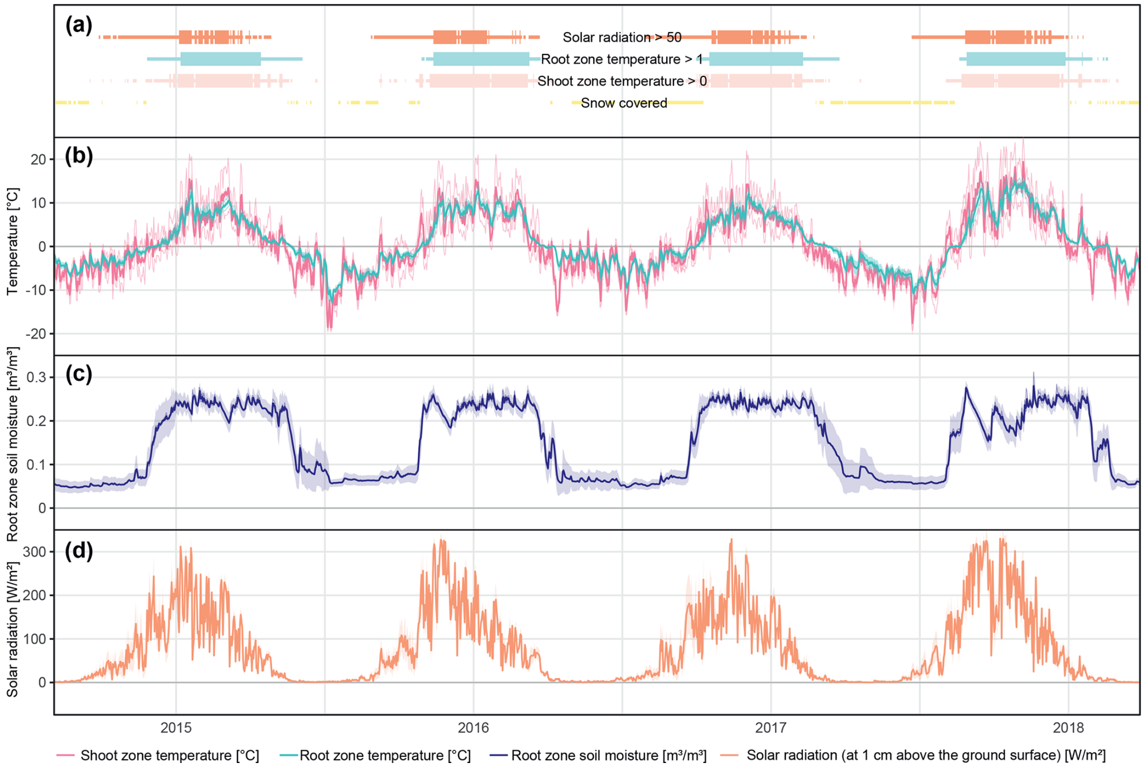


Figure 2. Micro-environmental data. Daily mean values of shoot and root zone temperatures **(b)**, soil moisture **(c)**, and global radiation **(d)**. Measurements were taken at each site individually but were averaged here over all sites for visualization. Shaded areas indicate standard deviations. Bars **(a)** show time spans for certain environmental conditions, with narrow bars marking the time at which the given condition was present at one or more (but not all) of the monitored sites, whereas broad bars mark the time for which the given condition was detected at all sites.

Table 4. Summary of collected environmental data: annual mean, minimum, and maximum values as well as mean values for each meteorological season. Numbers in parentheses represent site variability (coefficient of variation, CV).

Environmental parameter	Year	Mean	Min	Max	Mean spring	Mean summer	Mean autumn	Mean winter
Shoot zone temperature [°C]	2015	0.10 (11.65)	−13.66 (0.16)	21.24 (0.09)	−2.44 (0.49)	6.95 (0.18)	1.29 (0.99)	−5.50 (0.27)
	2016	0.13 (7.91)	−19.53 (0.12)	21.10 (0.07)	−1.39 (0.83)	8.40 (0.14)	0.30 (3.46)	−6.86 (0.17)
	2017	0.04 (28.54)	−15.70 (0.08)	21.97 (0.06)	−1.68 (0.73)	7.28 (0.16)	−0.07 (11.84)	−5.48 (0.30)
	2018	0.55 (1.78)	−19.373 (0.19)	25.156 (0.06)	−1.071 (0.89)	10.029 (0.11)	0.214 (5.14)	−7.782 (0.25)
Root zone temperature [°C]	2015	0.98 (1.17)	−7.01 (0.24)	14.27 (0.08)	−1.80 (0.59)	7.04 (0.19)	2.48 (0.44)	−3.88 (0.33)
	2016	0.96 (1.03)	−13.16 (0.15)	14.37 (0.1)	−1.48 (0.72)	8.76 (0.13)	2.03 (0.41)	−5.52 (0.22)
	2017	0.93 (1.2)	−9.76 (0.17)	13.57 (0.11)	−1.67 (0.57)	7.71 (0.14)	1.87 (0.59)	−4.30 (0.4)
	2018	1.31 (0.65)	−11.03 (0.19)	16.79 (0.1)	−1.76 (0.49)	10.45 (0.11)	1.67 (0.47)	−5.27 (0.31)
Soil moisture [$m^3\ m^{-3}$]	2015	0.15 (0.26)	0.05 (0.56)	0.28 (0.19)	0.09 (0.37)	0.23 (0.16)	0.15 (0.25)	0.06 (0.73)
	2016	0.14 (0.23)	0.06 (0.44)	0.27 (0.16)	0.12 (0.23)	0.23 (0.15)	0.12 (0.29)	0.06 (0.047)
	2017	0.15 (0.22)	0.05 (0.45)	0.27 (0.12)	0.10 (0.21)	0.24 (0.13)	0.14 (0.28)	0.07 (0.68)
	2018	0.15 (0.22)	0.05 (0.45)	0.312 (0.1)	0.13 (0.22)	0.21 (0.18)	0.14 (0.26)	0.06 (0.49)
Global radiation [$W\ m^{-2}$]	2015	73.11 (0.18)	0	809.34 (0.54)	74.38 (0.09)	169.70 (4.32)	41.82 (0.15)	4.72 (0.81)
	2016	75.80 (0.14)	0	823.93 (0.34)	93.94 (0.12)	165.04 (5.49)	39.51 (0.24)	3.53 (0.77)
	2017	70.86 (0.21)	0	791.81 (0.55)	78.45 (0.11)	166.59 (5.38)	32.27 (0.14)	4.26 (0.76)
	2018	85.57 (0.15)	0	846.38 (0.23)	117.15 (0.13)	190.84 (7.12)	28.59 (0.23)	3.25 (0.85)

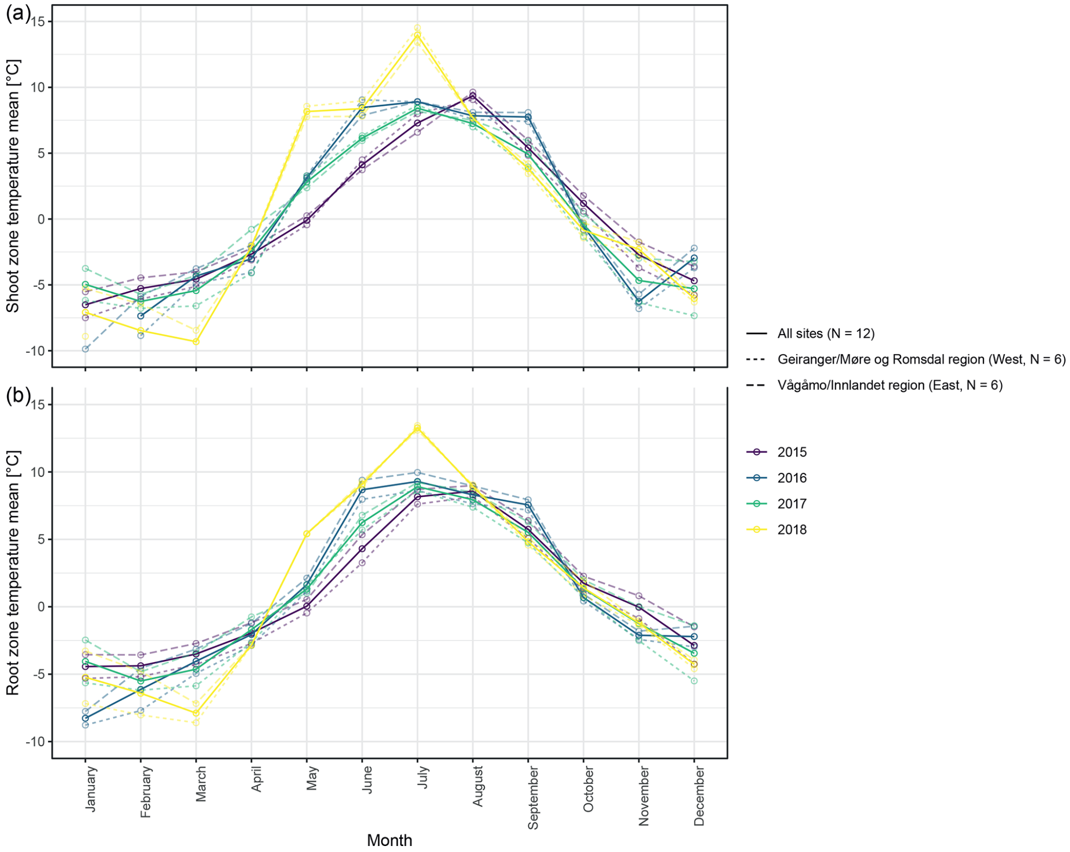


Figure 3. Mean monthly shoot **(a)** and root **(b)** zone temperatures from 2015 to 2018, for visualization purposes averaged (i) over the measured sites per study region and (ii) over all measured sites.

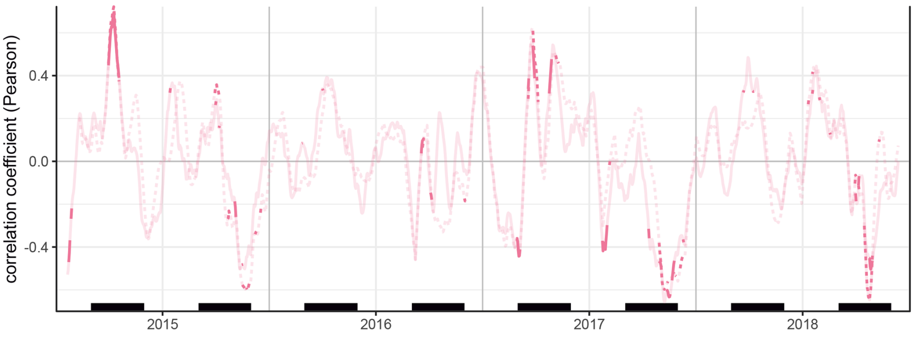
ing spring temperatures, and, counterintuitively, high winter temperatures led to a delayed growth start (Fig. 5).

4 Discussion

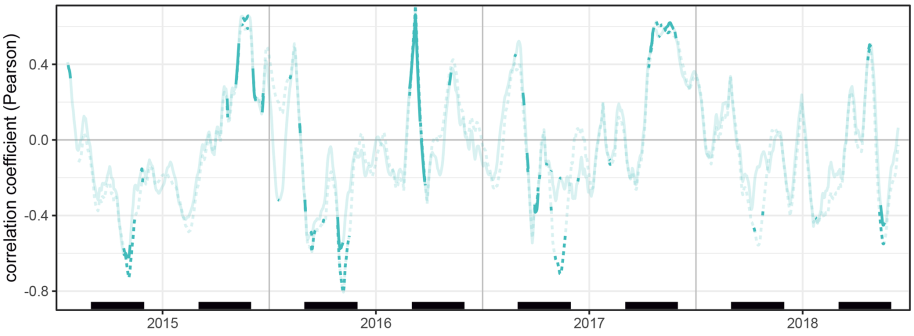
In this study, we demonstrated that our focal species *Empetrum hermaphroditum* displayed distinct annual patterns of stem diameter variability in response to near-ground environmental drivers and in close accordance with distinct conditions caused by the local topographical characteristics of the studied wind-blown ridge positions. Previous dendroecological studies of shrub growth have commonly used macroclimatic data, such as free atmospheric air temperature, in combination with ring width measurements (e.g., Bär et al., 2007, 2008; Hollesen et al., 2015; Weijers et al., 2018a). While a direct comparison of annual growth derived from our dendrometer measurements and such ring width measurements at the studied sites revealed high synchrony (Fig. A9), dendrometer measurements have the potential to reveal much deeper insights into complex functional aspects of stem diameter variability and, in combination with on-site environmental data, might help in rethinking climate–growth relations. For example, while a phase of winter stem shrinking has been described in trees (Winget and Kozlowski, 1964; Zweifel and Häsler, 2000), the distinct and strongly pronounced phase found in our sampled specimens might be described as a unique feature of shrub growth, which we documented for the first time in this study. The reason why this phase has not been described earlier might be attributable to the methods used in the past to measure stem change in shrubs, which were insufficient to document intra-annual variability at the appropriate timescale. High-precision dendrometers can reveal these patterns in stem diameter variability, demonstrating the large amount of additional information gained from this method compared to traditional measuring methods (Knüsel et al., 2021). For our focal species *Empetrum hermaphroditum*, dendrometer measurements yielded several novel insights into phenology and growth physiology.

At the same time, common challenges of dendrometer use, including the separation of reversible (water-related) and irreversible (growth-related) stem increment, which have been widely discussed for trees (Zweifel, 2016; Cruz-García et al., 2019; Knüsel et al., 2021) proved similarly complex for our data. Here, the observed strong contraction and expansion patterns of the stems, most likely controlled by stem water variability within the plant, linked to the extreme thawing

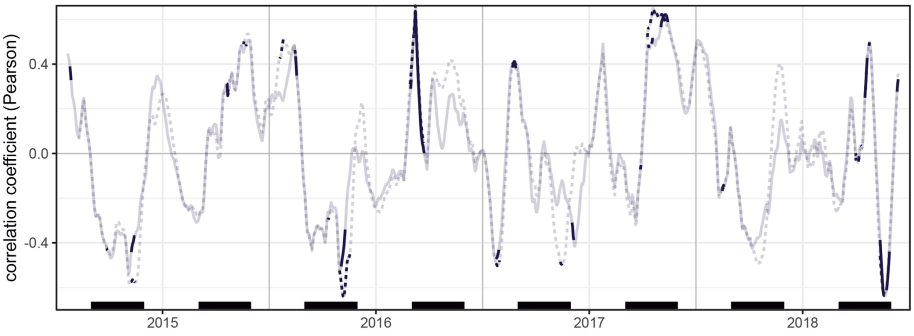
(a) Air temperature



(b) Soil temperature



(c) Soil moisture



(d) Radiation

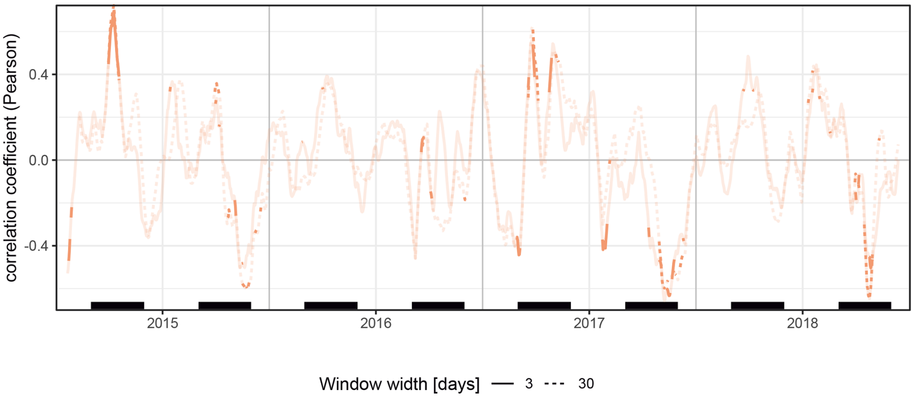


Figure 4. Moving Pearson's correlation coefficients for daily rates of radial stem diameter variability against measured daily values of on-site environmental parameters (T_{SZ}, T_{RZ}, $\mathrm{SM}_{\mathrm{RZ}}$, $\mathrm{GR}_{\mathrm{SZ}}$). Results are shown for window widths of 3 (solid lines) and 30 (dashed lines) days. Non-significance ($p > 0.05$) is indicated by transparency, and black bars show meteorological seasons. All individual specimens are entered into the analysis separately.

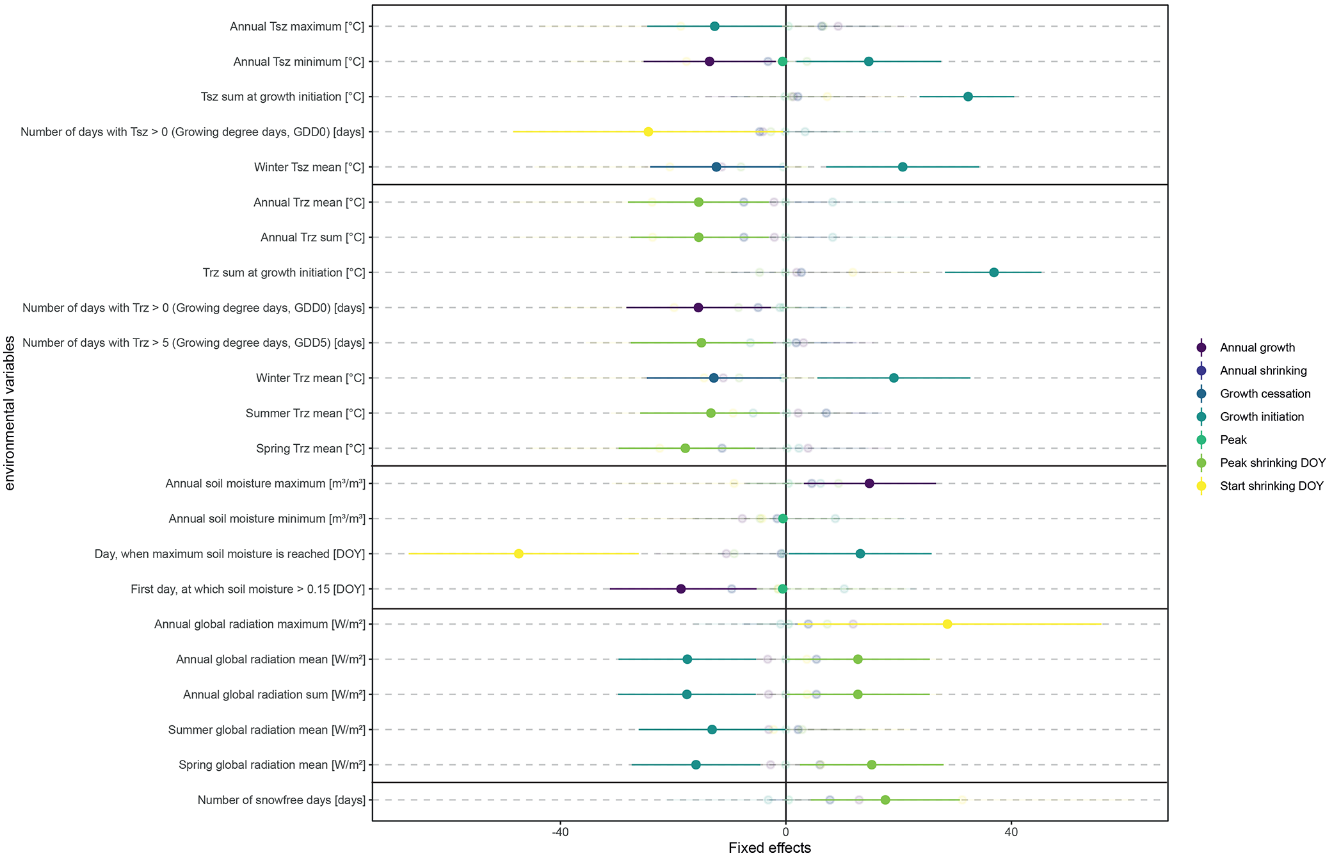


Figure 5. Fixed effects and associated confidence intervals from linear mixed-effect models, modeling key parameters of stem change (dependent variables) from key environmental parameters characterizing on-site environmental conditions (for years with a total annual growth > 0). The environmental parameters are presented in Table 1, while the dependent variables included (i) total annual growth, defined as irreversible stem increment in comparison to the previous year; (ii) total annual shrinking, defined as stem shrinking during the winter months, after the end of the growing season; (iii) timing of the main growing season (start and end); (iv) peak growth, defined as the maximum daily growth rate; and (v) timing of the winter shrinking phase, including the start of stem shrinking (usually co-occurring with the maximum annual stem diameter) and peak shrinking, or the day when the minimum winter stem diameter is reached. All dates were given as day of the year (DOY). Only those environmental parameters which were significantly linked to at least one growth parameter are included in the plot. Nontransparent colors indicate significance.

and freezing processes prominent at our study sites, provided an additional challenge. To fully explore these processes and possible links to transpiration dynamics and carbon fluxes, on-site measurements of the vapor pressure deficit, as a measure of atmospheric water demand, might yield additional insights (Novick et al., 2016; Peters et al., 2021; Zweifel et al., 2021). Furthermore, our study showed high inter-plant and inter-site variation in total annual growth, which has been previously described in *E. hermaphroditum* (Bär et al., 2008) and could be a result of internal growth variation within the multi-stemmed plant itself, which has not yet been fully explored (Bär et al., 2007). Overall, further studies are necessary to fully explore how dendrometer measurements compare to traditional measurement methods and which methodical adjustments are necessary for the extraction of physiologically meaningful data. Still, the comparative data presented in Fig. A9 clearly show that both types of measurement have the potential to reveal important physiological aspects of stem diameter variability and growth.

4.1 Radial stem growth variation

In general, we found total annual growth to be largely determined by peak growth. Thus, we cannot confirm a clear relation of the growing-season length and overall growth (Rammig et al., 2010; Blok et al., 2011; Prislan et al., 2019). The predominant role of peak growth in controlling total growth suggested that the shrubs were usually able to invest in new cells following the rise in water availability caused by thawing conditions in spring, most likely affected by prior carbohydrate storage. At the same time, an early growth start after favorable winter conditions may not be efficient in terms of total growth if conditions in early summer prevent the survival of the formed cells. For most snow-free ridges, budburst and flowering are not influenced by snowmelt and can therefore occur early on, causing high vulnerability to late frost events (Weijers et al., 2018b). This is in accordance with the findings of Choler (2018) and Weijers et al. (2018a), who suggested a strong influence of subzero temperatures in spring, counteracting improved conditions during summer, which would lead to the observed decoupling of the growing-season length from total realized growth. In our data, we found strong evidence of this relation in inter-annual comparison, with low growth rates in 2018 despite favorable summer conditions after an early growth start followed by a short cold snap and ground frost. Additionally, for some specimens we found total annual growth to be limited by long periods of snow cover during the previous winter, which might prevent *E. hermaphroditum* from photosynthetic activity and resource accumulation and thus may limit a crucial precondition of growth success. In accordance with Buchwal et al. (2013), we assumed that during years of no apparent radial growth, dwarf shrubs might prioritize growth in the more protected and long-living belowground segments, instead of investing in the more vulnerable shoots. This ability to reduce cambial activity to a minimum and cease aboveground wood formation is a trait common among woody plants (Wilmking et al., 2012).

