2022 ERDKUNDE Vol. 76 · No. 3 · 199–226

ON GROWTH PATTERNS AND MECHANISMS IN ARCTIC-ALPINE SHRUBS

Svenja Dobbert, Roland Pape and Jörg Löffler

With 10 figures, 1 table and 1 supplement
Received 19 July 2022 · Accepted 12 October 2022

Summary: 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 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. We started our analysis 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. The results 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. It 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 environmental 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.

Keywords: Arctic-alpine vegetation change, dendrometer, growth physiology, climate-growth relations, Norway

https://doi.org/10.3112/erdkunde.2022.03.04 ISSN 0014-0015 (Print) · ISSN 2702-5985 (Online)

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.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. 2021), 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. Over the past decades this led 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). 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 on the terrestrial impact of climate change (Forbes et al. 2010, Myers-Smith et al. 2011, Fraser et al. 2014, Carlson et al. 2016, Bjorkman & Gallois 2020, Collins et al. 2021, IPCC 2021). Observed and predicted vegetational shifts of this scale are of high importance to the carbon balance of ecosystems (Joos et al. 2001, Mishra & Riley 2012, Nauta et al. 2014, Alday et al. 2020), putting a large carbon pool at risk by promoting carbon release from permafrost thawing (Schuur et al. 2013, Schuur et al. 2015). At the same time, these shifts 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 & 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). While some areas appear remarkably stable in the face of rapidly warming conditions (Callaghan et al. 2021), others even experience a “browning” of vegetation (Bhatt et al. 2013, Phoenix & Bjerke 2016, Lara et al. 2018, Myers-Smith et al. 2020). This reversed trend may be 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, a 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 on the growth of 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 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 are mainly controlled by near-surface climatic conditions. Micro-topography has a strong influence here, modifying the general climate conditions (Löffler 2003, Bär et al. 2007, Körner 2012). Therefore, other effects might play an additional role in promoting or impeding shrub growth. These include 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 (Hollesen et al. 2015, Weijers et al. 2018a, Francon et al. 2020a). 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).

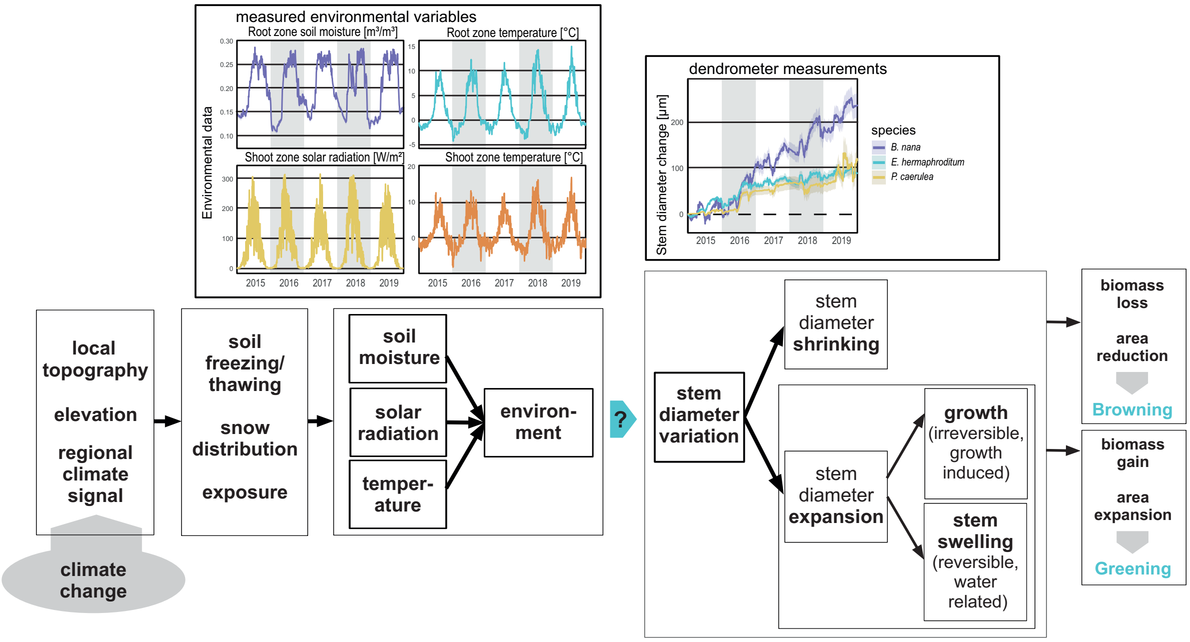

Fig. 1: Stem diameter change can be interpreted as an indicator for shrub growth and consequent shrubification, resulting in biomass gain and greening of the affected areas across tundra ecosystems. Thus, we here explore the important link between on-site environmental conditions and stem diameter measurements 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.