4.2 Environmental controls of shrub growth

E. hermaphroditum at the monitored ridge positions is faced with unique near-ground environmental conditions, which are a feature of the heterogeneous topography that characterizes alpine terrain (Scherrer and Körner, 2011). These conditions are caused by the exposed, wind-blown nature of the ridges and thus are distinctly different from the immediate surroundings and to some extent decoupled from the regional climate signal. They include high exposure to global radiation and very little, temporary snow cover during the winter months, associated with very low temperatures (Wundram et al., 2010). In general, the effects of winter snow cover on shrub growth are a critical topic in arctic and alpine ecology, with findings ranging from positive (Blok et al., 2015; Addis and Bret-Harte, 2019) to negative (Schmidt et al., 2010) growth responses, depending on the snow depth and vegetation type.

Our results highlight the importance of the unique winter conditions for early growth, indicating that for our sampled evergreen species, the degree to which photosynthetic activity was effective in synthesizing carbohydrates during the winter months was especially important. During this time, extreme temperatures prevent cell production and differentiation, resulting in a carbon overflow (Körner, 2015; Saccone et al., 2017), which gives *E. hermaphroditum* the ability to start growth activity as soon as liquid water is available in the root zone (Starr and Oberbauer, 2003). In general, carbon assimilation may be greater or lower than the demand for plant functions, resulting in periods of carbon surplus and deficit, respectively (e.g., Martínez-Vilalta et al., 2016). Though there is never a critical depletion of carbohydrates in alpine plants, resources at or shortly after snowmelt and thus at the onset of the growing season are still diminished – due to respiratory consumption during winter (Körner, 2021). Any surplus of carbohydrates gained by photosynthetic activity in late winter and spring is, therefore, likely to be beneficial for growth throughout the growing period. Such continued photosynthetic activity was found in *E. hermaphroditum*, as well as several other evergreen shrub species before (e.g., Gimeno et al., 2012; Bienau et al., 2014; Wyka and Oleksyn, 2014; Blok et al., 2015), and photosynthetic activity of high-latitude vascular plants and shrubs has previously been observed under extreme thermal conditions (Semikhatova et al., 1992; Lundell et al., 2008). Accordingly, we concluded that growth initiation might be driven by the constantly increasing radiation with the astronomic rise of the angle of the sun. At that time of the year, energy transfer from global radiation into thermal heat was low, but radiation was high enough for photosynthetic activity, which might explain the decoupling of thermal and radiation drivers of growth initiation. Under snow-free conditions, it is likely that, in our study design, global radiation is directly linked to soil thawing close to the soil surface, which was previously linked to growth onset (Descals et al., 2020). Furthermore, we found growth initiation in *E. hermaphroditum* to be positively linked to winter temperatures, indicating that low winter temperatures were correlated with an early start of the growing season, in contrast to common assumptions relating high temperatures during late winter to an early growth start (Dolezal et al., 2020). This highlights the influence of high radiation on energy storage during periods of absent snow cover, which are usually accompanied by low temperatures, whereas mild winters are often associated with cloudy, humid weather and snow cover on the ridges.

Photosynthetic activity during winter, however, forced by the exposure of the plant to high incoming solar radiation (Saccone et al., 2017), causes continued water transport under extreme temperatures, increasing the risk of cavitation (Tyree and Sperry, 1989; Venn and Green, 2018) while long and severe ground frosts might limit access to soil moisture and frost-triggered droughts might thus result in tissue damage caused by an internal water deficit (Mayr et al., 2006). Yet, *E. hermaphroditum* at our studied sites proved mostly frost-hardy, drought-tolerant, and highly adapted to these conditions (Carlquist, 1989; Hacke et al., 2001). In this context, we assume that *E. hermaphroditum* uses cell dehydration to actively protect living cells from the consequences of freezing (e.g., ice nucleation), causing the radial stem contraction during phases of extreme subzero temperatures evident in our data. In trees, radial stem shrinkage has been related to sap flow and tree water content (Winget and Kozlowski, 1964; Zweifel and Häsler, 2000; Zweifel et al., 2006; Tian et al., 2019). When temperatures sink below approximately −5 °C, extra-cellular water begins to freeze, inducing the osmotic withdrawal of intra-cellular water and thus cell and ultimately stem shrinkage (Zweifel et al., 2000; King et al., 2013). As such, stem shrinkage could be interpreted as a result of freezing processes causing living cell shrinkage because of water losses, as well as a strategy to avoid frost damage, especially where the protective effects of snow cover are missing (Kuprian et al., 2014; Neuner, 2014; Charra-Vaskou et al., 2016).

Furthermore, our findings confirmed commonly assumed positive effects of temperatures on radial stem growth in *E. hermaphroditum* to some extent (Shaver and Chapin, 1986; Shevtsova et al., 1997; Hollesen et al., 2015; Ackerman et al., 2017; Bråthen et al., 2018), with optimum growth conditions within a soil temperature span of 5 to 10 °C, which is in accordance with previously reported temperature thresholds for alpine plant distribution (Körner and Paulsen, 2004; Rossi et al., 2008; Steppe et al., 2015). On the other hand, our analysis indicated no direct relationship between total growth and near-surface temperatures, and a clear link between near-surface thermal conditions and stem diameter variability was lacking, suggesting more complex relations, probably influenced by the evident temperature extremes at our chosen sites, as well as complex interconnections with soil water availability (Körner and Hiltbrunner, 2018). A critical temperature threshold, as present in many trees (Rossi et al., 2007, 2008; Deslauriers et al., 2008) and found for xylem growth of alpine rhododendron shrubs (Li et al., 2016), could not be determined for *E. hermaphroditum*. In trees, the timing of the maximum growth and growth cessation in cold environments has been linked to day length (Heide, 1985; Rossi et al., 2006; Duchesne et al., 2012). This cannot be confirmed for our monitored shrubs because of the high variability observed between specimens. Therefore, timing of these critical parameters is most likely controlled by different factors in shrubs than those assumed for trees. Here, our results highlight soil moisture availability as the main driver for the end of the growing season. This accounts for the species dependency on a damp climate and high rainfall (Bell and Tallis, 1973).

Overall, we conclude that surviving during extreme winters was the main principle governing *E. hermaphroditum* growth when existing at alpine ridge positions, causing unique adaptations to local micro-site conditions. Additionally, our results highlight the overall importance of the root zone soil moisture as the key driver of growth in *E. hermaphroditum*.

4.3 Potential response to environmental change

The fine-scale data provided by dendrometer measurements proved highly important, since they allowed for a detailed growth analysis, revealing a growth mechanism that is highly adapted to the local micro-environmental conditions at our studied exposed ridge positions. The ability of continuing photosynthetic activity throughout the year and thus of aggregating resources for use in early cell formation, as observed in other evergreen plants (Wyka and Oleksyn, 2014), might provide a competitive advantage of the evergreen species over deciduous species in the same habitat, limiting the risk of losing resources through competition. However, it is most likely a unique feature of the snow-free ridge positions and thus not present at other micro-topographic positions, where the energy budget and water balance are strongly altered (Dahl, 1956; Fritts, 1976; Löffler et al., 2006; Pape et al., 2009).

To sustain the continued metabolism throughout the year, we found that the overall growth mechanism of *E. hermaphroditum* was mainly defined by moisture, as well as solar radiation. Hence, temperatures mainly played a role in freezing and thawing processes, on an intra-annual scale. We can thus confirm that while there is a link between shrub growth and warming conditions, it is most likely not uniform and highly variable over spatial and temporal scales (Elmendorf et al., 2012). The high local adaptation explains the wide distribution and competitive ability of the species at these sites (Bienau et al., 2014, 2016; Löffler and Pape, 2020) and highlights the prominent role of on-site near-ground environmental conditions in controlling growth processes (Zellweger et al., 2020). In a changing climatic regime, this dependency on specific winter radiation conditions and soil moisture availability might become a disadvantage, complicating the adaptation to warming winters and longer snow-covered periods, coupled with prolonged dry periods during summer (Hollesen et al., 2015; Weijers et al., 2018a), which might cause early growth cessation. Thus, we conclude that changing winter conditions and altered snow regimes represent one of the most serious threats to evergreen shrub growth in tundra ecosystems and *E. hermaphroditum* will not be able to persist at exposed positions in a changing climate or respond with longer periods of dormancy to warming conditions. This will potentially promote the spread of competing deciduous species and thus contribute to the arctic–alpine greening trend.

Appendix A

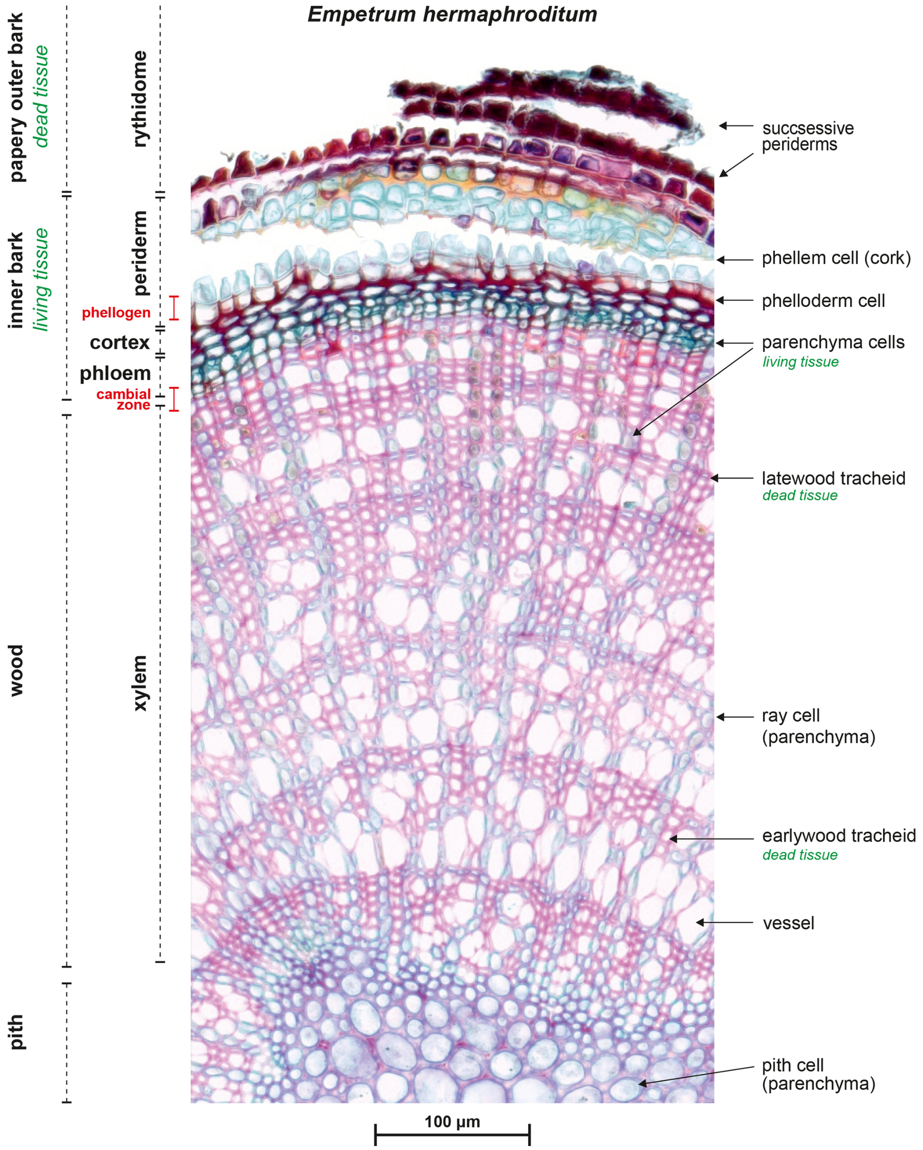


Figure A1. Radial micro-slide of a stem from *Empetrum nigrum* ssp. *hermaphroditum* (1 : 1000 magnification). The outermost layers of the papery outer bark, which repeat the successive pattern of the shown periderm, were lost while cutting. In our dendrometer approach, we removed the outer layers of the bark, most likely down to the phellogen. As shown here, the loose bark structure allows removal without severe damage of the inner tissue. We aimed at mounting our dendrometer sensor as close to the still protected cambial zone to obtain data on physiologically active stem diameter variability such as growth, excluding swelling and shrinking of the passive outer bark tissue.

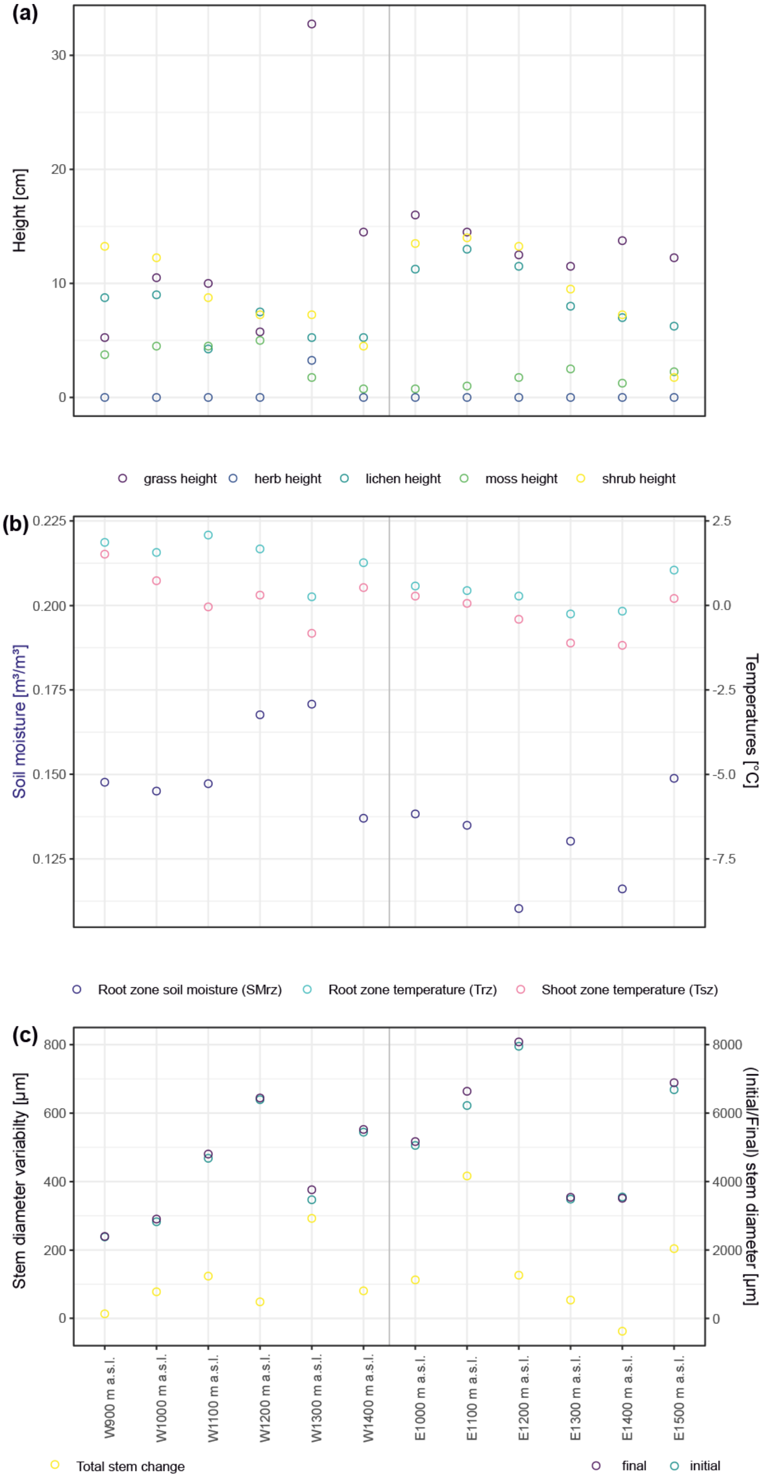


Figure A2. Summary of canopy height at the 12 studied sites by major vegetation type **(a)**. Trees are not included because there were no trees present. Panel **(b)** shows micro-environmental conditions averaged over the studied period, as well as minima and maxima for temperatures measured within the shoot and root zones and for soil moisture in the root zone. Panel **(c)** summarizes the total stem diameter change as well as stem diameter at the start and end of the studied period (2015–2018).

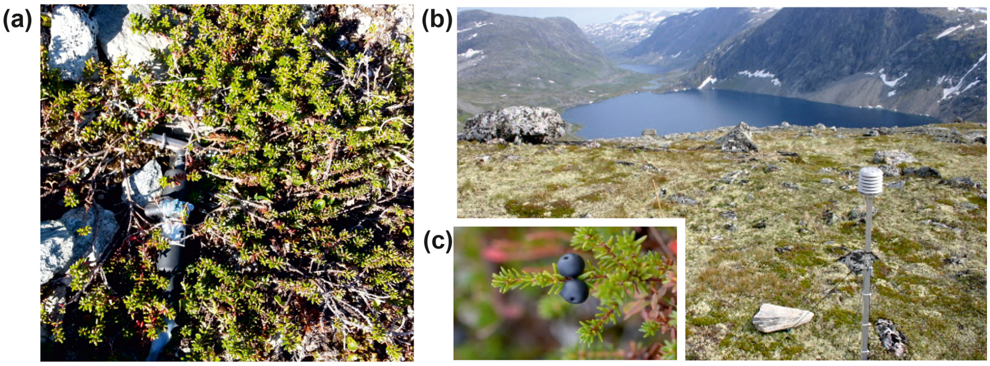


Figure A3. Dendrometer setup **(a)**, the studied species *E. hermaphroditum* in the studied region in central Norway **(b)**, and the species fruits and leaves **(c)**.

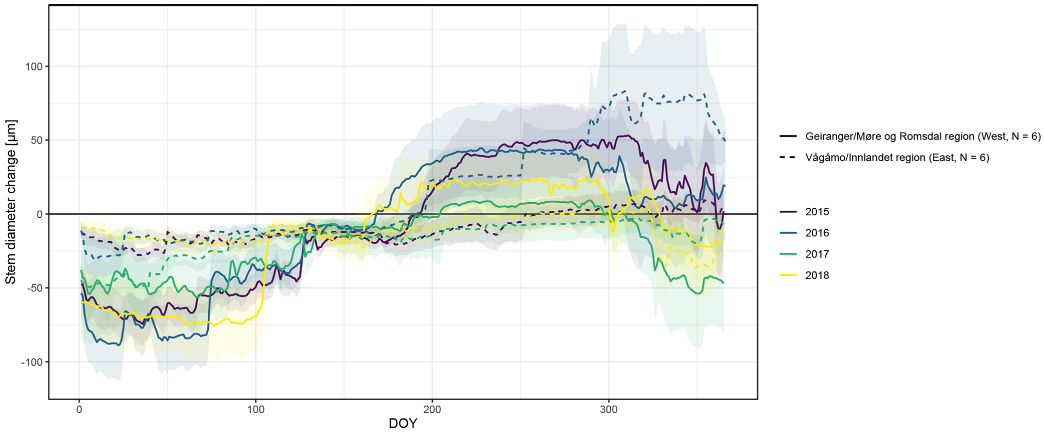


Figure A4. Observed stem diameter change averaged over the monitored specimens within each of the two study regions (Vågåmo, Innlandet, region (east, $N = 6$) and Geiranger, Møre og Romsdal, region (west, $N = 6$)). Transparency indicates standard deviation.

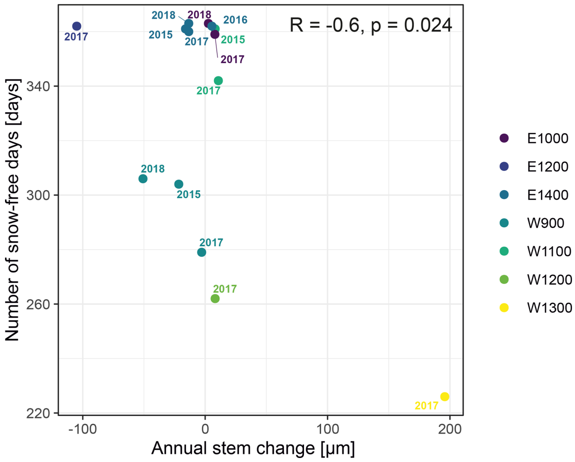


Figure A5. Number of snow-free days and annual stem diameter change in years in which no irreversible growth occurred (total annual growth = 0). Colors indicate the monitored specimens at the individual sites (E denotes east; W denotes west; numbers indicate elevation, m a.s.l.).

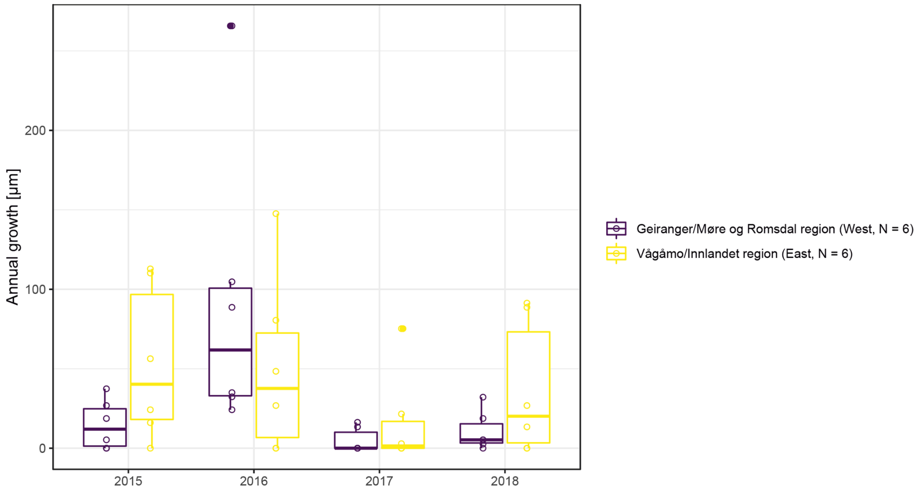


Figure A6. Boxplots of observed annual growth within each of the two study regions (Vågåmo, Innlandet, region (east, $N = 6$) and Geiranger, Møre og Romsdal, region (west, $N = 6$)).

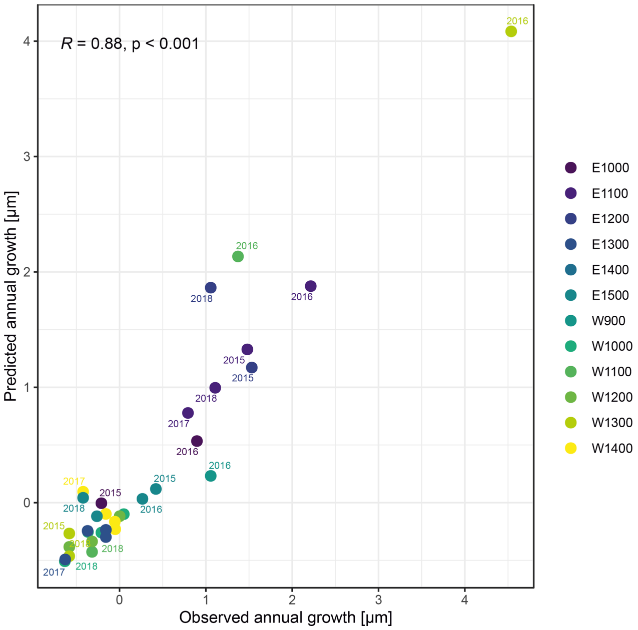


Figure A7. Observed annual growth and annual growth predicted by a linear regression model including timing (growth initiation and growth cessation), as well as peak growth as independent variables. Colors indicate the monitored specimens at the individual sites (E denotes east; W denotes west; numbers indicate elevation, m a.s.l.).

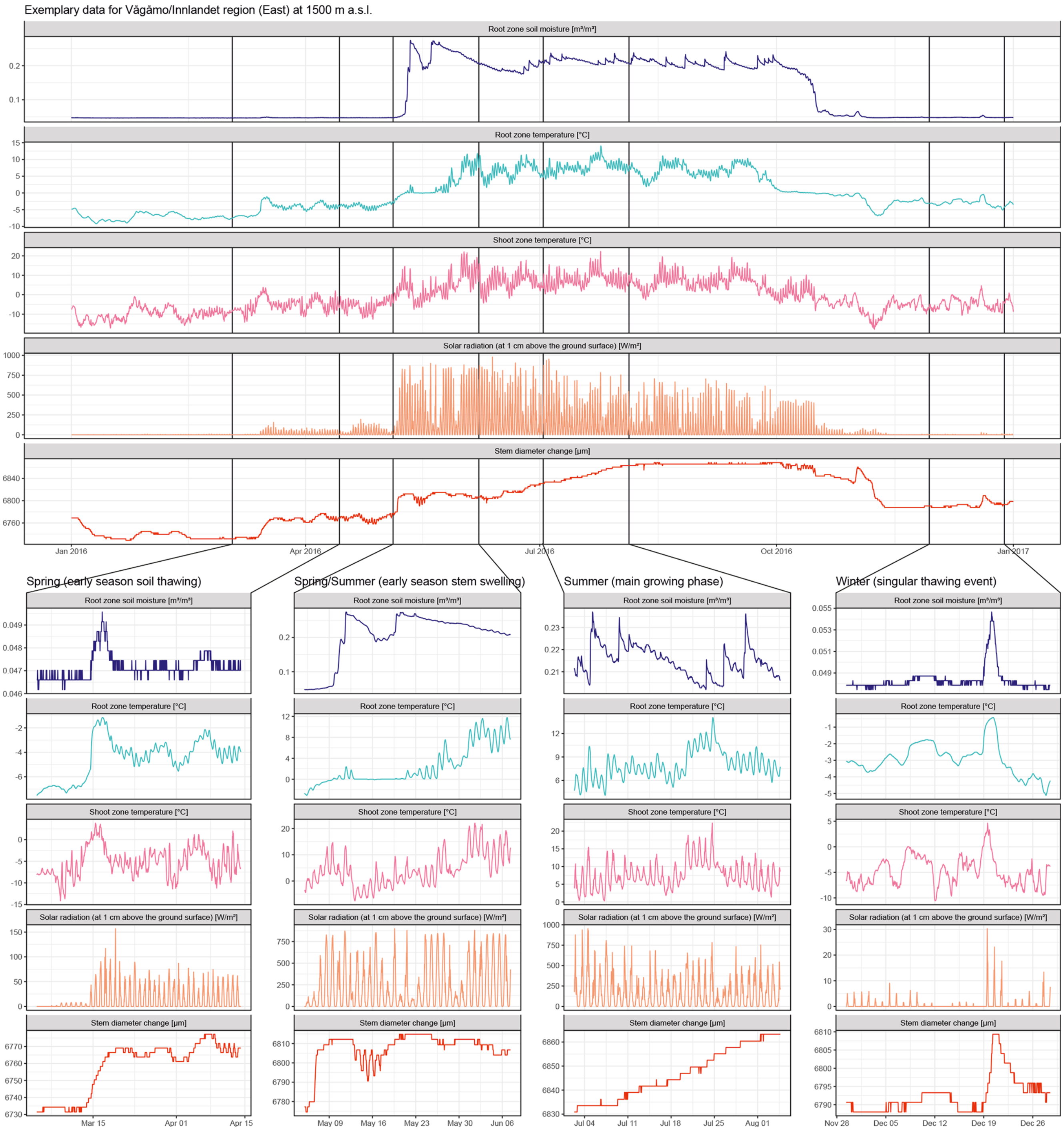
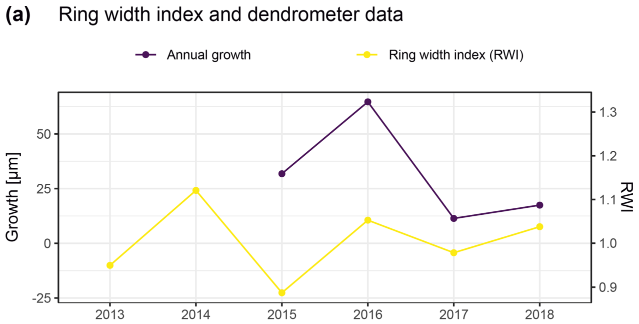
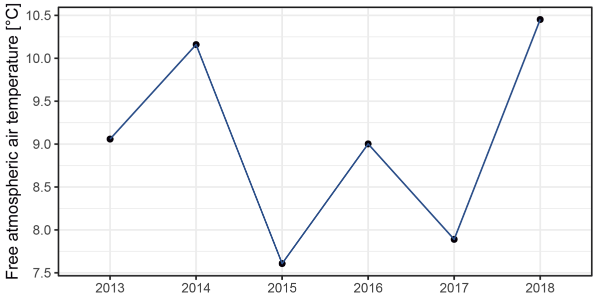


Figure A8. Raw data for one exemplary specimen from the Vågåmo, Innlandet, region at 1500 m a.s.l. Here, we present hourly data of stem diameter variability and the respective micro-environmental conditions. The four sections show important phases of the annual stem diameter variability and their relation to the micro-environment in detail. Coupling of soil moisture and stem diameter during the winter and spring months, when water-induced stem swelling and shrinking occur and decoupling during the main growing phase is clearly evident. Additionally, the direct response of the stem diameter to singular soil thawing events in winter is clearly visible in the curves.



(a) Ring width index and dendrometer data



(b) Mean summer temperatures (June, July, August)

Figure A9. Comparison of annual growth measured using dendrometers (see "Material and methods") and ring width derived by measuring annual growth rings of 12 specimens from similar positions on exposed ridges, presented here as the ring width index (RWI). Ring width was measured from multiple micro-slices per specimen (following Bär et al., 2006; **a**). Panel **(b)** shows free atmospheric air temperatures measured at 2 m above ground in both study regions. Such temperature data are commonly used for comparison of climate–growth relationships in dendroecological studies. With this figure we aimed to reproduce previous studies (Bär et al., 2006, 2007) for comparison with our dendrometer measurements.

Data availability. All underlying data pertinent to the results presented in this publication are publicly available in a data publication in ERDKUNDE – Archive for Scientific Geography (https://www.erdkunde.uni-bonn.de, last access: 8 March 2022; https://doi.org/10.3112/erdkunde.2021.dp.01, Löffler et al., 2021).

Author contributions. JL had the idea, designed the research platform, conducted the fieldwork, and together with RP ran the long-term project. SD analyzed the data, led the writing of the manuscript, and arranged the figures, with contributions from RP and JL.

Competing interests. The contact author has declared that neither they nor their co-authors have any competing interests.

Acknowledgements. The authors thank Eike Albrecht, Niklas Beckers, Elise Dierking, Nils Hein, Stef Weijers, and Dirk Wundram for collaboration within our LTAER project; Ole Øvsteng and Anders Svare for hospitality; and both the landowners and Norwegian authorities (Vågå and Stranda municipalities) for overall support. This work was supported by the Open Access Publication Fund of the University of Bonn.

Financial support. This research has been supported by the Deutsche Forschungsgemeinschaft (grant nos. LO 830/16-1 and LO 830/32-1).

This open-access publication was funded
by the University of Bonn.

Review statement. This paper was edited by Michael Bahn and reviewed by five anonymous referees.

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6 Contrasting growth response of evergreen and deciduous arctic-alpine shrub species to climate variability

DOBBERT, S.; PAPE, R.; LÖFFLER, J. (2021): Contrasting growth response of evergreen and deciduous arctic-alpine shrub species to climate variability. Ecosphere 12 (8), e03688. DOI: 10.1002/ecs2.3688.

Abstract

Broad-scale changes in arctic-alpine vegetation and their global effects have long been recognized and labeled one of the clearest examples of the terrestrial impacts of climate change. Arctic-alpine dwarf shrubs are a key factor in those processes, responding to accelerated warming in complex and still poorly understood ways. Here, we look closely into such responses of deciduous and evergreen species, and for the first time, we make use of high-precision dendrometers to monitor the radial growth of dwarf shrubs at unprecedented temporal resolution, bridging the gap between classical dendroecology and the underlying growth physiology of a species. Using statistical methods on a five-year dataset, including a relative importance analysis based on partial least squares regression, linear mixed modeling, and correlation analysis, we identified distinct growth mechanisms for both evergreen (*Empetrum nigrum* ssp. *hermaphroditum*) and deciduous (*Betula nana*) species. We found those mechanisms in accordance with the species respective physiological requirements and the exclusive micro-environmental conditions, suggesting high phenotypical plasticity in both focal species. Additionally, growth in both species was negatively affected by unusually warm conditions during summer and both responded to low winter temperatures with radial stem shrinking, which we interpreted as an active mechanism of frost protection related to changes in water availability. However, our analysis revealed contrasting and inter-annually nuanced response patterns. While *B. nana* benefited from winter warming and a prolonged growing season*, E. hermaphroditum* showed high negative sensitivity to spring cold spells after an earlier growth start, relying on additional photosynthetic opportunities during snow-free winter periods. Thus, we conclude that climate–growth responses of dwarf shrubs in arctic-alpine environments are highly seasonal and heterogenic, and that deciduous species are overall likely to show a positive growth response to predicted future climate change, possibly dominating over evergreen competitors at the same sites, contributing to the ongoing greening trend.

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Contrasting growth response of evergreen and deciduous arctic-alpine shrub species to climate variability

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Citation: Dobbert, S., R. Pape, and J. Löffler. 2021. Contrasting growth response of evergreen and deciduous arctic-alpine shrub species to climate variability. Ecosphere 12(8):e03688. 10.1002/ecs2.3688

Abstract. Broad-scale changes in arctic-alpine vegetation and their global effects have long been recognized and labeled one of the clearest examples of the terrestrial impacts of climate change. Arctic-alpine dwarf shrubs are a key factor in those processes, responding to accelerated warming in complex and still poorly understood ways. Here, we look closely into such responses of deciduous and evergreen species, and for the first time, we make use of high-precision dendrometers to monitor the radial growth of dwarf shrubs at unprecedented temporal resolution, bridging the gap between classical dendroecology and the underlying growth physiology of a species. Using statistical methods on a five-year dataset, including a relative importance analysis based on partial least squares regression, linear mixed modeling, and correlation analysis, we identified distinct growth mechanisms for both evergreen (*Empetrum nigrum* ssp. *hermaphroditum*) and deciduous (*Betula nana*) species. We found those mechanisms in accordance with the species respective physiological requirements and the exclusive micro-environmental conditions, suggesting high phenotypical plasticity in both focal species. Additionally, growth in both species was negatively affected by unusually warm conditions during summer and both responded to low winter temperatures with radial stem shrinking, which we interpreted as an active mechanism of frost protection related to changes in water availability. However, our analysis revealed contrasting and inter-annually nuanced response patterns. While *B. nana* benefited from winter warming and a prolonged growing season, *E. hermaphroditum* showed high negative sensitivity to spring cold spells after an earlier growth start, relying on additional photosynthetic opportunities during snow-free winter periods. Thus, we conclude that climate–growth responses of dwarf shrubs in arctic-alpine environments are highly seasonal and heterogenic, and that deciduous species are overall likely to show a positive growth response to predicted future climate change, possibly dominating over evergreen competitors at the same sites, contributing to the ongoing greening trend.

Key words: arctic-alpine greening and browning; *Betula nana*; climate–growth relations; dendrometer; *Empetrum nigrum* ssp. *hermaphroditum*; growth physiology; Norwegian Scandes; partial least squares regression.

Received 25 March 2021; accepted 31 March 2021; final version received 27 May 2021. Corresponding Editor: Debra P. C. Peters.

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INTRODUCTION

The change of vegetation within the tundra, the so-called "Arctic greening," has been identified as one of the clearest examples of the terrestrial impact of climate change (IPCC 2014). Observed from space over huge expanses of the circumpolar North (Myneni et al. 1997, Jia et al. 2003, Epstein et al. 2012, Berner et al. 2020), undergirded by plot-based evidence (Elmendorf et al. 2012), and attributed to warming at more than twice the rate of the rest of the planet (Chapin et al. 2005, Serreze and Francis 2006, IPCC 2014, Post et al. 2019), wide-ranging repercussions of this greening on ecosystems and their functioning are to be expected. Effects along a trophic cascade are observed, including declining herbivore populations, altered competition and predation, putting species at risk, and threatening endemic biodiversity (e.g., Fauchald et al. 2017, Ims et al. 2019). Moreover, vegetation trends of this scale are of immense importance to the carbon balance of tundra ecosystems (Joos et al. 2001, Mishra and Riley 2012, Alday et al. 2020), putting their large carbon pool at risk (Schuur et al. 2013, 2015). They also have major impacts on the global water cycle (Zwieback et al. 2019), and they lead, due to changes in the surface albedo, to self-amplifying feedbacks regarding the global climate system (Chae et al. 2015, Zhang et al. 2018, Bjorkman et al. 2020).

Addressing the mechanisms behind the observed greening, shrubification (i.e., an increased biomass and coverage of dwarf shrubs) has been identified as one key driver (Forbes et al. 2010, Myers-Smith et al. 2011, Fraser et al. 2014). Given, however, the pronounced spatial heterogeneity of the trend—which is slowing and even showing signs of browning in many regions (Bhatt et al. 2013, Phoenix and Bjerke 2016, Lara et al. 2018, Myers-Smith et al. 2020)—experts cannot yet agree on the direction of change (Abbott et al. 2016). A consensus is emerging that the underlying causes and future dynamics of tundra greening and browning trends are more complex, variable and scale-dependent than previously thought (Nielsen et al. 2017, Macias-Fauria et al. 2020). While at some places vegetation community composition shifts, greening is also promoted by increased plant productivity and growth (Alday et al. 2020). Longer growing seasons, increased thaw depth, and altered snow regimes may all influence vegetation changes (Bjorkman et al. 2020), and while growing season conditions (especially temperatures) are widely recognized as the main driver for growth in tundra shrubs (Blok et al. 2011, Hollesen et al. 2015, Francon et al. 2020), other effects, including those of winter warming, precipitation and snow cover, remain less studied. As such, the actual physiological processes and mechanisms behind the increased shrub growth are still poorly understood (Ackermann et al. 2017, Nielsen et al. 2017).

A better understanding of the observed patterns within arctic-alpine shrub growth is likely to emerge from an increased mechanistic understanding of the processes that actually underlie shrub growth (cf. Martin et al. 2017). The utilization of dendrometers to resolve the annual radial growth increment at finer functional and temporal scales than capable by classical ring-width–based dendroecological methods may hold an answer (Deslauriers et al. 2003). The achievable high temporal resolution enables fine-scale insights into short-term environmental effects (like frost spells) on the hydrological status and the xylogenesis of a shrub (Drew et al. 2010). Thus, dendrometer measurements bridge the gap between the ecophysilogically triggered short-term events of cell division and growth on the one hand and the time-integrated measure of total growth increment as assessed by ring widths (Köcher et al. 2012), on the other hand. Until now, the utilization of dendrometers, however, was mostly restricted to monitor tree growth (e.g., Duchesne et al. 2012, Cocozza et al. 2016, Liu et al. 2018).

Here, we, for the first time, make extensive use of high-precision dendrometers to monitor growth reaction of dwarf shrubs at the unprecedented temporal resolution, bridging the gap between classical dendroecology and its actual foundation, the underlying growth physiology of a species. By relating radial growth data to a set of physiologically meaningful environmental data that have simultaneously been recorded on-site, we shed light explicitly on those processes at the foundation of the observed changes in arctic-alpine environments. We are thus advancing the necessary understanding of widespread phenomena like greening and browning trends.

MATERIAL AND METHODS

Species and specimens

For this study, we chose two focal dwarf shrub species abundant across arctic-alpine ecosystems, one evergreen (*Empetrum nigrum* ssp. *hermaphroditum*, crowberry, hereafter *E. hermaphroditum)* and one deciduous (*Betula nana*, dwarf birch, hereafter *B. nana*). Both are almost circumpolar in distribution (see Büntgen et al. 2015 for distribution maps) with considerable effects on tundra communities and the observed arctic vegetation changes (Bell and Tallis 1973, Bret-Harte et al. 2001, Hollesen et al. 2015). At lower elevations, both species co-occur, with *B. nana* commonly surpassing *E. hermaphroditum* in growth height (as it reaches up to 1 m, Groot et al. 1997), thus likely to exert growth control by light limitation (Bret-Harte et al. 2001, Bär et al. 2007). At higher elevations, *E. hermaphroditum* decreases in growth height and remains the exclusive dwarf shrub within a matrix consisting of debris and graminoids (Bär et al. 2007). Both species are adapted to wet and cold climates (Bell and Tallis 1973, Groot et al. 1997), are able to tolerate comparatively low winter temperatures, and generally occur across a broad range of micro-habitats (Andrews et al. 1980, Stushnoff and Junttila 1986, de Groot et al. 1997, Ögren 2001). In this context, Löffler and Pape (2020) found a wide realized thermal niche for both species with optimum temperatures of >16.4°C for *B. nana* and >15.5°C for *E. hermaphroditum,* derived from the species frequency distribution across thermal regimes. More importantly, they highlight the importance of thermal conditions in autumn and winter, suggesting that as an evergreen species *E. hermaphroditum* is able to take advantage of favorable conditions when its deciduous congeneric, *B. nana*, is snow-covered and/or physiologically inactive (Löffler and Pape 2020).

Study sites

Our study is based on long-term monitored specimens from two study regions located in the alpine mountain region of central Norway, characterized by a steep regional climate gradient (Fig. 1). To the east, the Vågåmo/Innlandet region (61°53′ N; 9°15′ E) is located within the continental climatic section (C1; Moen 1999). With total annual precipitation of approximately 300–500 mm in the valleys, this area experiences the highest aridity found in Norway (Kleiven 1959). In contrast, our second study region to the west, the Geiranger/Møre og Romsdal region (62°03′ N; 7°15′ E), is located within the slightly to markedly oceanic climatic section (O1–O2; Moen 1999) of the inner fjords. It is characterized by humid conditions, with total annual precipitation of 1500–2000 mm in the valleys (Aune 1993). Measurements within the studied alpine regions indicated annual liquid precipitation of 900 mm in the West and 375 mm in the East. The additional amount of solid precipitation and its snow water equivalent remains unknown, but snowdrift leads to an uneven distribution of the snowpack within the complex alpine topography (Löffler 2005, 2007), leaving the studied plots on elevated ridges with discontinuous snow cover and deeply frozen ground in winter. In regard to temperature, those exposed sites represent the most extreme regimes found in the area where the mean annual ambient air temperature is 1.9°C (range −23.2°C [January] to +17.2°C [July]) in the west and −1.2°C (range −29.2°C [January] to +16.7°C [July]) in the east (e.g., Löffler 2003). The ridge positions used for sampling were stratified-randomly chosen to cover the elevational gradient, following the framework of our long-term alpine ecosystem research project (LTAER; e.g., Löffler and Finch 2005, Hein et al. 2014, Frindte et al. 2019, Beckers et al. 2020). They were placed at elevational levels from the tree line upwards, shifted by approximately 100 height-meters between regions to account for the depression of the elevational zonation toward the west (Löffler et al. 2006, Löffler and Pape 2020, Löffler et al., 2021). In accordance with the elevationally constrained range of the studied two species, we chose ten specimens from the oceanic region (700–1300 m a.s.l.) and 15 specimens from the continental region (900–1510 m a.s.l.) representing our chosen evergreen species, as well as five specimens from the oceanic region (700–1024 m a.s.l.) and ten specimens from the continental region (900–1510 m a.s.l.), representing our chosen deciduous species (Fig. 1). If available, we chose to monitor more than one site per elevational level, and at each site, the specimens were monitored for five full consecutive years (October 1, 2014–December 31, 2019), resulting in a total of 200 (((10 West + 15 East) *E. hermaphroditum* + (5 West + 10 East) *B. nana*) × 5 yr) dendrometer curves, each showing hourly stem diameter changes during the course of one year.