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. This includes 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. 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. 2022a). 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 study we were thus able to tackle the following research questions:

- How and to what extent are fine-scale physiological mechanisms of common shrub species controlled by the specific site conditions?
- How do these mechanisms and environmental controls vary on an inter-species level?
- How and to what extent do individual specimens optimize radial growth processes to maximize growth success at contrasting sites in arctic-alpine environemts?

- How is micro-site environmental change potentially affecting fine-scale physiological mechanisms and driving the observed large-scale vegetational shifts?

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). Within our study areas in Central Norway shrubs are close to reaching their elevational limit. For this study, 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*) (Fig. 2, Tab. 1). 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 & Tallis 1973, Bret-Harte et al. 2001, Coker & 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, in respect to their large spatial occurrence, 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).

P. caerulea

E. hermaphroditum

B. nana

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

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 & Junttila 1986, de Groot et al. 1997, Ögren 2001, Bär et al. 2007). However, both species prefer moderate site 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 & Coker 1973, Kameyama et al. 2008). *B. nana* commonly

Tab. 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	evergreen	circumpolar (Hultén 1968)

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 (Bret-Harte et al. 2001, Bär et al. 2007).

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 an alpineclimate 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 & Lillethun 1999). In contrast to the study region to the west, it is characterized

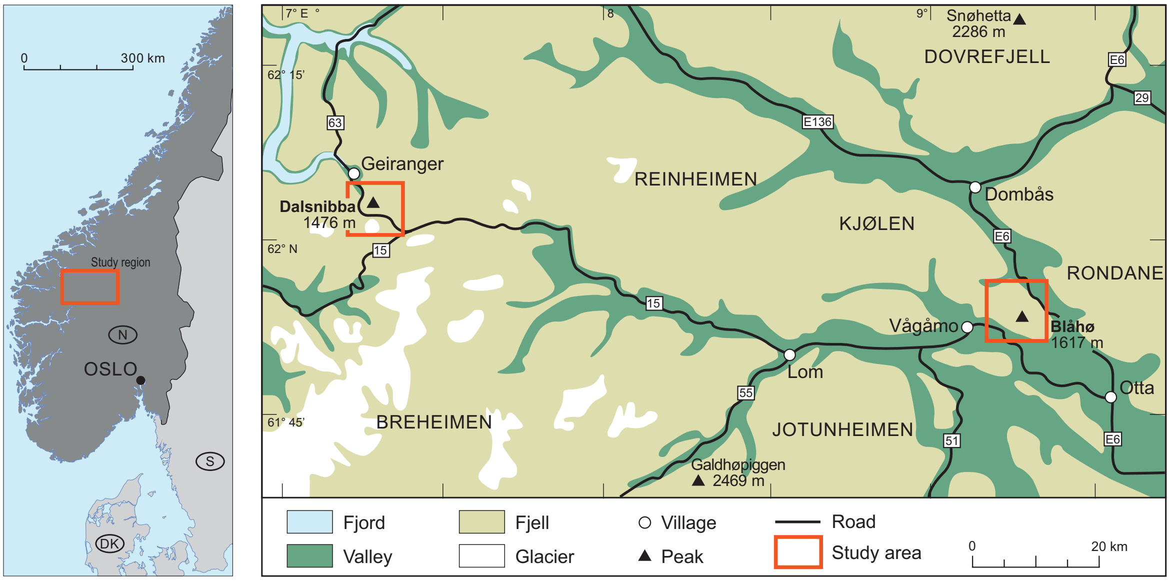

Fig. 3: Study areas in Central Norway with the location Geiranger/Møre og Romsdal region in the west and Vågå/Innlandet region in the east, marked with red squares, as well as their location in Norway (modified after Löffler et al. 2006).

by dry, semi-arid 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 a highly complex topography typical for alpine environments, where scales of a few tens of metres can give rise to high microclimatic variation (Scherrer & Körner 2011, Graae et al. 2017, Körner 2021) Snowdrift is leading to an uneven distribution of the snowpack (Wundram & Löffler 2008), influencing the local species composition (Jonasson 1981, Odland & Munkejord 2008) (Fig. 4).

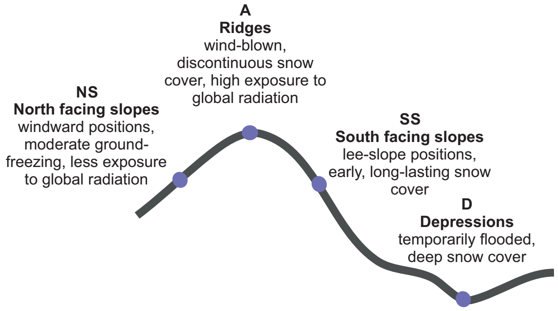

Fig. 4: Micro-topographic gradient and studied topographical positions

Consequently, the on-site environmental conditions monitored for this study vary considerably throughout the year, depending on topographical position: 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 are 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. 5). At the lower study sites (low alpine belt), the vegetation is dominated by shrub and heather communities. 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.

2.3 Study design and data collection

This study was designed to represent the full complexity of arctic-alpine shrub communities from the treeline to the highest local peak. Individual specimens were monitored along a regional climate gradient (oceanic-continental), the alpine elevation gradient, and along the micro-topographic gradient (Fig. 5). The result was a five-year dataset containing continuous, hourly measurements of shrub stem diameter variation and on-site environmental conditions. These measurements were taken from 2015/01/01 till 2019/12/31, with some additional data from 2014 and 2020. Our dataset enables for numerous opportunities for exploring climate-growth relations across scales within these highly relevant ecosystems (Fig. 6). Among other statistical methods, multi-scale modelling of complex patterns of stem diameter change from microsite environmental conditions enabled us to shed light on the physiological mechanisms behind radial stem growth.

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 & Bethel 1990, Duchesne et al. 2012, Ježík et al. 2016, Van der Maaten et al. 2018, Smiljanić & Wilmking 2018, Cruz-García et al. 2019). 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 & Bethel 1990, Duchesne et al. 2012, Ježík et al. 2016, Van der Maaten et al. 2018, Smiljanić & 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 & 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