Dendrometric data, monitoring setup, and environmental data collection

To monitor radial stem diameter variations, we used high-precision dendrometers (type DRO;

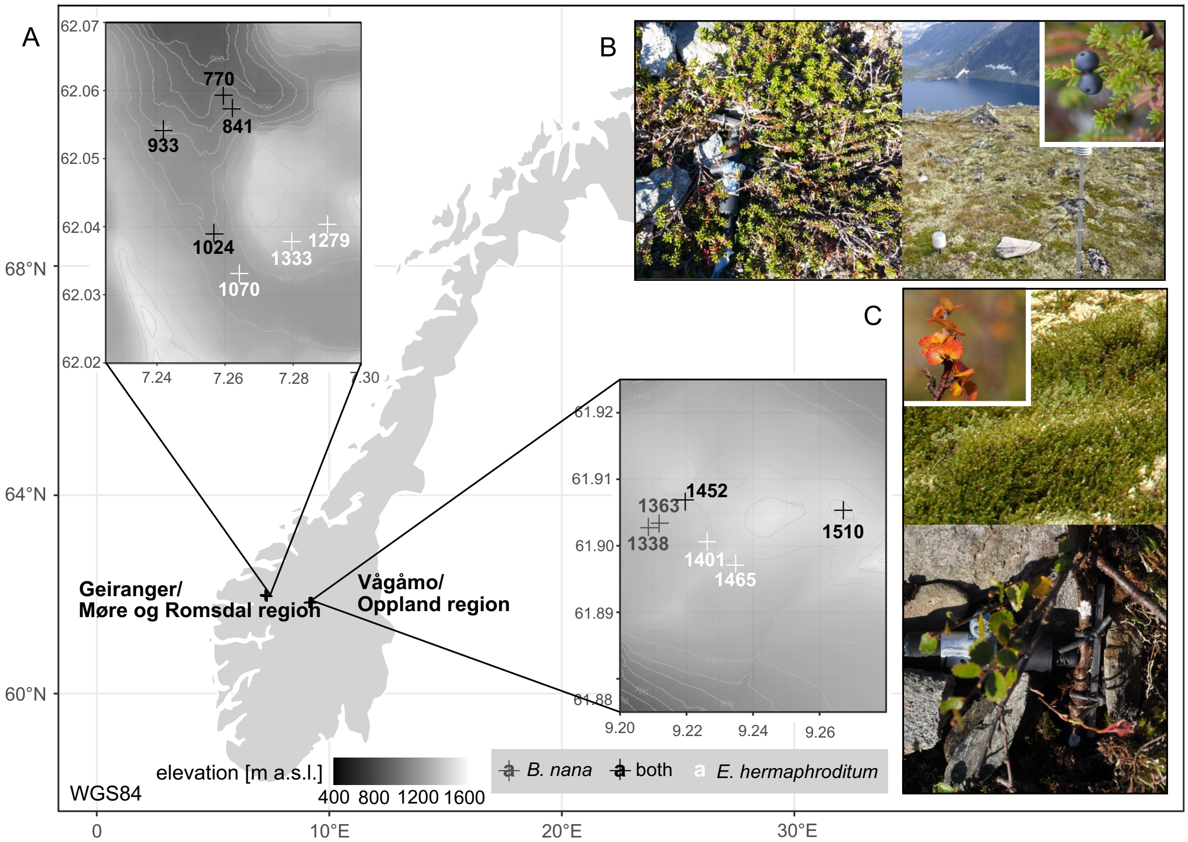

Fig. 1. Study regions in Central Norway and location of the individual study sites (A). At some sites both species were present and monitored (black), at others only one of the two focal species was found (gray, white). The shape file used to create the map was derived from the maps package (Becker et al. 2018) for the R software (R Core Team 2020), and the digital elevation model used is from the Norwegian Mapping Authority (2008). (B) and (C) show mounted dendrometers, and *E. hermaphroditum* (B), as well as *B. nana* (C) specimens at the studied sites.

Ecomatik, Dachau/Germany) mounted on one major aboveground stem horizontal to the ground surface on randomly chosen specimens, as close to the assumed root collar as possible (approximately 1–5 cm above ground). As addressed by Bär et al. (2006, 2007), this major stem is thought to represent the whole plant at least partly. However, how radial stem changes vary within the individual plant and between multiple stems of the same specimen is still not fully understood and might be a topic for further studies. We tried to account for this variation by sampling a high number of individual specimens. Also, we made sure that the chosen specimens were as representative for the observed local conditions at each site as possible, avoiding positions near stones and small depressions, inside the radius of other larger shrub species, and near patches of wind erosion. The temperature coefficient of the sensor used was <0.2 µm and measurements were taken at 1-min intervals and aggregated using the daily mean approach, averaging dendrometer data using the dendrometeR package (Van der Maaten et al. 2016), developed for the R statistical software (R Core Team 2020), which was primarily used in our analyses. Additionally, the annual stem diameter curves were normalized through subtraction of the previous year maximum to exclude year-related growth trends and maximize the separation of irreversible growth from water-related swelling and shrinking of the stem. This necessity arises because dendrometers are not measuring the absolute stem diameter, but rather changes in stem diameter relative to the start of the measurement cycle. Thus, the initial stem diameter, which ranged from 1829.1 to 10023.7 µm for *E. hermaphroditum,* and from 2851.8 to 12095.6 µm for *B. nana,* was removed from the annual curves. Finally, outliers were excluded, by defining cutoff ranges, using the interquartile range (IQR) and the 25th (Q1) and 75th (Q3) percentile (Q1/Q3 ± 1.5 × IQR). This led to a total exclusion of approximately 2% of daily measurements per curve.

At each site, we sampled one specimen of each species and took additional measures of micro-environmental parameters. These included soil temperatures (°C) at a depth of 15 cm below the ground surface within the root zone (hereafter "TRZ") and air temperatures at a location 15 cm above the ground surface within the shoot zone (hereafter "TSZ"), at 1-min intervals and recorded as hourly means using ONSET's HOBO loggers (type H21-002) and type S-TMB-002 temperature sensors (±0.2°C accuracy). For the TSZ measurements, the sensors were equipped with passively ventilated radiation shields. Additionally, we measured the volumetric soil water content (soil moisture, m^3 water/m^3 soil) 15 cm below the soil surface (hereafter "SMRZ") at all sites. The uncalibrated SMRZ was measured at 1-min intervals and recorded as hourly means using type S-SMD-M005 soil moisture sensors (±3% accuracy). Complementarily, we measured the hourly shoot zone global radiation (W/m^2) at 1 cm above the ground surface (hereafter "GRSZ") using a type S-LIB-M003 silicon pyranometer (±10 W/m^2 accuracy).

Our micro-environmental conditions were captured for the period from January 1, 2015, to December 31, 2019, with additional data used from the years 2014 and 2020 where needed. Missing data did not occur at the chosen sites.

Micro-environmental data

Averaged near-surface regimes of TRZ, TSZ, SMRZ, and GRSZ over all monitored sites are illustrated in Appendix S1: Fig. S1 and Fig. S2, as well as in Appendix S1: Table S1. The exposed ridge positions were characterized by extremely low winter temperatures and severe ground freezing, with high exposure to global radiation and only periodic snow cover. Temperatures usually started to increase in April or May. Lowest annual mean temperatures were measured in 2017 (TSZ = 0.371°C, TRZ = 1.230°C), highest in 2018 (TSZ = 0.912°C, TRZ = 1.614°C) with shoot and root zone conditions following, expectedly, a similar regime throughout the course of our study. The year 2015 stands out because of a comparatively long winter, with lasting low temperatures throughout the meteorological spring and soil moisture rising only gradually, indicating reoccurring freezing conditions. In contrast, the years 2019 and 2018 are characterized by an early rise in spring temperatures, followed by considerable spring cold snaps as evident by drops in the SMRZ regimes, indicating renewed soil freezing. Additionally, the winter 2015/2016 is characterized by the lowest temperatures measured throughout the studied period (Appendix S1: Figs. S1, S2).

Analysis of seasonal growth patterns

To discern seasonal growth patterns from the monitored dendrometer curves, we defined three distinct phases of stem variation, each as a temporal period (Fig. 2), as well as the radial stem change realized during this time period (Appendix S1: Table S2): (1) total annual growth, defined as growth-induced stem expansion (hereafter "growth"; following Zweifel 2016). Mathematically, we defined this phase as the current year's radial stem diameter maximum minus the previous year's maximum. As such, growth can take negative values if one year's stem increment fails to exceed the previous year's maximum stem diameter (see Fig. 2). We refer to those years as dormant years. Timewise, this phase lasts from the time when the stem diameter first exceeds the previous year's maximum, until the annual stem diameter maximum. As it represents irreversible stem expansion, this growth is most likely visible in the anatomical structure of the plant and should thus be directly comparable to classic measurement methods of radial stem growth, including ring width. (2) Reversible stem shrinking, associated with hydrological processes causing a temporary water deficit within the stem (Zweifel et al. 2014, Zweifel 2016) following the active growing phase and lasting until stem increment starts in the following year (hereafter "shrinking"). We define stem change during this phase as stem diameter maximum minus the next year's minimum. (3)

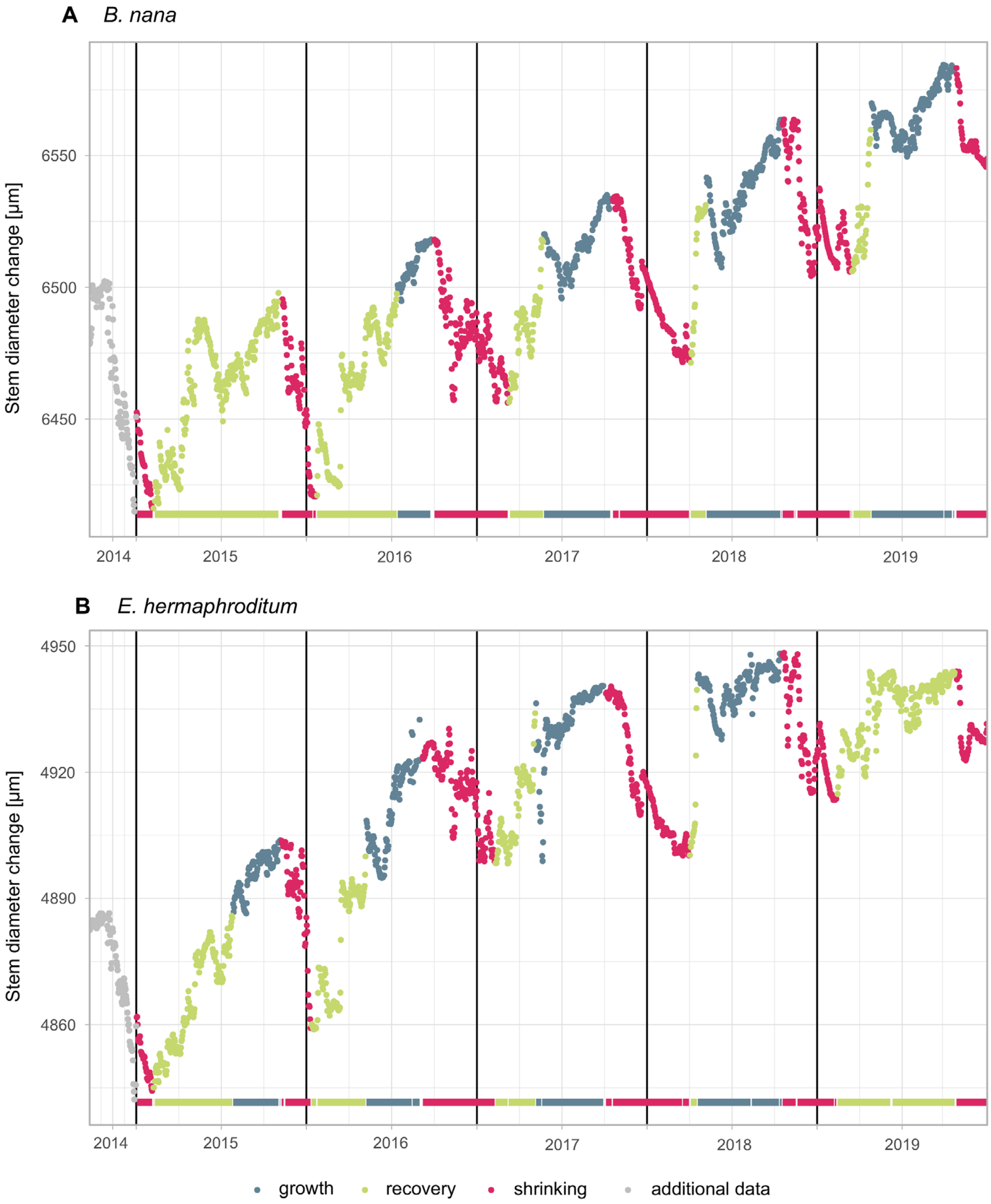

Fig. 2. Stem diameter variations in *B. nana* (A) and *E. hermaphroditum* (B). Measured daily radial stem change averaged over all studied sites (15 for *B. nana* and 25 for *E. hermaphroditum*). Colors represent phases of stem change. Additional relevant data beyond the defined studied period (2015–2019) is shown in gray. These data were used to identify the phases in 2015 (see *Material and Methods*).

Recovery, defined as stem swelling, also associated with hydrological processes reversing the previous shrinking. We define this phase similar to shrinking as the year's stem diameter minimum until the point where this year's stem diameter reaches the previous year's maximum (growth start). Mathematically, the stem diameter change during this phase can be calculated as the previous year's maximum minus this year's minimum. If one year's stem increment fails to exceed the previous year's maximum stem diameter, recovery is defined as the year's maximum minus the year's minimum instead.

For each phase, we calculated both, stem diameter change in terms of magnitude as well as temporal phase duration (number of days, Fig. 2), for each individual specimen and each of the monitored years. Appendix S1: Fig. S3 summarizes stem diameter variation sums realized in each of the previously defined phases and split by months.

Correlation and linear mixed-effects analysis

In order to reveal the relation between the observed growth patterns and micro-environmental conditions at the studied sites, we tested the influence of microclimate on individual shrub growth through correlation and linear mixed-effects analysis. We calculated Pearson's correlation coefficients between annual irreversible stem growth or shrinking in the years 2015–2019, and daily mean values for our environmental parameters TSZ, TRZ, SMRZ, and GRSZ, using the R statistical software (R Core Team 2020). To account for possibly time-lagged effects of the previous year's conditions on current growth, we included daily mean values for the period June (of the previous year) to September (of the current year) into the correlation analyses, similar to the analysis of growth chronologies as derived from ring-width series (e.g., Bär et al. 2008, Weijers et al. 2018). Here, additional micro-environmental measurements from 2014, prior to the start of our studied period, were included. For comparison, all analyses were performed individually for all specimens of *B. nana* and *E. hermaphroditum*.

To avoid generalizations which might arise from data averaging data measured at the individual sites into mean values, we additionally fitted linear mixed-effects models to our data, using the lme4 R package (Bates et al. 2015). For these models, we again chose annual irreversible stem growth as response variable, and monthly mean values for all environmental parameters as fixed effect. The individual specimens were included as random effect.

Additionally, Pearson's correlation coefficient was calculated between the response variable annual growth, shrinking and recovery (both duration and magnitude, defined as described above, and averaged for all individual specimens (15 for *B. nana* and 25 for *E. hermaphroditum*)) and seasonal means, minima and maxima for all measured environmental parameters. To assess the effect of the duration of both, growth and recovery, on total accomplished growth, we created linear mixed-effect models with annual growth as the dependent, and the duration of growth as well as the duration of recovery as independent variables. Here, the individual specimens were included as random effect similar to the previous analysis.

Finally, we aimed to further reveal temporal patterns of climate–growth relations by calculating moving window correlations for both focal species, using Pearson's correlation coefficient for each individual dendrometer curve and the corresponding environmental parameters (daily averaged values). These correlations were performed for moving window widths ranging from 3 to 180 d. Because the year-to-year variation in these patterns was very high for our data, we performed the correlations for the whole study period (2015–2019). Additionally, we averaged daily micro-environmental values for all parameters (TSZ, TRZ, SMRZ, and GRSZ) over preceding time windows with length of one day to up to one year and similarly correlated these values with averaged dendrometer data for each of the previously defined phases of stem change (Fig. 2). Here, we aimed to further highlight temporal patterns and year-to-year variation within these patterns.

Partial least squares regression

To complement the correlation analysis, we additionally analyzed the relation between annual growth and micro-environmental parameters applying partial least squares regression (PLSR; Wold 1975), also known as projection on latent structures (Abdi 2010). Our aim in applying this statistical approach was solely to use variable selection methods to assess the relative importance of certain micro-environmental conditions in promoting or hindering growth, and to define a subset of relevant conditions. Primarily intended for multidisciplinary problems (Wold 1980), PLSR has found application in ecological studies during the past decade (Carrascal et al. 2009, Frindte et al. 2019, Löffler and Pape 2020). Main advantages include that it works without distributional assumptions (Wold 1980, Dijkstra 1983, Vinzi et al. 2010) and deals efficiently with unreliability and heteroscedasticity issues (Martens and Næs 1989, Frindte et al. 2019). Moreover, the method is not limited, if the number of predictors exceeds the number of observations or if the predictors are highly correlated, as is the case with our data. This distincts PLSR from classical methods, like multiple linear regression and principal component regression, and makes it highly suitable for our purposes (Geladi and Kowalski 1986, Carrascal et al. 2009, Frindte et al. 2019). Following the approach successfully applied by Löffler and Pape (2020) to determine species thermal niches, we aggregated our (hourly) environmental data, rounding to 0.5°C for temperatures and 0.01 m^3/m^3 for soil moisture values. Subsequently, we counted and totaled the frequency of each value occurring within the rounded time-series. These calculations were performed for each meteorological season separately, resulting in sets of 35–124 predictor variables, which were subsequently scaled and centered. Previously calculated annual growth (which was found to be almost normally distributed, see Appendix S1: Fig. S4) served as the associated response variable. For final single response model estimation, we used the SIMPLS algorithm (de Jong 1993), implemented in the R package mdatools (Kucheryavskiy 2020). The optimal number of components in the PLSR model was found using Wold's R criterion (Wold 1978), and tenfold cross-validation was used to assess the explained variance during model calibration and validation. To assess the relevance of each independent variable from the created models, there are numerous methods available (reviewed by Mehmood et al. 2012). Based on assessments by Farrés et al. (2015) and Frindte et al. (2019), we considered the selectivity ratio (SR, defined as the ratio of explained to residual (unexplained) variance for each variable in the target projection vector), most appropriate for our data. From the SR, we derived the explained variance (SR/abs(SR +1)) for more contrastable results. In the resulting plots (Appendix S1: Figs. S5, S6), the variables with highest values represent the most important explanatory variables (Rajalahti et al. 2009). Finally, we increased the interpretability of these results by multiplying the SR of each variable by the sign of its corresponding regression coefficient, making it easy to identify which variables were positively or negatively related to the dependent variable (Rajalahti et al. 2009, Löffler and Pape 2020). Thus, we were able to clearly identify those environmental conditions that were significantly related to annually realized growth.

RESULTS

Our examined species showed surprisingly clear similarities in intra-annual stem diameter variation patterns, yet distinctive differences in total realized growth, with 2015 and 2019 being the most contrasting years, and an overall more positive growth trend for *B. nana* in comparison to *E. hermaphroditum* (Fig. 3 and Appendix S1: Fig. S7). In general, *B. nana* presented a greater spring increment rate followed by a short period of stem contraction, leading to an overall more strongly pronounced bimodal increment curve.

In accordance with the species physiological distinctions, we observed slight variations in growth start and end, with *E. hermaphroditum* starting growth earlier in most years (Appendix S1: Fig. S8). As an evergreen species, *E. hermaphroditum* is not restricted by leaf-forming processes in spring and can invest in radial stem growth earlier. As expected, growth in both species was significantly related to the duration of growth and recovery, with growth in *B. nana* showing slightly stronger dependency to duration ($R = 0.85$, $P < 0.001$) than *E. hermaphroditum* ($R = 0.52$, $P < 0.001$). Year-to-year variation in growth, as well as growth response to environmental parameters, was high for both species.

During the meteorological winter months, variation in both species was characterized by a very clear phase of radial stem contraction (shrinking;

Fig. 3). This shrinking phase usually started in September or October and lasted until the following spring, with remarkably little variation between the two species (Appendix S1: Fig. S8). It was characterized by short alterations in stem radius, directly linked to thawing and freezing conditions, indicating a strong influence of soil moisture availability on stem diameter during those months (Appendix S1: Fig. S9). However, the shrinking phase was not present in all individual specimens, and its absence was usually followed by dormancy or prolonged radial stem shrinking of the affected specimen during the following years (Appendix S1: Fig. S10), indicating an important role in mitigating the effects of low winter temperatures, which would otherwise inhibit further growth during the following growing season. In turn, these dormant years led to high inter-specimen variation in both species, the overall proportion of dormant years being 31% for *B. nana* and 48% for *E. hermaphroditum*. Here, it is important to note that such years of absent or negative stem change did not correspond in the two species and while stem shrinking followed similar patterns, correlation analysis revealed fundamental differences in micro-environmental controls. The moving window correlation (Fig. 4) showed shrinking in both species related to thermal conditions (TSZ and TRZ), yet, while *B. nana* responds with less shrinking to overall warmer conditions, *E. hermaphroditum* succeeds at higher temperatures with higher shrinking rates. This indicates that while both species are clearly compelled to actively reduce stem radius to mitigate the negative effects of extreme winter conditions, the underlying physiological mechanism differs. This distinction leads to an overall negative response to warming conditions in *E. hermaphroditum* and a contrasting positive response in *B. nana*.

On the contrary, our correlation analysis revealed a negative growth response of *B. nana* to high late summer temperatures and radiation (Figs. 4 and 5), evident in the years 2018 and 2019, which were characterized by comparatively warm summers. In contrast, in 2015, in which we measured the lowest summer temperatures, we found a more positive temperature-growth relation for both species, and, in the intermediate years 2016 and 2017, *B. nana* showed no clear dependency on summer and spring temperatures, responding positively to wet conditions characterized by high soil moisture and low radiation input instead (Appendix S1: Fig. S11). This indicates that raising summer temperatures and increasing summer radiation might affect *B. nana* negatively (Appendix S1: Fig. S11). PLSR results (Figs. 6 and 7) support those findings, indicating a negative influence of high summer soil temperatures, with *B. nana* being negatively affected by root zone temperatures exceeding 10°C. For *E. hermaphroditum,* we were able to identify a significant optimum range of root zone temperatures (7°–8°C), but higher temperatures (11°–12°C) had a negative effect as well.

Still, regarding climate–growth relations over all five monitored years, one of the clearest findings was a strongly contrasting response to winter conditions between the species (Figs. 4 and 5). *E. hermaphroditum* showed a clear positive growth response to unfavorable conditions during December to March, with low soil moisture content (indicating frozen ground and a lack of snow cover) and temperatures. In contrast, growth in *B. nana* was promoted by snowy winters, characterized by high soil moisture content and low global radiation (Fig. 5 and Appendix S1: Fig. S12). PLSR results strongly support those findings, marking low winter shoot zone temperatures as the most influential parameter in determining growth (Fig. 6), with the effects highly variable between species. Additionally, effects of winter warming might be slightly enhanced by relations to conditions during the following summer, which in turn might affect growth. We found mean winter temperatures and mean temperatures during the following summer significantly related throughout our studied period, although the relation was not very strong (TSZ, $R = 0.29$, $P < 0.001$, TRZ, $R = 0.31$, $P < 0.001$). The years 2015 and 2019, which showed the highest contrast in annual temperature regime (Appendix S1: Fig. S1), clearly demonstrated the strong negative effects of a long winter with late spring temperature increase on *B. nana*, as evident in 2015. Contrasting, our findings from 2019 highlight the negative sensitivity of *E. hermaphroditum* to temperatures rising early, followed by severe cold spells in spring and early summer (Fig. 3).