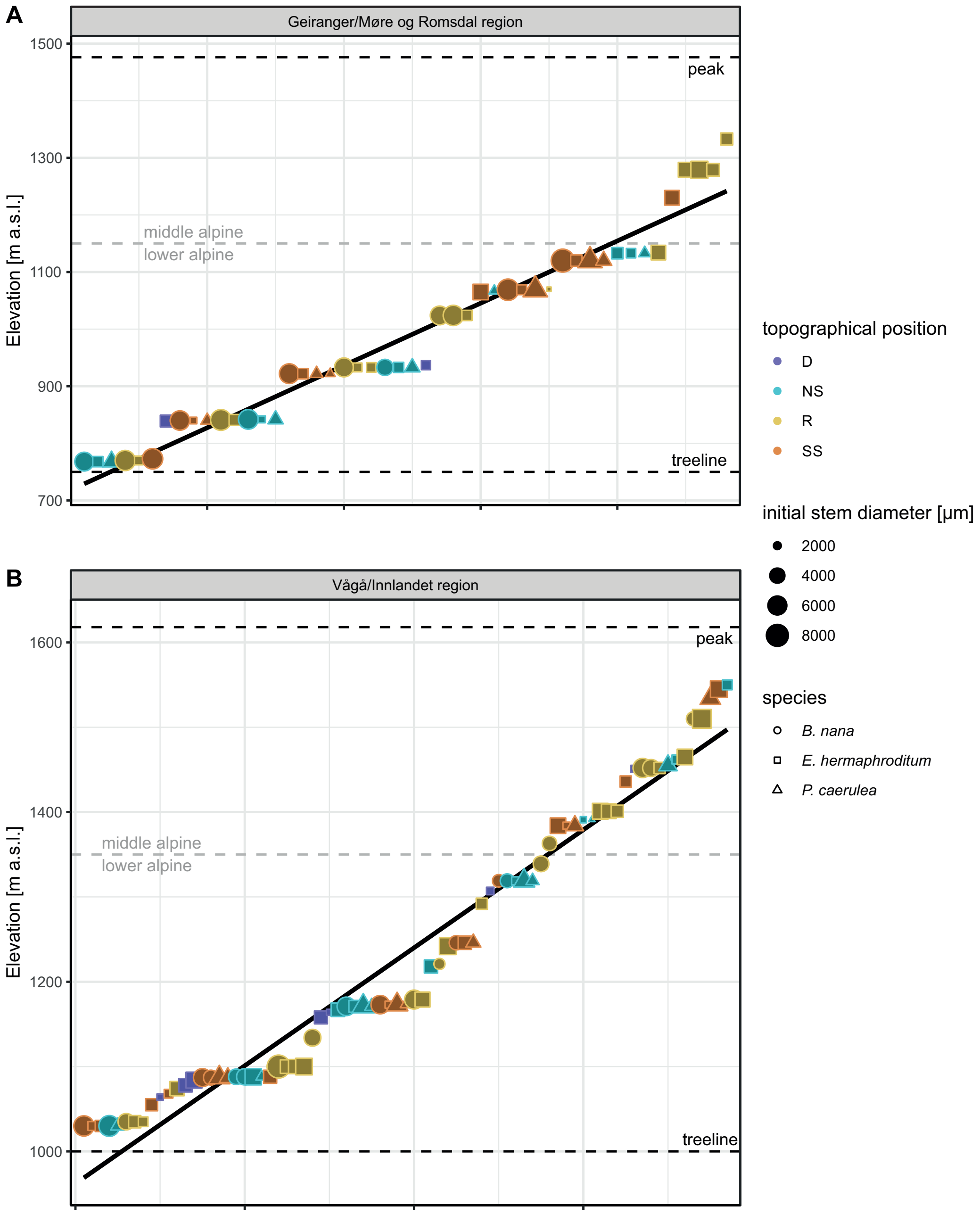

Fig. 5: Location of studied specimens along the elevational gradient in the Geiranger/Møre og Romsdal region (A) and the Vågå/Innlandet region (B). If possible, at each elevational band a broad variation of microtopographic positions and existent species was sampled. The size of the data points gives 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.

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 & 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, LÖFFLER et al. 2022).

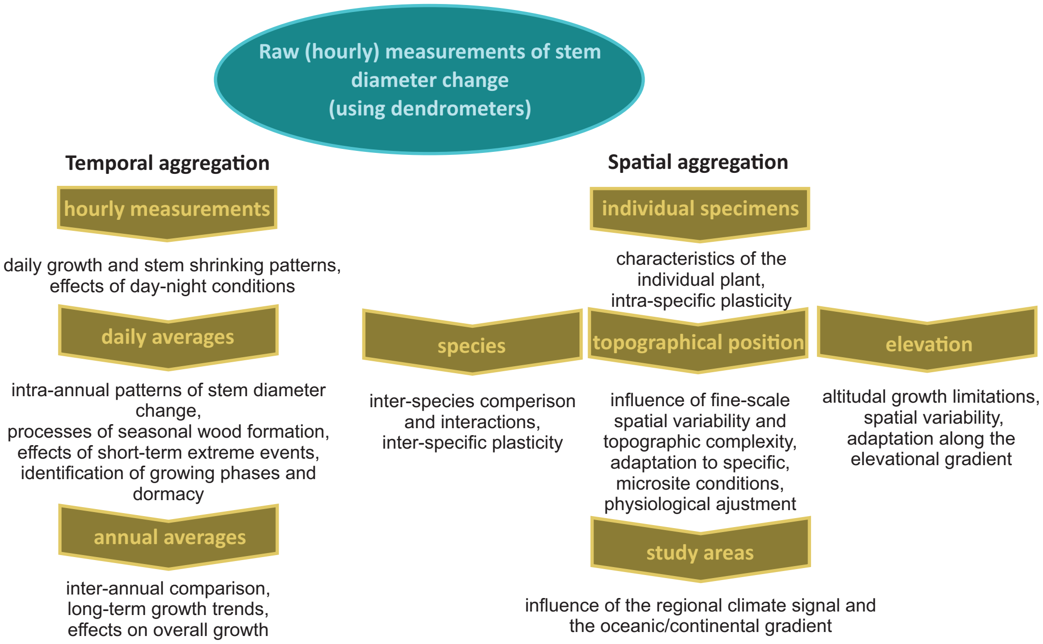

Fig. 6: Temporal and spatial aggregation of the measured data and the information potentially derived from each grouping step.

In this study, dendrometer measurements were taken using high-precision point dendrometers (type DRO; Ecomatik, Dachau/Germany), with a temperature coefficient of $<0.2\,\mu m\,K^{-1}$. These dendrometers were carefully mounted on one major aboveground 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 we avoided positions near exposed stones and small depressions which are common at most sites within the heterogenous alpine landscape. Additionally, positions inside the radius of other larger shrub species, and near patches of wind erosion were avoided. This was necessary to ensure accurate measurements representing the typical growing conditions found at each site.

With this monitoring design two main problems arose and were tried to address 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 already assessed 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 pool for further analyses. However, the intra-plant variability of secondary growth processes provides a multitude of opportunities for future research and might be specifically addressed through additional wood anatomical analyses. 2) Dendrometer measurements on trees are influenced by changing bark water content causing hygroscopic shrinkage and swelling of dead tissues and consequent uncertainties in stem diameter measurements (Zweifel & Häsler 2000, Gall et al. 2002, Ilek et al. 2016). 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 point 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. These time series provide important information on cambial activity, including cell formation and cell enlargement. Dendrometer measurements thus present an alternative to time-consuming traditional dendroecological methods (Deslauriers et al. 2007, Drew & Downes 2009, Miller et al. 2022). At the same time, the raw measurements provided by dendrometers contain information on stem dynamics 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 a mechanistical sound interpretation of radial stem variations. In trees, this issue has been addressed in recent years and two main approaches have emerged (Zweifel & 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. It 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. 7). 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 often not considered, making this approach mainly useful for regions with a longer growing season and no pronounced winter shrinkage (Van der Maaten et al. 2018, Liu et al. 2019). Using sigmoid models to identify intra-annual growth dynamic in shrubs proved to some extend successful for our focal species (Dobbert et al. 2022a). 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. 7). 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 (Suppl. I: Fig. S1a, S2a, S3a, Dobbert et al. 2022b).

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 proposed by Zweifel (2016) is based on the assumption of zero growth during periods of stem shrinkage. It thus provides 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

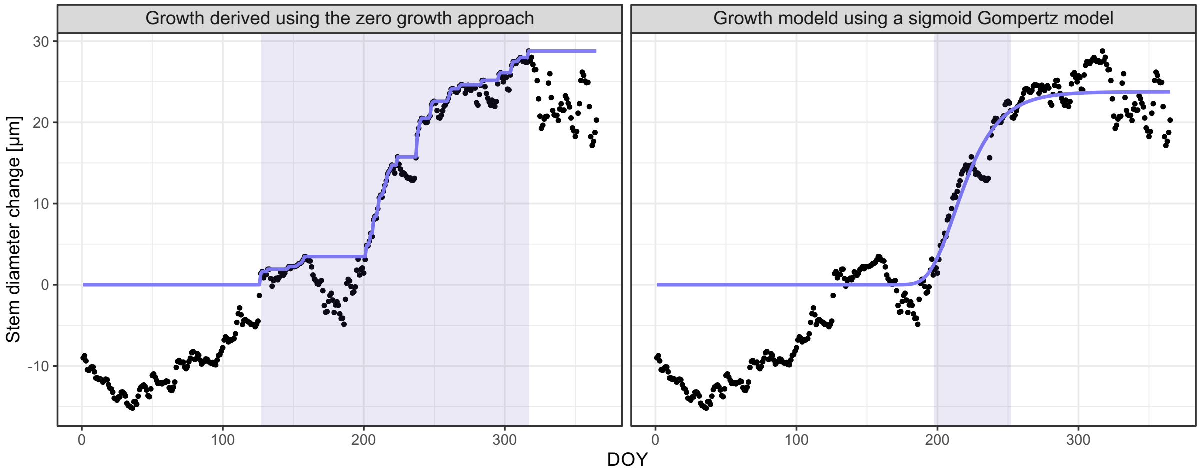

Fig. 7: Approaches to derive timing and magnitude of annual radial stem growth from raw measurements of stem diameter change of *E. hermaphroditum* in 2015. Shaded areas show the respective derived growing season. The threshold for the growing season from the Gompertz-model was defined as 5% and 95% of the total annual increment (e.g. van der Maaten et al. 2018).

lowering of the turgor pressure. This means 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 increasing growth 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. 7). This approach is 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 lead to complex hydraulic fluctuations within the stem, leading to periodic stem shrinking and swelling (Dobbert et al. 2021a, Dobbert et al. 2021b).