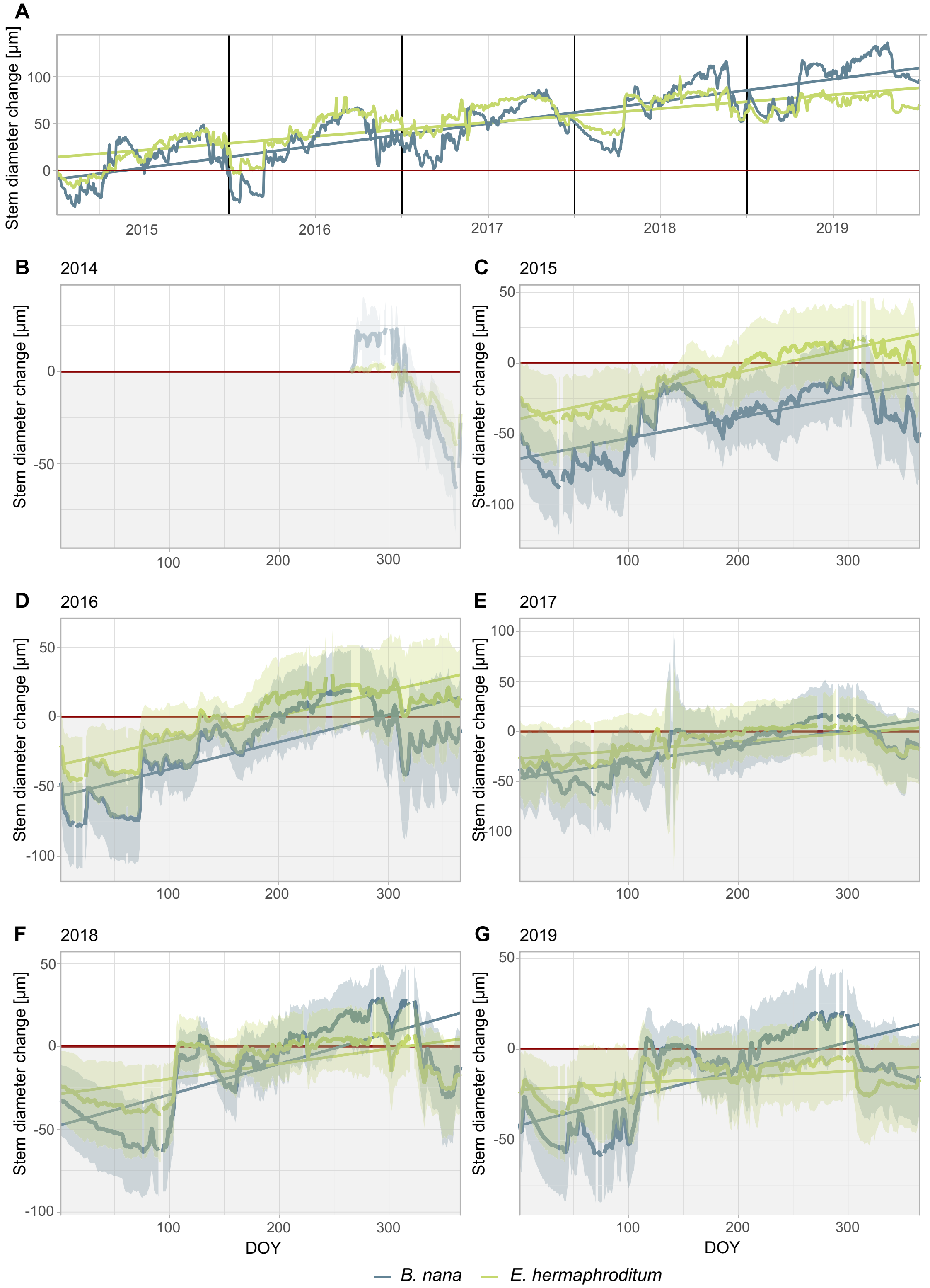

Fig. 3. Averaged annual stem diameter variations (± 1 SE) relative to previous years maximum (B–G) and

(Fig. 3. *Continued*)

stem diameter change relative to the start of the measuring period (A). Straight lines (dashed) represent linear trends. Gaps are caused by removed outliers. Measuring started in September 2014 and the measured changes in 2014 are therefore included (B), relative to the start of the measuring period. Transparency indicates standard deviation of all measured specimens.

Discussion

Dendroecological meaningful aboveground stem diameter curves can successfully be derived from both *B. nana* and *E. hermaphroditum* using high-precision dendrometers. In addition to annual growth characteristics measured by traditional methods (e.g., Bär et al. 2006, 2007, Macias-Fauria et al. 2012, Shetti et al. 2018, Le Moullec et al. 2019), we were thus able to directly track stem diameter changes on a daily time-scale. Net stem diameter change in woody plants is thought to represent the sum of expansion/shrinkage of living cells due to changes in turgor pressure and expansion/shrinking of xylem due to changes in xylem water tension (Lintunen et al. 2016, Lindfors et al. 2019). In most years, our focal species presented a phase of irreversible stem increment (usually associated with cambial activity, including cell enlargement and cell division, Rossi et al. 2008, Drew et al. 2010, Steppe et al. 2015, Zweifel 2016) during the summer months. This phase was missing in individual specimens, indicating reduced or inhibited cambial activity during those years, most likely caused by the extreme

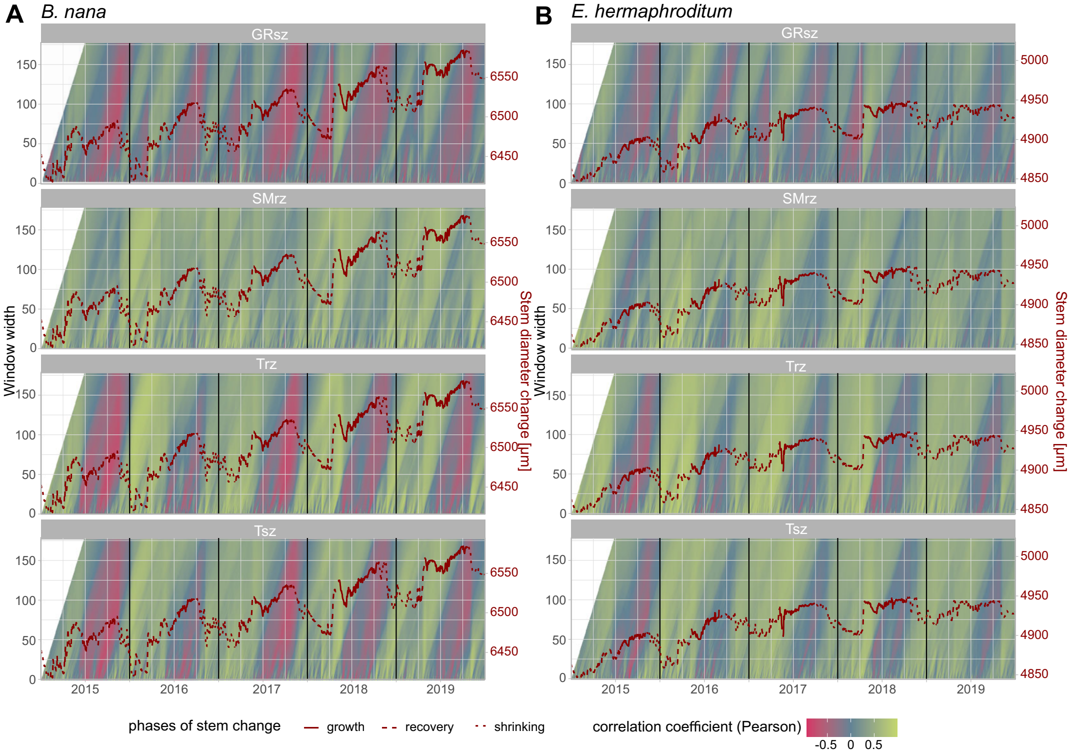

Fig. 4. Mow correlation for daily stem diameter change as shown in Fig. 2 and daily measurements of environmental data. Moving window correlations were performed for window widths ranging from 3 to 180 days (right-aligned), revealing temporal patterns of radial stem change and microenvironment relations. Additionally, radial stem change is indicated by the red line for direct comparison.

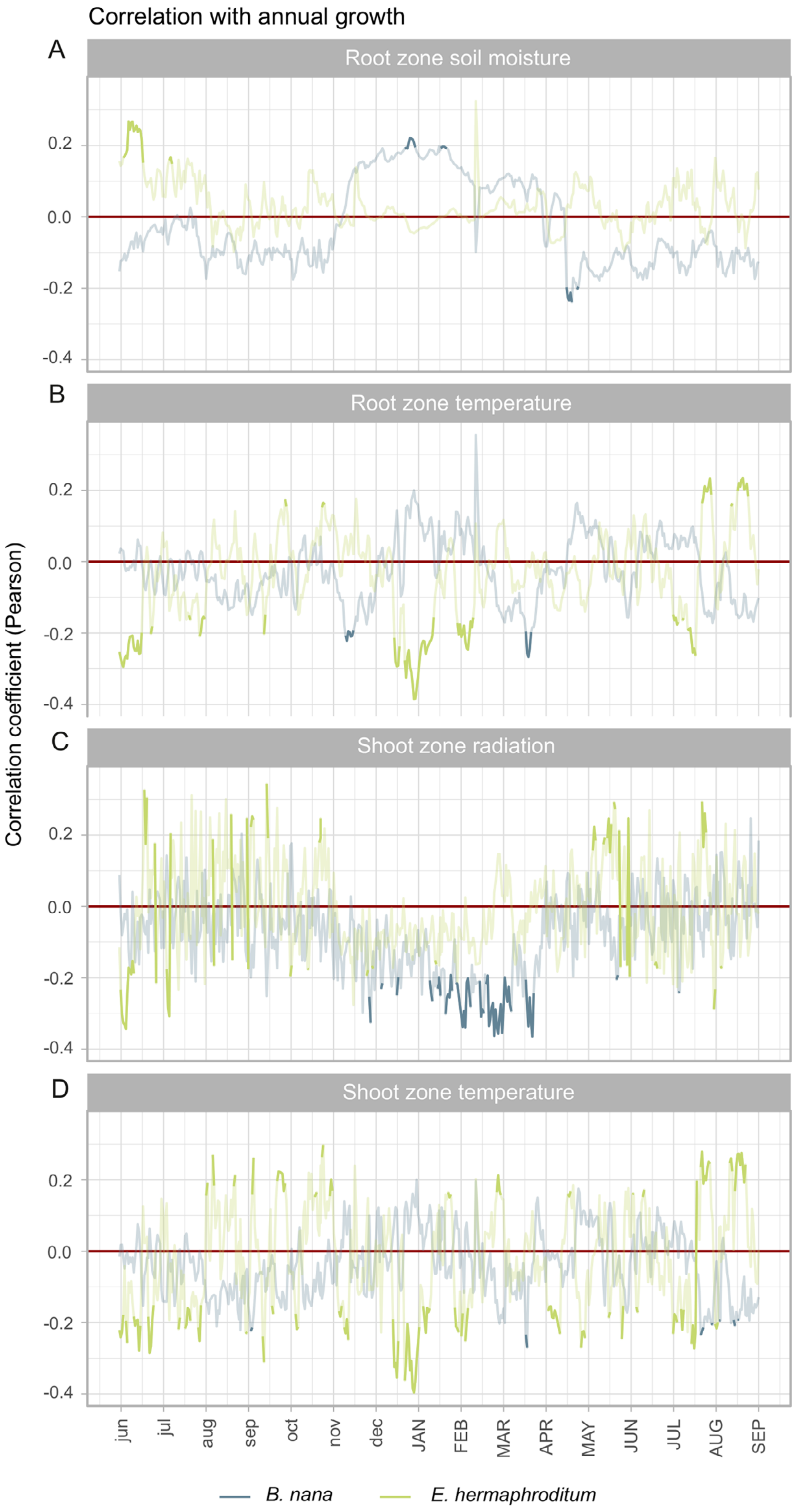

Fig. 5. Pearson's correlation coefficients calculated between total annual growth as derived from the

(Fig. 5. *Continued*)

dendrometer curves and daily environmental data, measured at the individual sites. Transparency indicates non significance. Abbreviations of months from the previous year are in lowercase letters and those of the current year are given in capitals.

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growing conditions and cold stress experienced at the studied sites (Wilmking et al. 2012). Throughout the rest of the year, most of our specimens showed very strongly pronounced reversible expansion/shrinkage, which can be attributed to underlying changes in water relations (distribution of water and water potential gradients between different compartments and parts of the plant, Lindfors et al. 2019). In this context, both *B. nana* and *E. hermaphroditum* showed short-term variations in stem radius, directly linked to fluctuations in soil moisture and

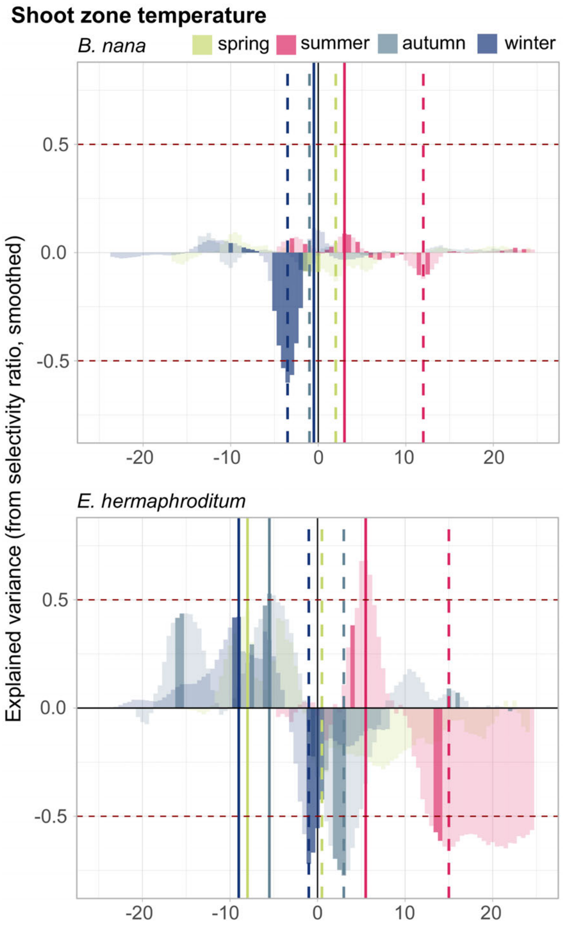

Fig. 6. Pearson's correlation coefficients calculated between total annual growth as derived from the dendrometer curves and daily environmental data, measured at the individual sites. Transparency indicates non significance. Abbreviations of months from the previous year are in lowercase letters and those of the current year are given in capitals.

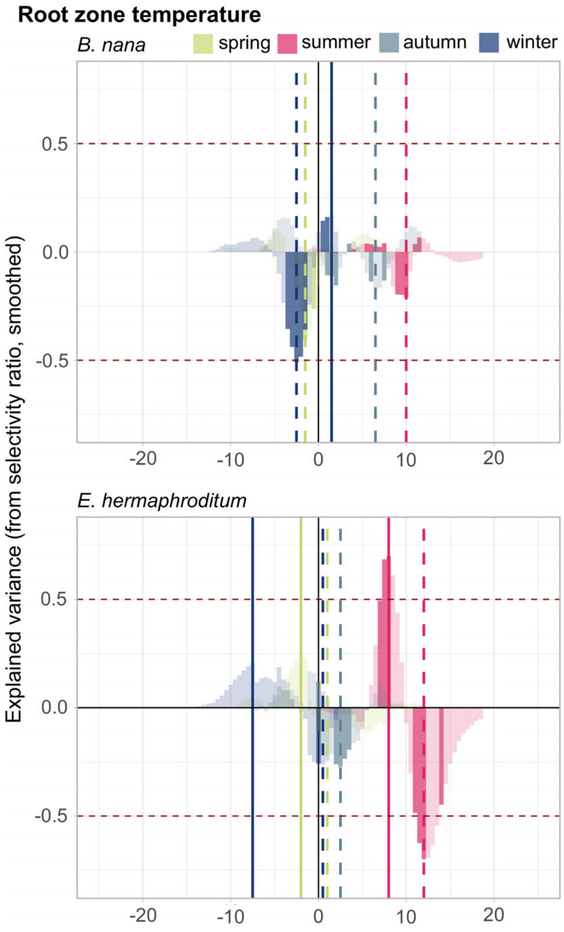

Fig. 7. Smoothed variance explained derived from selectivity ratio multiplied with the sign of its corresponding regression coefficient for shoot zone temperature (Tsz, independent variables) and total annual growth (dependent variable), derived from PLSR analysis. Shaded areas represent values rendered significant ($P < 0.05$). Colors represent seasons.

temperature, as well as a longer-term phase of stem shrinking which lasted throughout the winter months and can be interpreted as a form of protection from frost damage (Schott and Roth-Nebelsick 2018). In cold-climate ecosystems, effects of freezing and ice encasement have proven to be highly influential in trees (Lindfors et al. 2019) and in shrubs (Preece and Phoenix 2014, Milner et al. 2016). In general, it is believed that shrubs resist freezing damage by snow protection during the coldest part of the year (Körner 2012, Blok et al. 2015, González et al. 2019). As snow is sparse at our studied sites, there is a strong need for additional frost protection through physiological adaptation. Our results suggest that living cells of both *B. nana* as well as *E. hermaphroditum* are able to resist the effects of frost, possibly through actively reducing cell water content to avoid frost-induced cavitations, which may occur when xylem sap freezes and dissolved gases create air bubbles in the wider conduits (Fonti et al. 2010). Such dehydration processes, alongside ice nucleation and ice forming in the apoplast causing additional dehydration stress, have shown to lead to xylem diameter shrinkage in other woody plants, mainly through a reduced water potential (ψ; Zweifel and Häsler 2000, Améglio et al. 2001, Charra-Vaskou et al. 2016, Lintunen et al. 2016, Lindfors et al. 2019). Additionally, vessel size and anatomy might play a role here. In general, narrow vessels embolize less readily than wide ones, while bigger vessels allow for higher rates of photosynthesis and growth (Gorsuch et al. 2001). Thus, the narrow mean vessel diameter characteristic of *E. hermaphroditum* can be interpreted as a form of adaption to the extreme environments (Carlquist and Zona 1988). As a study by Nielsen et al. (2017) showed, *B. nana* can actively alter vessel lumen in response to environmental conditions, potentially increasing freezing resistance. Similar strategies have yet to be studied for *E. hermaphroditum*.

In general, the importance of the adaptive mechanisms described above is highlighted by the fact that the observed winter shrinking was missing in individual specimens, causing them to cease radial growth in the following years indicating a direct inhibiting influence on cambial activity (Wilmking et al. 2012). Overall, the growth and response patterns observed at the sampled ridge positions confirm that both *E. hermaphroditum* and *B. nana* might be able to adjust key xylem anatomical traits to annual fluctuations in micro-climatic conditions in order to optimize their total radial stem growth rate and avoid negative effects of extreme winter conditions.

However, even though the importance of unfavorable winter conditions is highlighted by our findings, their effects on total realized growth have shown to be highly contrasting in our focal species. In the context of future climate change, this is particularly important as temperature increase at high latitudes is expected to be higher during winter, and there are more extreme events expected during winters, including unseasonal warm periods, ground ice formation, and loss of snow cover (Post et al. 2009, Seneviratne et al. 2012, Vikhamar-Schuler et al. 2016). At our studied wind-blown ridge positions, characterized by shallow snow cover and consequent low winter temperatures, pronounced temperature amplitudes, and high year-to-year variability in winter, future changes in (micro-)environmental conditions might differ and are hard to predict (Löffler et al. 2006, Wundram et al. 2010). In recent years, there have been several studies recognizing the importance of winter warming on dwarf shrub development in addition to growing season conditions, which have long been the focus. Though there is no consensus regarding direction and magnitude of the effects, they generally agree that the response is highly species-specific (Bokhorst et al. 2010, Cooper 2014, Blok et al. 2015, Hollesen et al. 2015, Krab et al. 2018, González et al. 2019). In our focal species, this is evident by the highly contrasting response to winter conditions. Both *B. nana* and *E. hermaphroditum* are able to mitigate the effects of extreme negative temperatures, but only *E. hermaphroditum* shows a strong positive response to those conditions, benefiting from prolonged snow-free periods. This suggests that in contrast to deciduous species, *E. hermaphroditum* is able to continue photosynthetic activity and remain energetically effective in synthesizing carbohydrates during at least parts of the winter months (Gimeno et al. 2012, Wyka and Oleksyn 2014, Löffler and Pape 2020). While nutrition uptake and soil moisture access are extremely limited during those times, high global radiation can lead to additional photosynthetic opportunities (Körner 2015, Saccone et al. 2017). However, this implies that *E. hermaphroditum* has to sustain water transport to the canopy to some extent, risking cavitation in the xylem (Sperry 2003, Fonti et al. 2010, Bowling et al. 2018). Thus, we suggest that the negative relation found between winter shrinkage in *E. hermaphroditum* and temperatures is caused by this need for water transport in order to remain photosynthetically active in cold winters with high global radiation and little snow cover, consequently risking frost damage, evident in the high rate of dormant years. With this highly localized advantage over deciduous species such as *B. nana*, *E. hermaphroditum* is able to start growth activity as soon as liquid water is available in the root zone, and to acquire nitrogen early in the season (Bråthen et al. 2018), leading to a slightly earlier growth start. However, this phase of early growth is highly critical (Fonti et al. 2007, 2010), and Venn and Green (2018) found evergreen alpine shrub species strongly affected by freezing events very early in spring, before they become frost-hardened after snowmelt. This could explain the low growth rates found in *E. hermaphroditum* in 2019, a year characterized by such spring conditions. In contrast, *B. nana* might benefit from warmer winters, with increased nutrition availability (Sturm et al. 2005, Hagedorn et al. 2014) and high soil moisture content, indicating pronounced snow cover, and early snowmelt that allows the soils to drain and warm quicker and the flowering and leaf-forming processes to start earlier (Pop et al. 2000, Hollesen et al. 2015). Therefore, we found *B. nana* highly sensitive to prolonged snow cover and late temperature rise as was the case in 2015. Early snowmelt, evident in high soil moisture content during spring, on the contrary had a positive effect on *B. nana* growth. Such links between snow cover and shrub growth have been suggested before (Hallinger et al. 2010, Blok et al. 2015).

While the effects of winter conditions on shrub growth have only recently been addressed, summer conditions have long been recognized as a driver of radial growth, with most studies reporting positive effects (Bär et al. 2008, Elmendorf et al. 2012, Myers-Smith et al. 2015, Young et al. 2016, Weijers et al. 2018), and negative effects found in a few areas only (Myers-Smith et al. 2015, Young et al. 2016, Gamm et al. 2018), which were recently linked to soil moisture limitations (Buchwal et al. 2020). In years with comparatively short, cold summers, our results confirm summer temperatures as a driver of growth for both *B. nana* and *E. hermaphroditum*. On the contrary, in years with relatively warm summers, which dominated our study period, temperature-growth relations lost their significance and we found optimum summer temperatures in both species at our studied sites lower than the thermal niches previously identified by Löffler and Pape (2020) suggest (below a threshold of approximately 10°C). Additionally, our PLSR results suggest a thermal limitation of growth that arises from unconventionally high root zone temperatures in summer (Fig. 7). Those effects are most likely unique to the exposed positions we have studied, as it was not found in previous studies (e.g., Hollesen et al. 2015, Nielsen et al. 2017, Löffler and Pape 2020). Possible causes are interactions of temperature and moisture regimes, and the specific topography at the studied positions, as well as long-term adaption to the cooler alpine environment meeting unusually warm summers in recent years (IPCC 2014, Post et al. 2019). This corresponds well with recent findings by Gamm et al. (2018) and Buchwal et al. (2020), suggesting negative effects of rapid warming on *B. nana,* directly linked to soil moisture limitation. Yet, even though we found high summer temperatures a limiting factor to total annual growth, *B. nana* also responded positively to a prolonged growing season caused by raising summer temperatures, as found in our study and others (Pop et al. 2000, Li et al. 2016). The total effects of summer warming are therefore highly complex.

CONCLUSION

In contrast to several studies from past years (Bär et al. 2008, Meinardus et al. 2011, Dumais et al. 2014), we found both species highly adapted to local extreme environmental conditions throughout the year, but no clear dependency of radial stem growth on governing elevational or regional climatic signals. We can thus confirm findings that suggest a high sensitivity of growth patterns to topographic heterogeneity (Ropars et al. 2015, 2017, Young et al.

2016, Nielsen et al. 2017), which overrides governing regional climate signals (Pape and Löffler 2016, 2017). In terms of coping with climate changes, the high adaptability found in both species can be interpreted as an indicator for high phenotypic plasticity evolved in response to the high micro-environmental heterogeneity of the region. This might provide a crucial advantage, possibly allowing the species to persist locally in a changing environment (Turcotte and Levine 2016, Pfennigwerth et al. 2017, Graae et al. 2018). However, the extent of phenotypic plasticity can be limited by ecological and evolutionary constraints (Valladares et al. 2007, Henn et al. 2018), and our results suggest the existence of a thermal threshold restricting the cold-adapted arctic-alpine species in terms of rising summer temperatures. Additionally, even though both species evidently developed distinct coping mechanisms in response to extreme conditions, species-specific responses differed a great deal, indicating a crucial role of interspecific interactions and competition in future community-level changes. Overall, our findings suggest a long-term positive growth response of *B. nana* to warming conditions and emphasize the importance of winter warming and growing season length in this process. This is in accordance with findings by Hollesen et al. (2015) and Nielsen et al. (2017). Thus, our results support the hypothesis of warming conditions leading to a possible dominancy of *B. nana* (Bret-Harte et al. 2001, Deslippe et al. 2011, Deslippe et al. 2011, Henry et al. 2012) at exposed positions, where evergreen species like *E. hermaphroditum* currently rely on their ability to benefit from cold, snow-free winters by continued photosynthetic activity. However, our findings also point to possible difficulties of both focal species to adapt to warming summer conditions, which will increase the complexity of future changes. Additional long-term monitoring and examination of specimens from different topographic positions and from different species are therefore of crucial importance in understanding climate–growth relations and the direction of such changes. Overall, our results highlight the importance and complexity of seasonal effects on tundra shrub growth and confirm a possible advantage of deciduous over evergreen species, leading to the greening trend observed across arctic-alpine regions (Tape et al. 2006, Gough et al. 2012).

ACKNOWLEDGMENTS

The authors thank Niklas Beckers, Elise Dierking, Nils Hein, Stef Weijers, and Dirk Wundram for collaboration within our LTAER project, Ole Øvsteng and Anders Svare for hospitality, and both the landowners and Norwegian authorities (Vågå and Stranda municipalities) for overall support. Parts of this study were supported by the Deutsche Forschungsgemeinschaft (DFG) (grants LO 830/16-1, LO 830/32-1).

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DATA AVAILABILITY STATEMENT

Data are available from Erdkunde: Archive for Scientific Geography: https://doi.org/10.3112/erdkunde.2021.dp.01.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3688/full

7 How does spatial heterogeneity affect inter- and intraspecific growth patterns in tundra shrubs?

DOBBERT, S.; PAPE, R.; LÖFFLER, J. (2021): How does spatial heterogeneity affect inter- and intraspecific growth patterns in tundra shrubs? J Ecol 109 (12), p. 4115–4131. DOI: 10.1111/1365-2745.13784.

Abstract

Arctic and alpine ecosystems are strongly affected by rapidly changing environmental conditions, resulting in profound vegetation shifts, which are highly heterogeneous and hard to predict, yet have strong global impacts. Shrubs have been identified as a key driver of these shifts. In this study, we aim to improve the understanding of how such broad-scale vegetation changes are locally impacted by inter- and intraspecific plasticity and topographically driven heterogeneity in microsite conditions.

We assessed continuous stem diameter variation of three dominant tundra shrub species at daily resolution during 5 years, using high-precision dendrometers, thus bridging the gap between classical dendroecology and plant physiology. From this data, we identified distinct growth patterns which we linked to microsite environmental drivers.

The observed patterns appeared highly variable depending on site and species, strongly influenced by characteristics of the individual plant. As the main driver of this variability, we identified fine-scale topographic complexity, causing the sampled specimens to adjust locally by developing distinct growth strategies. We found these strategies strongly related to snow-cover variation and associated freezing and thawing. Predicted changes in winter conditions and associated snow regimes will therefore have strong effects on shrub growth and community structure, yet, these effects are highly complex and not uniform in direction.

Synthesis. The ability to adapt in a heterogeneous environment appeared highly differentiated between species and closely connected to intraspecific plasticity. Here, we identified spatial variability related to local topography as a main indicator for potential future redistribution and niche shifts in response to environmental change.

Received: 18 June 2021 | Accepted: 12 September 2021

DOI: 10.1111/1365-2745.13784

Journal of Ecology
BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

How does spatial heterogeneity affect inter- and intraspecific growth patterns in tundra shrubs?

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Funding information
Deutsche Forschungsgemeinschaft, Grant/Award Number: LO 830/16-1 and LO 830/32-1

Handling Editor: Robert G. Björk

Abstract

1. Arctic and alpine ecosystems are strongly affected by rapidly changing environmental conditions, resulting in profound vegetation shifts, which are highly heterogeneous and hard to predict, yet have strong global impacts. Shrubs have been identified as a key driver of these shifts. In this study, we aim to improve the understanding of how such broad-scale vegetation changes are locally impacted by inter- and intraspecific plasticity and topographically driven heterogeneity in microsite conditions.
2. We assessed continuous stem diameter variation of three dominant tundra shrub species at daily resolution during 5 years, using high-precision dendrometers, thus bridging the gap between classical dendroecology and plant physiology. From this data, we identified distinct growth patterns which we linked to microsite environmental drivers.
3. The observed patterns appeared highly variable depending on site and species, strongly influenced by characteristics of the individual plant. As the main driver of this variability, we identified fine-scale topographic complexity, causing the sampled specimens to adjust locally by developing distinct growth strategies. We found these strategies strongly related to snow-cover variation and associated freezing and thawing. Predicted changes in winter conditions and associated snow regimes will therefore have strong effects on shrub growth and community structure, yet, these effects are highly complex and not uniform in direction.
4. *Synthesis*. The ability to adapt in a heterogeneous environment appeared highly differentiated between species and closely connected to intraspecific plasticity. Here, we identified spatial variability related to local topography as a main indicator for potential future redistribution and niche shifts in response to environmental change.

KEYWORDS

arctic–alpine vegetation change, climate–growth relations, dendrometer, ecophysiology, growth variation, linear mixed effect models, partial least squares regression

1 | INTRODUCTION

In a rapidly changing climate, there is an increasing need to understand how communities and ecosystems respond to environmental change. With tundra ecosystems experiencing temperatures rising at thrice the global rate (AMAP, 2021; Post et al., 2019), massive changes in vegetation structure and ecosystem functioning are taking place already (Bjorkman et al., 2018; Elmendorf, Henry, Hollister, Björk, Boulanger-LapointeHenry, et al., 2012; Epstein et al., 2017; IPCC, 2014). In the past decades, an increased biomass and coverage of shrubs in response to changes in climate has led to major vegetation shifts. The observed greening of wide areas of the circumpolar Arctic has profound implications for the global climate system (Bjorkman & Gallois, 2020; Carlson et al., 2016; Collins et al., 2021; Forbes et al., 2010; Fraser et al., 2014; Myers-Smith et al., 2011). In recent years, however, this trend has been recognized as highly heterogeneous and complex, with the direction of change still poorly understood (Abbott et al., 2016; Elmendorf, Henry, Hollister, Björk, Bjorkman, et al., 2012; Macias-Fauria et al., 2020; Myers-Smith et al., 2020; Nielsen et al., 2017; Phoenix & Bjerke, 2016). As growing seasons are lengthening (Epstein et al., 2017), snow-cover conditions are changing (Xu et al., 2013) and extreme winter warming events are more frequently causing snowmelt in midwinter (Bjerke et al., 2017), questions are rising about the ability of dominant tundra species to adapt within the necessary timeframe to survive under these changing conditions.

An individual plant's ability to thrive in a changing environment has been linked to multiple factors, including its evolutionary history, genetic constraints, environmental influences and plasticity, both on an inter- and intraspecific level (Funk et al., 2017; Henn et al., 2018; Matesanz et al., 2012; Violle et al., 2012). Phenotypic plasticity, the ability of a species to alter its phenotype in response to environmental variation (Kingsolver & Huey, 1998), as well as genetic adaption (Hoffmann & Sgrò, 2011), play a key role in determining the individual plant's ability to shift optimal trait values with changing environmental conditions. In ecology, plasticity is therefore closely linked to range size and climatic niche breadth (Callaway et al., 2003; Duputié et al., 2015; Graae et al., 2018; Henn et al., 2018; Malyshev et al., 2016). Inter- and intraspecific variability have long been recognized as a key element of community ecology with strong implementations on ecosystem-level processes in response to environmental change (Firn et al., 2019; Hendry, 2016; Violle et al., 2012). This fact has led numerous studies (e.g. Duputié et al., 2015; Firn et al., 2019; Pfennigwerth et al., 2017; Valladares et al., 2014) to look at inter-plant variability in response to climate change research, where species are challenged to cope with modified environmental drivers, that may lead to range and niche shifts. In this context, variation in functional traits is often used as indicator for this variability, while physiological adjustment and consequent variation in growth patterns have not yet been utilized in this context. Furthermore, models of species distribution and range limits still rarely consider plasticity and such models are often restricted by small datasets. How plasticity, in response to heterogeneous environments, connects with the factors determining a species niche, remains poorly understood (Pérez-Ramos et al., 2019).

In this context, we examined variations in stem diameter across three dominant shrub species within a heterogeneous oroarctic (Virtanen et al., 2016) setting along steep geographical gradients. We derived fine-scale growth curves from continuous stem diameter measurements using high-precision dendrometers, thus bridging the gap between classical dendroecology and plant physiology. We expected to discern distinct growth patterns from these curves, adapted to site-specific environmental conditions, and reflected by inter-site variability in stem diameter change. Our objectives were to specify this variability within growth patterns, answering (a) how these patterns differ between species and along topographic gradients, (b) how they are linked to site- and topography-specific environmental drivers and (c) how growth variance between individual specimens is affected. We assumed that answering those questions will allow us to infer conclusions about drivers of radial growth in shrubs and derive valuable information regarding the overall plasticity of the examined shrub species, which would facilitate predictions of possible range and niche shifts in response to future climate change.

2 | MATERIALS AND METHODS

2.1 | Species and specimens

For this study, we selected three shrub species abundant across the tundra, two evergreen (*Empetrum nigrum* ssp. *hermaphroditum* (Hagerup), crowberry, and *Phyllodoce caerulea* (Linnaeus), blue mountain heath), and one deciduous species (*Betula nana* (Linnaeus), dwarf birch). All three species have a near circumpolar distribution (Büntgen et al., 2015; Hultén, 1968), exert considerable effects on tundra communities (Bell & Tallis, 1973; Bret-Harte et al., 2001; Coker & Coker, 1973), and play a key role in the 'greening of the Arctic' (Crawford, 2008; Myers-Smith et al., 2015). Regarding interspecific interaction, *B. nana* commonly surpasses both *E. hermaphroditum* and *P. caerulea* in height (Coker & Coker, 1973; de Groot et al., 1997), and is thus likely to influence growth of its competitors by restricting their exposure to solar radiation (Bär et al., 2007; Bret-Harte et al., 2001). At higher elevations (>1,100–1,300 m a.s.l.), *B. nana* and *P. caerulea* cease to exist while *E. hermaphroditum* remains within a matrix consisting of debris and graminoids (Bär et al., 2007). While *B. nana* and *E. hermaphroditum* occur across a broad range of micro-habitats and are able to tolerate comparatively low winter temperatures (Andrews et al., 1980; de Groot et al., 1997; Ögren, 2001; Stushnoff & Junttila, 1986), *P. caerulea* usually grows best at habitats with prolonged snow cover (more than 100 days annually) and primarily prefers slopes (Coker & Coker, 1973; Kameyama et al., 2008).

2.2 | Study sites

Our study is based on long-term monitored specimens from two study regions located in two contrasting alpine regions of central Norway. To the east, the Vågå/Innlandet region (61°53′N; 9°15′E) is located within the continental climatic section (C1; Moen & Lillethun, 1999). With a total annual precipitation of approximately 300–500 mm in the valleys, this area experiences the highest aridity found in Norway (Kleiven, 1959). Mean annual ambient air temperature is −1.2°C (range: −29.2 to +16.7°C) (measured between 1991 and 2002, Löffler, 2003). Our second study region to the west, the Geiranger/Møre og Romsdal region (62°03′N; 7°15′E), is located within the slightly to markedly oceanic climatic section (O1–O2; Moen& Lillethun, 1999) of the inner fjords. It is characterized by humid conditions, with total annual precipitation of 1,500–2,000 mm in the valleys (Aune, 1993) and a mean annual ambient air temperature of 1.9°C (range: −23.2 to +17.2°C) (measured between 1991 and 2002, Löffler, 2003). Additionally, our own measurements within the studied regions (in the alpine parts) and within the study period indicated an annual liquid precipitation of 900 mm in the west and 375 mm in the east. The additional amount of snow and its water equivalent remains unknown, but snowdrift leads to an uneven distribution of the snowpack within the complex alpine topography (Löffler, 2007). The study sites within the regions were stratified-randomly chosen to cover the elevational gradient, following the framework of our long-term alpine ecosystem research project (LTAER; e.g. Frindte et al., 2019; Hein et al., 2014; Löffler et al., 2021; Löffler & Finch, 2005). They were placed to represent the different elevational bands at 100-m intervals from the tree line upwards, shifted by approximately 100 height-metres between the Western and Eastern study region to account for the depression of the elevational zonation towards the west. The tree line, defined as the upper elevational limit of the occurrence of subalpine birch trees (*Betula pubescens* ssp. *czerepanovii*), and, as such, the lower limit of the alpine belt (Dahl, 1986), is located at approximately 1,000 m a.s.l. in the Eastern study region and at approximately 750 m a.s.l. in the Western region. In accordance with the local micro-topography, we chose sites from four distinct micro-topographical positions at each of the elevational bands: (a) exposed ridge positions (R), (b) positions within local depressions (D), (c) south-facing slopes (SS) and (d) north-facing slopes (NS). For a detailed depiction of the study design see Figure S1. Because of the topographic preferences of the studied species, we measured *P. caerulea* at the slopes (SS and NS) only. Additionally, a small proportion of the measurements contained missing data, resulting in gaps in the dendrometer curves. This was attributed to technical errors, and we therefore discarded the affected specimens from the study. This resulted in a lack of data for *B. nana* within local depressions (D). All chosen specimens were monitored for five consecutive years, resulting in a total of 570 annual dendrometer curves. For the total number of sampled specimens at each position, see Figure 1.

2.3 | Data collection

To monitor stem diameter variations, we used high-precision dendrometers (type DRO; Ecomatik, Dachau/Germany) mounted on one major above-ground stem horizontal to the ground surface for each specimen, as close to the assumed root collar as possible (approximately 1–5 cm above the ground). As addressed by Bär et al. (2006 and 2007), this major stem is thought to represent the whole plant at least partly. We tried to account for this variation between stems of the same plant by sampling a high number of individual specimens. During the mounting process of the dendrometers, we removed the dead outer bark to place the sensor as close to the living tissue as possible, following a common practice for dendrometer measurements of trees (e.g. Grams et al., 2021; Oberhuber et al., 2020; Wang et al., 2020). This ensures that hygroscopic shrinkage and swelling of dead tissues from the outer bark does not influence the diameter measurements. The sensor used had a temperature coefficient of <0.2 μm/K. Measurements were taken at 1 min intervals and aggregated, averaging dendrometer data into time series of daily

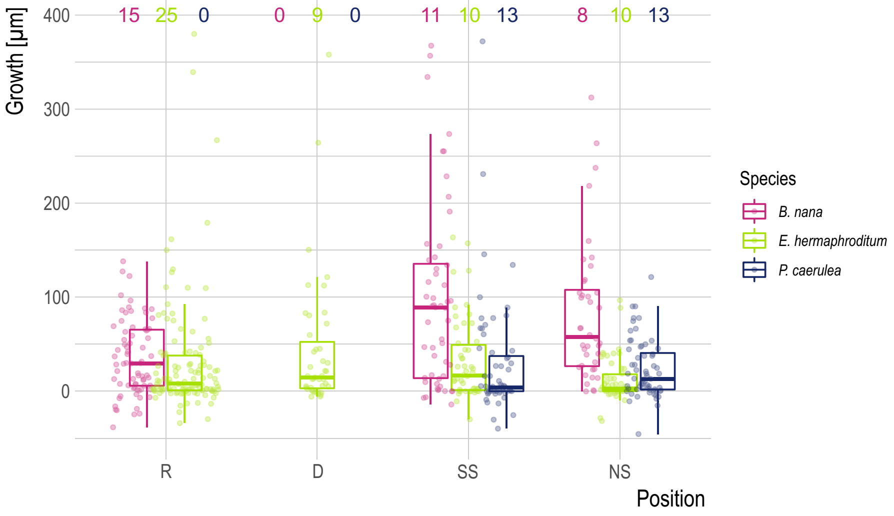

FIGURE 1 Summary of radial stem growth at the monitored topographical positions, showing the median and the 25th and 75th percentiles (box), as well as the smallest and largest value no further than 1.5*interquartile range from the hinge respectively (whiskers). Each value within the plot represents one annual value derived from stem diameter measurements (see Section 2). Numbers at the top show the number of specimens of each focal species, which were monitored at the respective position

mean values, using the R statistical software (R Core Team, 2020). When choosing microsites, we avoided positions near stones and small depressions, inside the radius of other larger shrub species, and near patches of wind erosion. At each site, we sampled one or more specimens of each species, if available, and took additional measures of microsite environmental parameters. These included soil temperatures (°C) at a depth of 15 cm below the ground surface (within the root zone; hereafter 'Trz') and air temperatures at 15 cm above the ground surface (within the shoot zone; hereafter 'Tsz'), measured at 1 min intervals and recorded as hourly means. For these recordings, we used ONSET's HOBO loggers (type H21-002) in combination with type S-TMB-002 temperature sensors (±0.2°C accuracy). For measurements of Tsz, the sensors were equipped with passively ventilated radiation shields. Based on this setup, we were able to accurately capture near-ground thermal conditions, which are often decoupled from the governing macro-climatic temperature signal (Körner, 2021; Körner & Hiltbrunner, 2018; Löffler et al., 2006). Additionally, we measured the volumetric soil water content (soil moisture, m^3 water/m^3 soil) 15 cm below the soil surface (hereafter SMrz) at all sites. The uncalibrated SMrz was measured at 1 min intervals and recorded as hourly means using ONSET's type S-SMD-M005 soil moisture sensors (±3% accuracy). Those measurements proved especially valuable in the final analysis, as they, apart from the intended assessment of soil moisture, allowed for the fine-scaled analysis of freezing and thawing conditions within the root zone as derived from the availability of liquid water. To complement these data, we additionally inferred snow cover estimates from daily temperature amplitude. We assumed that a daily Tsz amplitude of less than 5K indicated that a layer of snow restricted daily air temperature fluctuations at the measured height of 15 cm. The respective periods were therefore defined as snow covered. The threshold of 5K was carefully chosen in accordance with the data. All the collected data covered a period of five full calendar years from 1 January 2015, to 31 December 2019, with some additional data collected in 2014. Missing data did not occur at any of the chosen sites.

2.4 | Statistical analysis

All statistical analyses were conducted using R v. 4.0.3 (R Core Team, 2020). For all analyses, significance levels were set at $\alpha = 0.05$. The stem diameter curves produced from the continuous dendrometer measurements were split by calendar years and the resulting annual stem diameter curves were normalized through subtraction of the previous year's maximum to exclude year-related growth trends and to maximize the separation of growth-related expansion from water-related swelling and shrinking of the stem. This necessity arises because dendrometers are not measuring the absolute stem diameter, but rather changes in stem diameter relative to the start of the measurement cycle. Additionally, singular outliers, which might occur due to mechanical influence to the sensor, were removed, by defining cut-off ranges, using the interquartile range (IQR) and the 25th (Q1) and 75th (Q3) percentile ($Q1/Q3 \mp 1.5*IQR$; Figure 2). Finally, for each year, a set of complementary growth characteristics was derived from the raw data: (a) growth, defined as the amount of stem diameter increase within 1 year, compared to the previous year (maximum stem diameter − maximum stem diameter of the previous year), (b) increment, defined as the total stem diameter increase (maximum stem diameter − minimum stem diameter) and (c) (annual) stem diameter change, defined as the absolute stem diameter increase within the span of the year (stem diameter at the end of the year − stem diameter at the beginning of the year) (Figure 2; Figure S2). While annual growth describes growth-related stem diameter expansion, the two latter include potentially reversible stem diameter shrinking, which is commonly associated with hydrological processes (Zweifel, 2016; Zweifel et al., 2014). In this way, we differentiated between growth-induced stem expansion (growth), which is most likely visible in the anatomical structure of the plant and thus directly comparable to classic measurement methods of radial stem growth in shrubs, and additional processes causing radial stem change (e.g. temporary water deficits), which are uniquely captured by our dendrometer measurements. In addition, we derived (d) the maximum annual stem diameter (including the initial stem diameter at the start of the year) from the dendrometer curves.

To assess whether there are governing trends or patterns in variation between individually measured sites and plants, depending on elevation or topographical position, we first performed a principal component analysis (PCA), using the R package VEGAN (Oksanen et al., 2020). In this analysis we included growth characteristics (annual growth, annual increment and annual stem change), as defined above. PCAs were computed for each species separately. The results (Figure S3) revealed no clear governing patterns between elevational bands and between the two study sites. The clearest distinctions were visible between topographical positions. For this reason, we chose to focus on this parameter for most of the subsequent analysis.

To understand the influence of microsite environmental drivers on growth, we then calculated Pearson's correlation coefficients and determined the significance of the coefficient through 500 bootstrapped iterations using the R package WBOOT (Weiss, 2016). Correlation coefficients were calculated between annual growth and monthly, as well as seasonal, mean values for our environmental parameters Tsz, Trz and SMrz. To account for possibly time-lagged effects of the previous year's conditions, we included monthly mean values for the period June (of the previous year) to December (of the current year) into the correlation analyses, similar to the analysis of growth chronologies as derived from ring-width series (e.g. Bär et al., 2008). Data from each topographical position, and from each species, entered into the analysis separately.

In addition, we applied partial least squares regression (PLSR; Wold, 1975) with the aim to use variable selection methods to assess the relative importance of certain environmental parameters in promoting or hindering growth and to thus substantially expand on the results of the correlation analysis. Developed for multidisciplinary problems (Wold, 1980), PLSR has found application in ecological studies during the past decade (Carrascal et al., 2009; Frindte et al., 2019; Löffler & Pape, 2020), yet the approach described here is

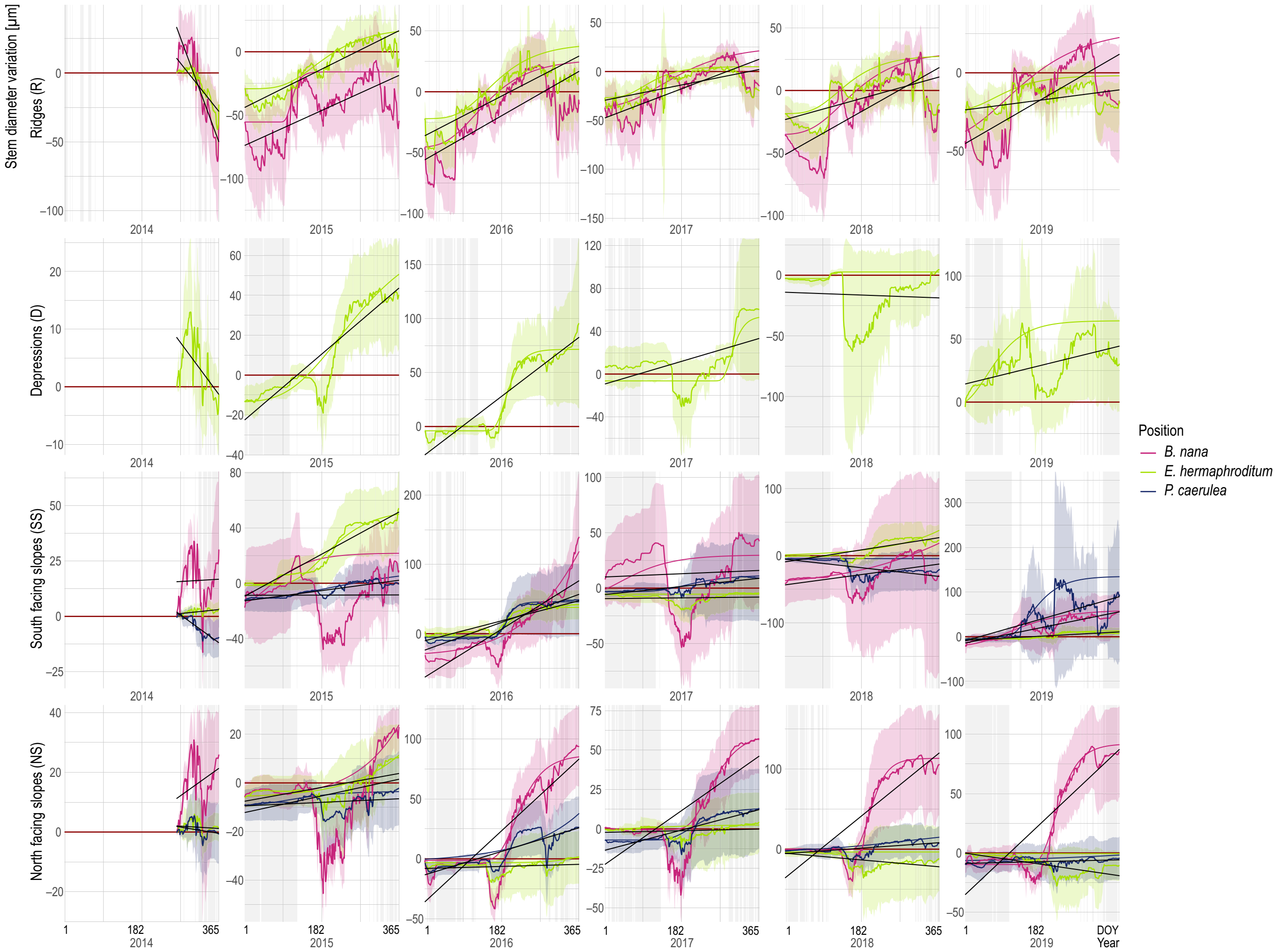

FIGURE 2 Annual stem diameter variations relative to previous years maximum or start of the measuring period (for 2014), as derived from dendrometer measurements and aggregated to daily mean values. Measurements of individual specimens were averaged for each focal species and topographical position. Black lines indicate linear trends. Additional lines show fitted sigmoid Gompertz models derived from the original data. Grey areas indicate snow cover, derived from the daily amplitude in air temperature measurements (see Section 2)

comparatively novel. Main advantages include that it works without distributional assumptions (Dijkstra, 1983; Vinzi, 2010; Wold, 1980) and deals efficiently with unreliability and heteroscedasticity issues (Frindte et al., 2019; Martens & Næs, 1989). Moreover, the method is not limited, if the number of predictors exceeds the number of observations, or if the predictors are highly correlated, which makes PLSR highly suitable for our data (Carrascal et al., 2009; Frindte et al., 2019; Geladi & Kowalski, 1986). Following the approach successfully applied by Löffler and Pape (2020) to determine species thermal niches, we aggregated our environmental data, rounding to 0.2°C for temperatures and 0.01 m^3/m^3 for soil moisture values. Subsequently, we counted and totalled the frequency of each value occurring within the time series. These calculations were performed for each meteorological season separately, resulting in sets of predictor variables, which were subsequently scaled and centred. Annual growth served as the associated response variable. For final single response model estimation, we used the SIMPLS algorithm (de Jong, 1993), implemented in the R package mdatools (Kucheryavskiy, 2020). The optimal number of components in the PLSR model was found using Wold's R criterion (Wold, 1978) and 10-fold cross-validation was used to assess the explained variance during model calibration and validation. From the numerous methods available to assess the relevance of each independent variable from the created models (reviewed by Mehmood et al., 2012), we chose the selectivity ratio (SR), based on assessments by Farrés et al. (2015) and Frindte et al. (2019). This parameter is defined as the ratio of explained to residual (unexplained) variance for each variable in the target projection vector. From the SR, we derived the explained variance (SR/abs(SR + 1)) for more contrastable results. In the results, the variables with highest SR represent the explanatory variables with the highest influence on growth (Rajalahti et al., 2009). We increased the interpretability of these results by multiplying the SR of each variable by the sign of its corresponding regression coefficient, making it easy to identify which variables were positively or negatively related to the dependent variable (Löffler & Pape, 2020; Rajalahti et al., 2009). Like the correlations, the analysis was conducted for each of the topographic positions and for each species separately.

Finally, we aimed to explore the variation in the stem diameter change patterns captured by the dendrometers, as well as the effects of environmental influences on this variation. We ran a set of linear mixed effects models, using the lmer function from the LME4 R package (Bates et al., 2015). This modelling approach has found wide application in ecological settings in recent years as it is an excellent tool to decompose the variability within grouped, complex data (Aller et al., 2019; Bolker et al., 2009; Firn et al., 2019; Henn et al., 2018). First, we fitted linear mixed effect models to the previously aggregated total annual growth values (dependent variable) and seasonally aggregated environmental parameters (independent variable), to further explore climate–growth relations. In contrast to the approaches described above, our complex study design can be implemented into this modelling approach by including species and topographical position as random effects, controlling variation in slope and intercept of the resulting models. In all created models, our response variables were log transformed. Models were created for each of the growth characteristics defined above, which entered as response variables. For total annual growth, years with negative values (net stem diameter shrinking) were defined as not growing and set to zero. After selecting these response variables, we grouped our data by a set of characteristics, that is, species, topographical position, year and site (including both elevation and study region). Furthermore, we included the initial stem diameter at the beginning of the year, rounded to the nearest decimal, as a grouping variable. By including these grouping factors as random effects into the models, we investigated the percentage of variance explained by each factor, which was derived from the models using the VarCorr function (Bates et al., 2015) in R. To represent the study design (Figure S1) within the model structure, we nested topographical position within the site parameter and species within position and site. The final models included no fixed effects and thus had the form Growth ~ (1 | site/position/species) + (1 | year) + (1 | initial stem diameter), as implemented into the lmer function of the LME4 R package (Bates et al., 2015). Aside from the full models, we created additional models for each species separately, removing the variable species from the random effects. Following this statistical exploration of spatial and temporal variability, we tested the role of microsite environmental variation within and between the grouping characteristics defined above and how this variation influenced annual growth. Therefore, we included seasonal means of measured environmental parameters (Tsz, Trz and SMrz) as fixed effects, creating one full model including all fixed and random effects and the response variable growth: Growth ~ environmental parameters + (environmental parameters | position) + (environmental parameters | site) + (environmental parameters | year) + (environmental parameters | species) + (1 | initial stem diameter), as implemented into the lmer function of the LME4 R package (Bates et al., 2015). From this model we then derived explained variance estimates (conditional, R_c^2, and marginal, R_m^2), as well as the partitioned variance, using the R package MUMIN (Barton, 2020; Nakagawa & Schielzeth, 2013). In that way, we quantified the percentage of variance in growth, which can be explained by environmental variation between sites, years and topographical position. More importantly, we quantified the proportion of variance in growth, which cannot be explained by those factors and can therefore probably be partly attributed to specimen-specific internal biology and/or other biotic/abiotic factors not accounted for by the study. All environmental data were standardized (scaled by means and standard deviations) prior to model fitting to make coefficients comparable (Grace & Bollen, 2005).

The full analysis thus consisted of four different statistical approaches to assess variation in growth-environment relations across species and positions. Combined, our results should provide a clear understanding of how the chosen three species are influenced by their respective local environment.

3 | RESULTS

3.1 | How do microsite environmental conditions vary within the study area?

Each of the four sampled topographical positions was characterized by distinct regimes of near-surface environmental conditions (Tsz, Trz and SMrz) with different degrees of variation between the positions (Figure 3; Figure S4). However, a number of subordinate trends in inter- and intra-annual environmental variation were present at all sites: Temperatures usually started rising in spring (April or May). Lowest mean temperatures were measured in 2017, highest in 2018, with shoot and root zone conditions following, expectedly, a similar regime throughout all years. The year 2015 stands out because of a comparatively long winter, with lasting low temperatures throughout the meteorological spring and soil moisture rising only gradually, indicating reoccurring freezing conditions. However, according to our calculations regarding snow cover, snowmelt did not occur unusually late in 2015. In contrast, the years 2019 and 2018 were characterized by relatively short, cold winters with an early rise in spring temperatures, followed by considerable spring cold snaps (as evident by drops in the SMrz regimes), indicating renewed soil freezing. The successive winters 2015/2016 and 2016/2017 were characterized by comparatively little snow cover at all positions.

In terms of variability between the positions (Figure S3), a number of microsite environmental variations were represented in our data, resulting from the complex topographical conditions given in the studied alpine region. Here, we found differences in snow cover caused by snowdrift and timing of snowmelt to be most crucial. Extremely low winter temperatures and severe ground freezing, with high exposure to global radiation and only periodic snow cover, resulting in a slightly earlier temperature rise in spring (Figure 3), characterized the exposed ridge positions (R). In contrast, the positions within depressions (D) experienced no ground freezing in winter due to an isolating and mostly continuous snow cover during these months, coupled with little exposure to global radiation and very wet conditions, resulting in SMrz measurements

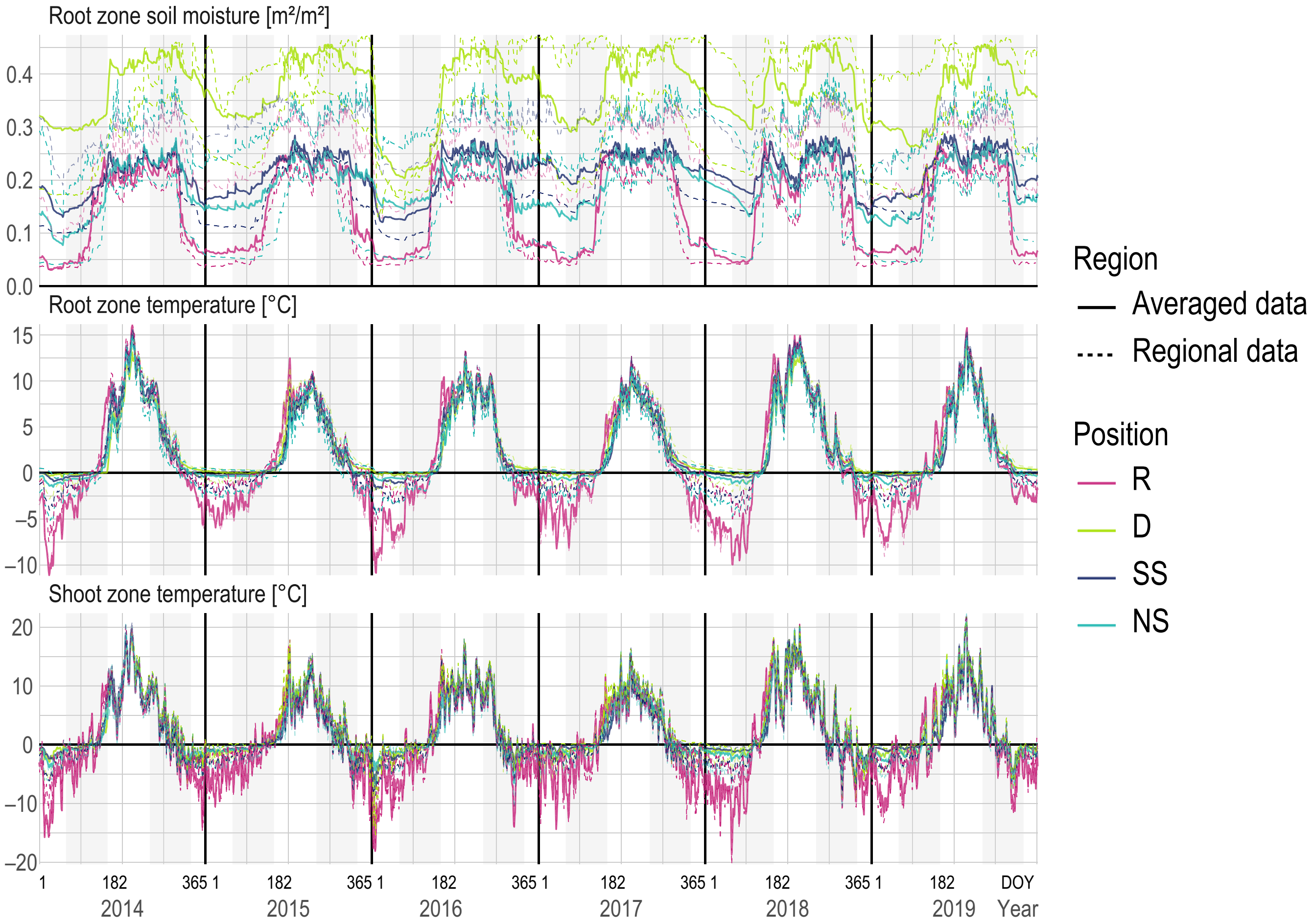

FIGURE 3 On-site environmental data. Shoot zone temperature (Tsz), root zone temperature (Trz) and root zone soil moisture (SMrz) regimes (daily means, derived from hourly measurements) averaged over all studied sites, aggregated by topographical position. Shaded areas indicate meteorological seasons

surpassing all other positions throughout the studied period. South- and north-facing slopes (SS and NS) showed very similar regimes. Here, snow protection leads to only moderate ground freezing in winter, whereas the slightly differentiated soil moisture regimes are most likely caused by differing exposure to global radiation, leading to differences in snowmelt timing (Figures 2 and 3). In addition to this variation between micro-topographical positions, soil moisture also varied between the two study regions, with markedly higher soil moisture values in the oceanic region in the west, compared to the continental region in the east. Here, it is worth noting that despite this high environmental variability, variation patterns between topographical positions were very similar in both regions (Figure 3).

3.2 | How do inter- and intra-annual growth patterns differ between species and along topographic gradients?

At each of the sampled topographical positions, stem diameter variability followed a distinct pattern of stem expansion and contraction (Figures 2 and 4). These patterns were surprisingly similar between species, even though total realized growth varied considerably, with *B. nana* on average surpassing the evergreen species at all positions, yet thriving especially at the slopes. In contrast, *E. hermaphroditum* showed the highest annual stem diameter increase within the depressions (D), and both evergreen species showed little annual growth at the north-facing slopes (NS), with an especially prominent contrast to the south-facing slopes (SS) for *E. hermaphroditum*, which was not visible in *P. caerulea* (Figure 1; Figure S5). Thus, interspecific variability in annual stem diameter expansion was highest at the slopes. Overall mean growth (148 µm, *SE* = 56) was highest in 2016 for *B. nana* at south-facing slopes and lowest (2.5 µm, *SE* = 1) in 2019 for *E. hermaphroditum* at the north-facing slopes.

The main growth phase usually started during the meteorological spring at the exposed ridge positions (R) and in early to late summer at all other positions. The ridge positions showed a distinct phase of radial stem contraction during winter, which was missing at most of the other positions and which can therefore be attributed to the unique winter conditions experienced at the mostly snow-free ridges (Figure 4). In contrast, some specimens at the slopes (SS and NS) and within the depressions (D), all of which are mostly snow covered throughout the winter months, showed additional winter stem expansion, mostly during the winter 2016/2017. This phenomenon

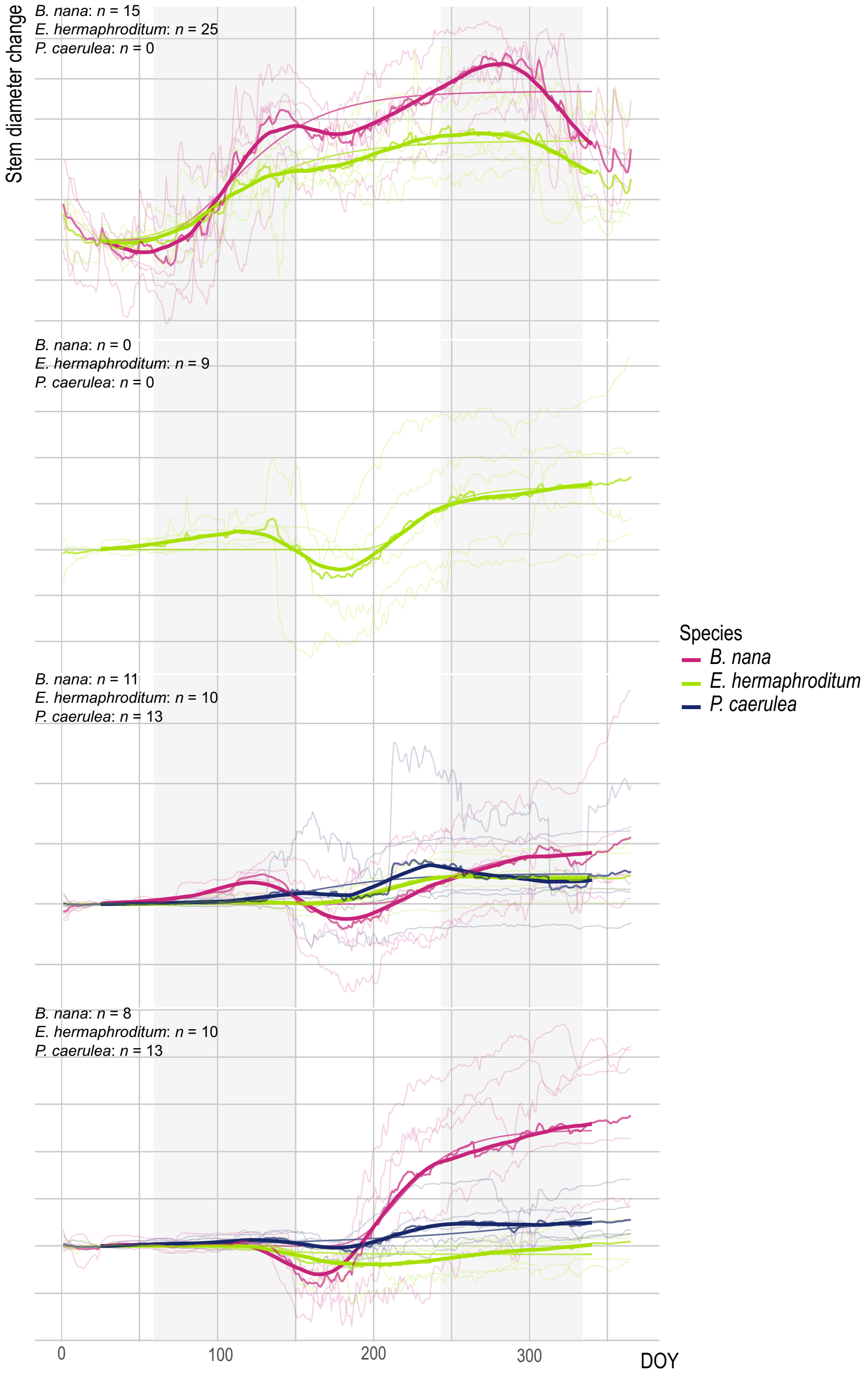

FIGURE 4 Schematic representation of annual stem diameter variation for each focal species at each topographical position. Curves were derived from dendrometer measurements. Thin lines represent the average across all available individual annual curves with the day of the year (DOY) on the *x*-axis, while thick lines represent smoothed versions of these curves. Numbers at the top show the number of included specimens. For each specimen, five annual curves were included. Additional lines show fitted sigmoid Gompertz models derived from the original data. Since the curves show schematic representations derived from the original data, there are no absolute values or units given (*y*-axis)

was present in *E. hermaphroditum* and *B. nana* and can most likely be attributed to hydrological processes within the stem and additional water uptake (Figure 2). Additionally, at these snow-covered positions, the winter was usually followed by a more or less pronounced phase of stem contraction in May or June, sometime after snowmelt and preceding the summer growth phase (Figure 4). Length and magnitude of this phase varied considerably between years and species, with *B. nana* usually showing a higher amplitude in stem contraction and expansion than the evergreen species (Figure 2).

Year-to-year variability in growth characteristics was high at all positions, obscuring a clear temporal growth trend over the studied period of 5 years (Figure S6). Because this inter-annual variability showed no synchrony across species, it can most likely be attributed to interspecific variation in response patterns to environmental conditions.

3.3 | How are growth patterns linked to site- and topography-specific environmental drivers?

Our analysis of growth response to microsite environmental conditions revealed complex patterns and highly differentiated response patterns, depending on species and topographical position. At the exposed ridge positions (R), for instance, *E. hermaphroditum* showed a strong response to temperatures, especially during winter, profiting from cold winters, associated with high global radiation (Figure 5; Figures S7–S9). For *B. nana*, on the other hand, warm summers and high soil moisture during winter, the latter indicating wet and snowy conditions, were most influential.

In the depression (D), our correlation analysis indicated a clear positive effect of soil moisture on *E. hermaphroditum* growth throughout the year, which was, however, not significantly reflected in PLSR analysis, indicating fine-scale complexity. The effect might be less pronounced in the PLSR analysis, because the depressions experience comparatively high levels of soil moisture at all times, thus showing a reduced range. In this context, it is worth noting that none of our analysis showed a negative effect of soil moisture at these positions, which is in strong contrast with the south-facing slopes (SS), where high soil moisture had negative impacts throughout the year, especially for *E. hermaphroditum* (Figure 5). Additionally, linear mixed effect models and correlation analyses revealed a negative effect of unusually high spring soil temperatures on total annual growth in the depressions, especially during May (Figures S9; Figure 5), while the PLSR analysis revealed a negative effect of subzero temperatures, associated with soil freezing, during spring. As such, when growing at positions within local depressions, *E. hermaphroditum* thrived during years of prolonged spring cold and associated snow cover (e.g. 2015, 2016), showing a shorter and less pronounced shrinking phase in early summer and an earlier growth start under these conditions (Figure 2). Because the depressions are usually frost protected by an isolating snow cover, this indicates that *E. hermaphroditum* might rely on this protection until well into the spring and responds to unexpected cold spells and soil freezing later in the year after an early temperature rise with contraction of the stem, as shown in 2018 (Figure 2).

A similar pattern existed at the slopes (SS and NS), where *E. hermaphroditum* followed the severe late frost spell in 2018 with prolonged stem shrinking at most of the monitored sites, possibly caused by cell damage (Figure 2). Furthermore, annual growth measured at the slopes showed the least pronounced relation to microsite environmental parameters, indicating that an interaction of multiple factors is influencing growth here. Still, for *E. hermaphroditum*, our

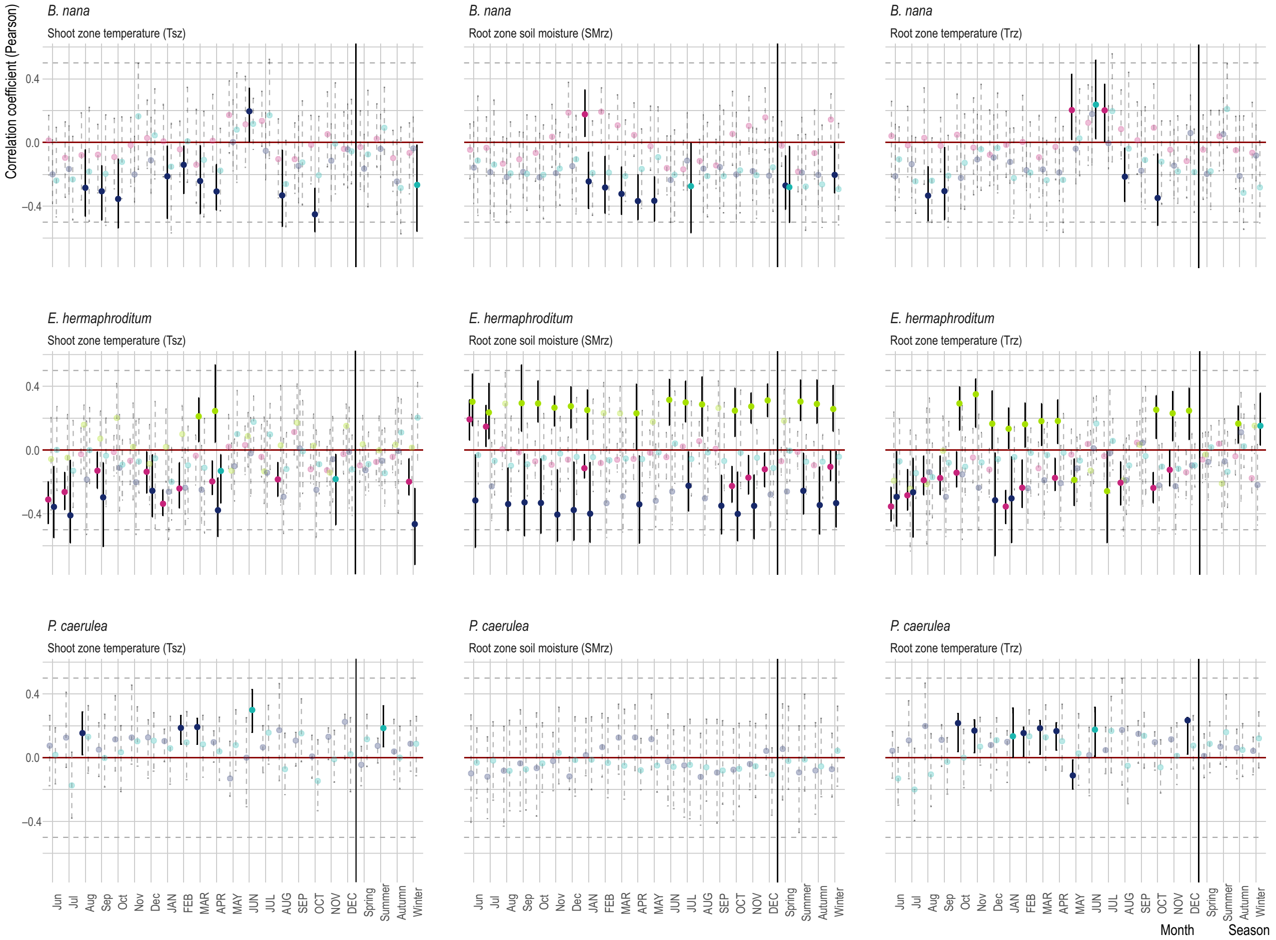

FIGURE 5 Pearson's correlation coefficient for annual growth derived from stem diameter measurements (see Section 2) and monthly, as well as seasonally, aggregated environmental parameters. Significance is indicated by non-transparency and lines show 95% confidence intervals, with dotted lines additionally indicating significance. Lowercase months on the *x*-axis correspond to previous year months

analysis revealed a stronger (and mostly negative) impact of soil moisture in comparison to temperatures, which might be attributed to the complex patterns of snow coverage present at these positions (Figure 5).

Across all topographical positions, *B. nana* showed more positive relations to temperatures throughout the year, compared to the evergreen species (Figure S9). Optimum temperatures revealed by the PLSR analysis were in general higher for *B. nana* as well, especially during summer (Figures S8 and S9). In general, all species were driven by soil moisture availability, including a high influence of winter and spring freezing conditions.

3.4 | How is growth variance between individual specimens affected?

Linear mixed effect models revealed high variation of growth between sites, species, positions and years, as well as high variability in growth response to microsite environmental conditions. This variation was to some extend reflected in the PCAs (Figure S3), which showed distinctions between the topographical positions, yet no clear patterns in growth variation related to elevation or study region. Through linear mixed effects modelling, we were able to attribute 94% of variance in total annual growth to temporal and spatial environmental variation and initial stem diameter (Figure 6b), leaving 6% of growth variance unexplained. We identified soil moisture, related to seasonal soil freezing, as the strongest contributor to this variation, and, accordingly, winter and spring conditions most influential. Because of the highly complex topography found in the studied regions, these conditions varied considerably between positions, explaining most of the observed differences in annual growth patterns. Inter-annual temporal variation in climate and environmental variation associated with the elevational gradient, as well as the overall regional climate signal had considerably less explanatory power (Figure 6). Directly comparing the sources of variance in growth parameters (Figure 6a) confirmed this result. Here, it is worth noting that the initial stem diameter at the start of the study period played a significant role for overall radial growth and that variance in maximum stem diameter, which is in turn strongly linked to this initial stem diameter, was highly dependent on topographical position, elevation and region and thus almost completely explainable by these parameters. Furthermore, the percentage of variance in growth parameters explained by variation between species was comparatively small (Figure 6a).

Collectively, our results indicate that radial stem growth and its response to local microsite conditions are closely linked to local topography, which is the strongest contributor to microsite environmental heterogeneity.

4 | DISCUSSION

Our results clearly show that patterns of stem change in shrubs are closely linked to microsite environmental conditions, with this link evidently present across temporal scales (i.e. intra- and inter-annually). In trees, such patterns of stem diameter change have been interpreted as the result of irreversible stem increment, associated with cambial activity (Rossi et al., 2008; Steppe et al., 2015; Zweifel, 2016), as well as reversible expansion or shrinking, attributed to underlying changes in water relations (Lindfors et al., 2019). As such, these processes have been strongly linked to the overall physiology of the individual plant, which results both from physiological constraints and from adaptive strategies (Duputié et al., 2015; Zweifel, 2016). Our results can therefore be interpreted as an indication of physiological adjustments of the individual plants, controlling shrub growth at the monitored sites (Martin et al., 2017). Further studies using experimental or modelling approaches to directly target these ecophysiological adjustments might be of help in further defining the underlying processes of climate–growth relationships.

We found the observed patterns of stem change strongly variable, depending on species, location and associated microsite environmental conditions. The main factor contributing to this variability was local topography, with species playing a surprisingly small role in explaining variation in growth patterns, indicating that multiple species might develop similar growth strategies in response to site-specific local environmental conditions. In general, we found a high variability of overall radial growth, which might be a result of physiological plasticity, or a remodelling of the plant's physiology to meet local environmental conditions (Callaway et al., 2003; Seebacher et al., 2015). To what extend genetic structure and varying genotypes play a role here, requires further studies (Chevin et al., 2010; Hoffmann & Sgrò, 2011). However, given the wide genetic variation found for example in *E. hermaphroditum* across three populations in northern Sweden (Szmidt et al., 2002), it can be assumed that both genotypic adaption and phenotypic plasticity play a major role in contributing to the observed intraspecific variation. In general, our results emphasize the importance of topographically driven heterogeneity in environmental conditions for understanding and predicting vegetation shifts, including distribution and redistribution of species in response to climate change, which has been recognized in recent years (Graae et al., 2018; Körner, 2016; Ropars et al., 2015; Young et al., 2016).

Furthermore, our results indicate a high complexity in temperature–growth relationships. All three studied species showed high variation across seasons and topographical positions, with especially *E. hermaphroditum* exhibiting negative responses at specific positions. Consequently, there was no clear relation between high temperatures and growth in our data, contrasting the prominent assumption of temperatures being the key driver of plant life in arctic and alpine environments (Graae et al., 2018; Körner, 2021; Raunkiær, 2015). Accordingly, the increase in shrub growth currently observed in these regions is commonly linked to a rise in temperatures (e.g. Bär et al., 2008; Hollesen et al., 2015; Liang & Eckstein, 2009). Conversely, our results highlight the importance of topography-controlled soil moisture, snow conditions and associated freeze–thaw cycles (Dobbert et al., 2021).

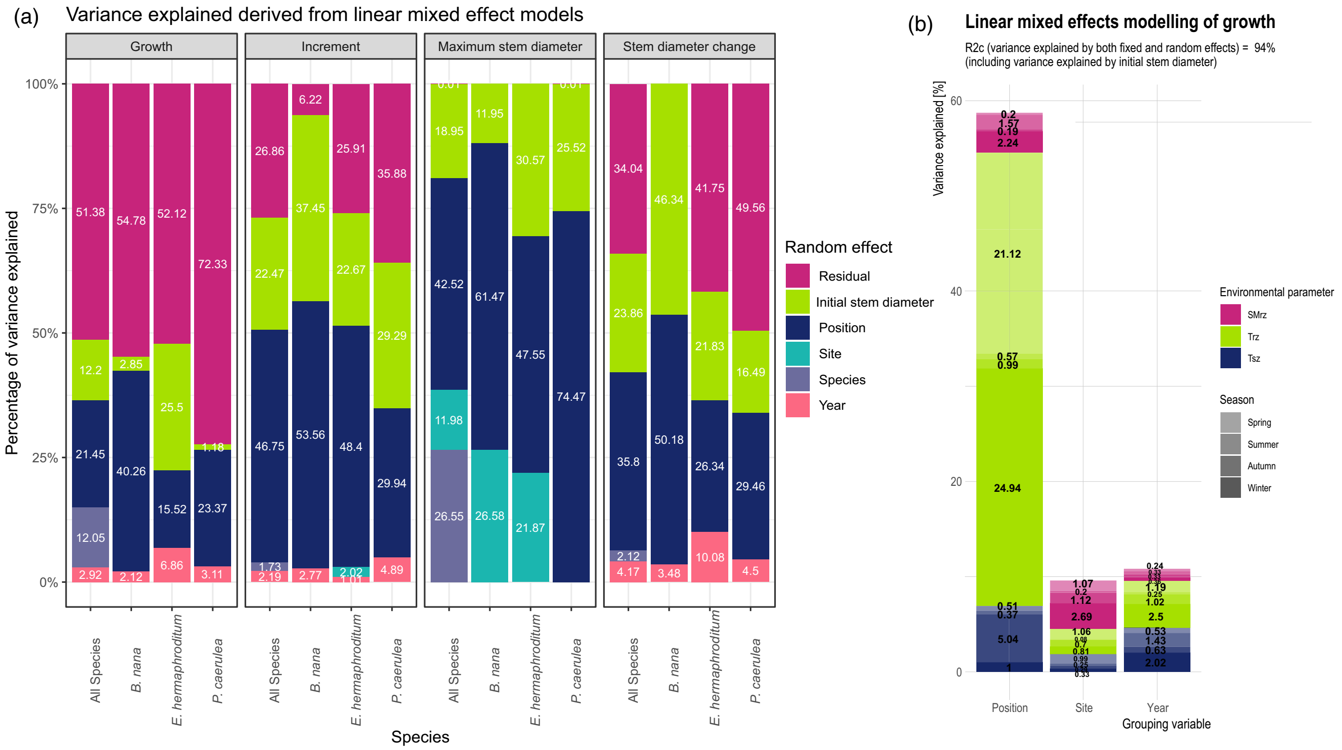

FIGURE 6 Partitioned variance in growth parameters explained by variation in spatial and temporal grouping variables (a). For each growth parameter (growth, stem increment, maximum stem diameter and stem diameter change) four models were fitted, one including all data, and one for each focal species. The models included no fixed effects and thus had the form Growth ~ (1 | site/position/species) + (1 | year) + (1 | initial stem diameter), as implemented into the lmer function of the LME4 R package (Bates et al., 2015). (b) Includes micro-environmental parameters and shows variance in total annual growth explained by variation in seasonally aggregated environmental conditions between topographical position, site (including region and elevation) and year. All results for (b) are derived from a singular model of the form Growth ~ environmental parameters + (environmental parameters | position) + (environmental parameters | site) + (environmental parameters | year) + (environmental parameters | species) + (1 | initial stem diameter), as implemented into the lmer function of the LME4 R package (Bates et al., 2015). This model is thus able to explain variance in total annual growth to a large extend

At most monitored positions, freezing after snowmelt, caused by spring cold spells, resulted in stem contraction, reduced growth or stem shrinkage during the rest of the growing season. In some cases, stem shrinkage even lasted into the following year, indicating cambial cell damage (Choler, 2018; Weijers et al., 2018). This proved especially dangerous for our evergreen species on the north-facing slopes, where the individual plants are highly adapted to the protective snow cover and are usually able to start growth activity directly after snowmelt, as soon as liquid water becomes available in the root zone (Bråthen et al., 2018). Unusually discontinuous snow cover and early snowmelt during this crucial phase might have left our specimens vulnerable to spring cold spells and many seemed unable to recover from such conditions during 2018 and consequently showed less overall growth during the following growing season. At positions where protective snow cover is usually present, a reduced snow cover during the winter months (clearly expressed during the winter 2016/2017) resulted in rapid stem expansion and reduced growth during the following years, possibly attributed to freezing processes and cell damage. Through isolating effects, mitigating the influence of extreme temperatures, as well as shielding from global radiation, snow cover is altering the thermal conditions at the micro-scale. Predicted changes in snow conditions (AMAP, 2017; Bjerke et al., 2017; Xu et al., 2013) are therefore likely to significantly alter species composition across all topographical positions. However, current studies aiming to predict these changes have found them highly complex and spatial variable (AMAP, 2017; Niittynen et al., 2018; Rizzi et al., 2018). Our data suggest that snow protected the plant from negative effects of soil freezing and extreme temperatures (Blok et al., 2015; González et al., 2019; Körner, 2012). Consequently, a reduction in isolating snow cover duration (Callaghan et al., 2011), for instance, might mitigate the effects of winter warming and a prolonged growing season for deciduous species like *B. nana* and increase the risk of growth-inhibiting spring cold spells and soil freezing for *E. hermaphroditum* at positions where the species is currently adapted to frost protection. Here, an increase in frequency of winter warming events and associated snowmelt (Bjerke et al., 2017) would expose the plants to unfamiliar and potentially fatal freeze-and-thaw stress, forcing the individual plant to adopt coping strategies.

We found indications for such coping strategies at the ridge sites, for both *B. nana* and *E. hermaphroditum*, with *E. hermaphroditum* showing a positive growth response to cold winter conditions, possibly using the associated high solar radiation input for additional photosynthetic activity (Bråthen et al., 2018; Löffler & Pape, 2020). At the same time, *P. caerulea* was limited to those positions where snow cover provides protection from extreme temperatures until well into spring, when the growth processes begin. For both *E. hermaphroditum* and *B. nana*, our measurements revealed a distinct phase of stem contraction at the ridge positions, presumably an active response mechanism protecting the plant from frost damage by reducing cell water content to avoid frost-induced cavitations (Fonti et al., 2010). Such dehydration processes, alongside ice nucleation and ice forming in the apoplast causing additional dehydration stress, have shown to lead to xylem diameter shrinkage in other woody plants (Améglio et al., 2001; Charra-Vaskou et al., 2016; Lindfors et al., 2019; Lintunen et al., 2016). Both *B. nana* and *E. hermaphroditum* are generally considered frost-hardy species (González et al., 2019; Hollesen et al., 2015). They are able to withstand extreme winter conditions with prolonged soil freezing at the exposed ridges. As such, our findings suggest that the ability to adopt coping strategies in response to extreme environmental conditions is highly species dependent. For instance, *P. caerulea* indicated comparatively low adaptive or maladaptive plasticity in response to frost. This might leave the species vulnerable to predicted future climate changes.

In contrast, our results suggest that *B. nana* and *E. hermaphroditum* have developed adaptive growth strategies to varying degrees, which are in accordance with the microsite environmental conditions at their respective topographical positions and strongly related to the snow regime. Our sampled *E. hermaphroditum* specimens were able to thrive at both of the most extremes of the sampled topographical positions (ridges and depressions), indicating a high plasticity and capacity to adapt in diverse environments. However, at the same time, *E. hermaphroditum* showed high sensitivity to spring cold spells at the north-facing slopes and no positive response to warming conditions. *B. nana*, on the other hand, was similarly adapted to local microsite conditions at the ridges, but, at the same time, able to profit from rising temperatures and to thrive at all monitored positions simultaneously. Such an acclimatization has been interpreted as an indicator for the species' capacity to tune their physiological characteristics to changing conditions, which in turn is linked to their ability to avoid migration or extinction under climate change (Matesanz et al., 2010; Nicotra et al., 2010; Valladares et al., 2014). We here support the assumption that the individual plant's physiology can vary considerably within populations, in response to the local environment (Banta et al., 2012; Graae et al., 2018; Leimu & Fischer, 2008; Savolainen et al., 2007) and further highlight the importance of integrating physiological plasticity into our understanding of species distribution and niche shifts (Valladares et al., 2014). Following this mechanistic understanding for our three focal species, we suggest that *P. caerulea* is likely to show the least persistence in a changing environment, as the species currently inhabits a comparatively narrow niche (Graae et al., 2018; Wasof et al., 2013), predominantly caused by limited adaptive thermal plasticity. Both *E. hermaphroditum* and *B. nana* are likely to show higher resilience to changing conditions than *P. caerulea*, based on their more pronounced plasticity towards thermal conditions. At an interspecific level, we argue that deciduous species, like *B. nana*, are most likely to profit from the predicted environmental changes, thus further contributing to the ongoing greening trend. However, on a broader scale, other factors might additionally affect species composition. For example, both our studied regions are not majorly affected by reindeer grazing, whereas grazing was generally shown to be a major influencing factor on shrub growth in other areas, with highly species-specific effects (Grellmann, 2002; Pape & Löffler, 2016, 2017; Weijers & Löffler, 2020). Furthermore, our study illustrates how growth trends are usually not uniform in space and time, and generalization across sites consequently might result in a too simplistic view of future vegetation changes in the highly relevant ecosystems of the tundra regions.

5 | CONCLUSIONS

Overall, our findings demonstrate that species in heterogeneous environments adapt locally by adjusting their growth strategies to fine-scale microsite conditions, in accordance with their physiological plasticity. This allows them to potentially occupy wide ecological niches and is closely linked to the adaptive capacity of the species as a whole. Physiological plasticity can, thus, be directly linked to a species ability to cope with potentially rapid climate change (e.g. Pérez-Ramos et al., 2019; Seebacher et al., 2015). However, this plasticity varies a great deal between species and we found no clear link to leaf habit here (e.g. Funk et al., 2017; Lavorel & Garnier, 2002). On an intraspecific level, our results support principal findings by Pfennigwerth et al. (2017), suggesting that multiple populations and individuals within a species may not exhibit a single, universal response to climatic variation. While past studies have emphasized the role of the elevational gradient in this context (Henn et al., 2018; Pfennigwerth et al., 2017), our results conversely show no clear evidence of a strong connection between elevation or larger-scale climatic region and radial growth (Figure S3). Instead, we identified environmental variation associated with micro-topography as the main driver of the variability in response patterns. Thus, our findings highlight fine-scale spatial complexity as a main indicator for a species' adaptive capacity, which is, in turn, strongly linked to local topography. Therefore, intraspecific variability in physiological characteristics has the potential to yield highly relevant information on future niche shifts, and might even be used to predict changes in a species' geographical range in the face of environmental change. Regarding the broad-scale vegetational changes observed across the arctic and alpine regions, our findings highlight the fine-scale complexity of these developments, and elevate the importance of locally differentiated microsite conditions and species-specific response patterns in determining future community development. We thus stress the importance of a fine-scale perspective in arctic and alpine tundra ecosystem research.

ACKNOWLEDGEMENTS

The authors thank the associate editor and anonymous reviewers for their constructive suggestions, which helped to improve the manuscript, and Niklas Beckers, Elise Dierking, Nils Hein, Stef Weijers and Dirk Wundram for collaboration within our LTAER project, Ole Øvsteng and Anders Svare for hospitality, and both the landowners and Norwegian authorities (Vågå and Stranda municipalities) for overall support. Parts of this study were supported by the Deutsche Forschungsgemeinschaft (DFG) (grants LO 830/16-1, LO 830/32-1).

CONFLICT OF INTEREST

Svenja Dobbert, Roland Pape and Jörg Löffler declare that they have no conflict of interest.

AUTHORS' CONTRIBUTIONS

J.L. had the idea, designed the research platform, conducted the fieldwork and together with R.P. ran the long-term project; S.D. analysed the data, led the writing of the manuscript and arranged the figures, with contributions from R.P. and J.L.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13784.

DATA AVAILABILITY STATEMENT

All underlying data pertinent to the results were recently published in 'ERDKUNDE---Archive for Scientific Geography' (https://www.erdkunde.uni-bonn.de) under the following https://doi.org/10.3112/erdkunde.2021.dp.01.

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How to cite this article: Dobbert, S., Pape, R., & Löffler, J. (2021). How does spatial heterogeneity affect inter- and intraspecific growth patterns in tundra shrubs? *Journal of Ecology*, 109, 4115–4131. https://doi.org/10.1111/1365-2745.13784