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, Pape et al. 2009, Körner 2021), and the fact that most meteorological stations are located in valleys (Price & 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 & Birks 1997, Engler et al. 2009). However, within the complex alpine terrain with contrasting elevations, high topographic heterogeneity, and consequent microhabitat differentiation (Barry 2008, Pape et al. 2009, Wundram et al. 2010, Körner 2021), incorporating fine-scale spatial variability of near-surface conditions is essential. Especially small-stature shrubs are experiencing near-surface conditions which are often decoupled from the overall climatic regime (Hiltbrunner & Körner 2018, Löffler & Pape 2020), rendering macroclimatic, as well as gridded, data problematic. 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 (Randin et al. 2013, Körner & Hiltbrunner 2018, Körner 2021) (Fig. 8). 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 & Molau 2007, Bär et al. 2008). For this study, 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 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 with lowest values during winter (Fig. 9, Fig. 10). 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. 9, Fig. 10).

In recent years, the spatial and temporal heterogeneity of shrub encroachment, often decoupled from the overall warming trend (Martin et al. 2017, Brodie et al. 2019, Myers-Smith et al. 2020), has shifted the focus from thermal conditions during

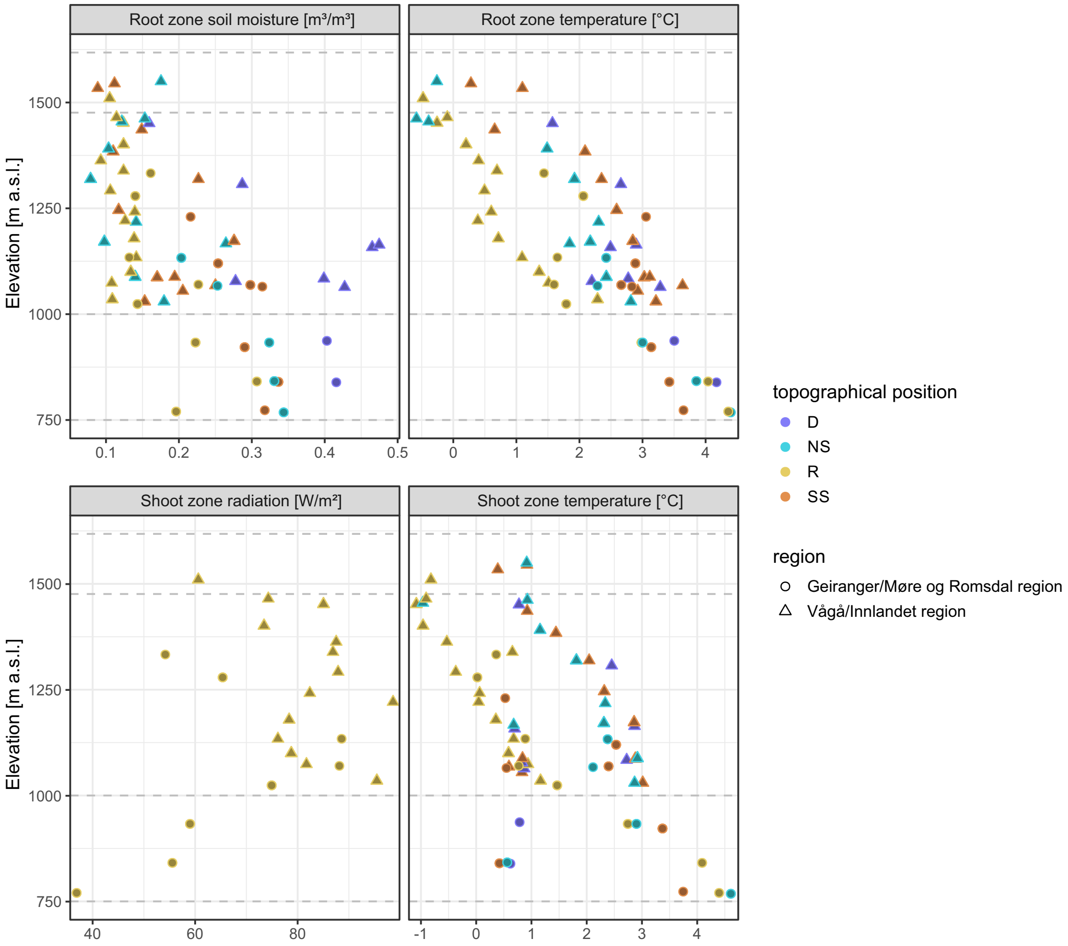

Fig. 8: Observed on-site environmental conditions along the elevational gradient within the two studied regions. Dotted lines represent the treeline and highest peak in each region: Light grey for the Geiranger/Møre og Romsdal region, and dark grey for the Vågå/Innlandet region.

the growing season. Additional environmental factors controlling growth processes and, consequently, shrubline dynamics and vegetational shifts are now considered as well (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. 10). 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.

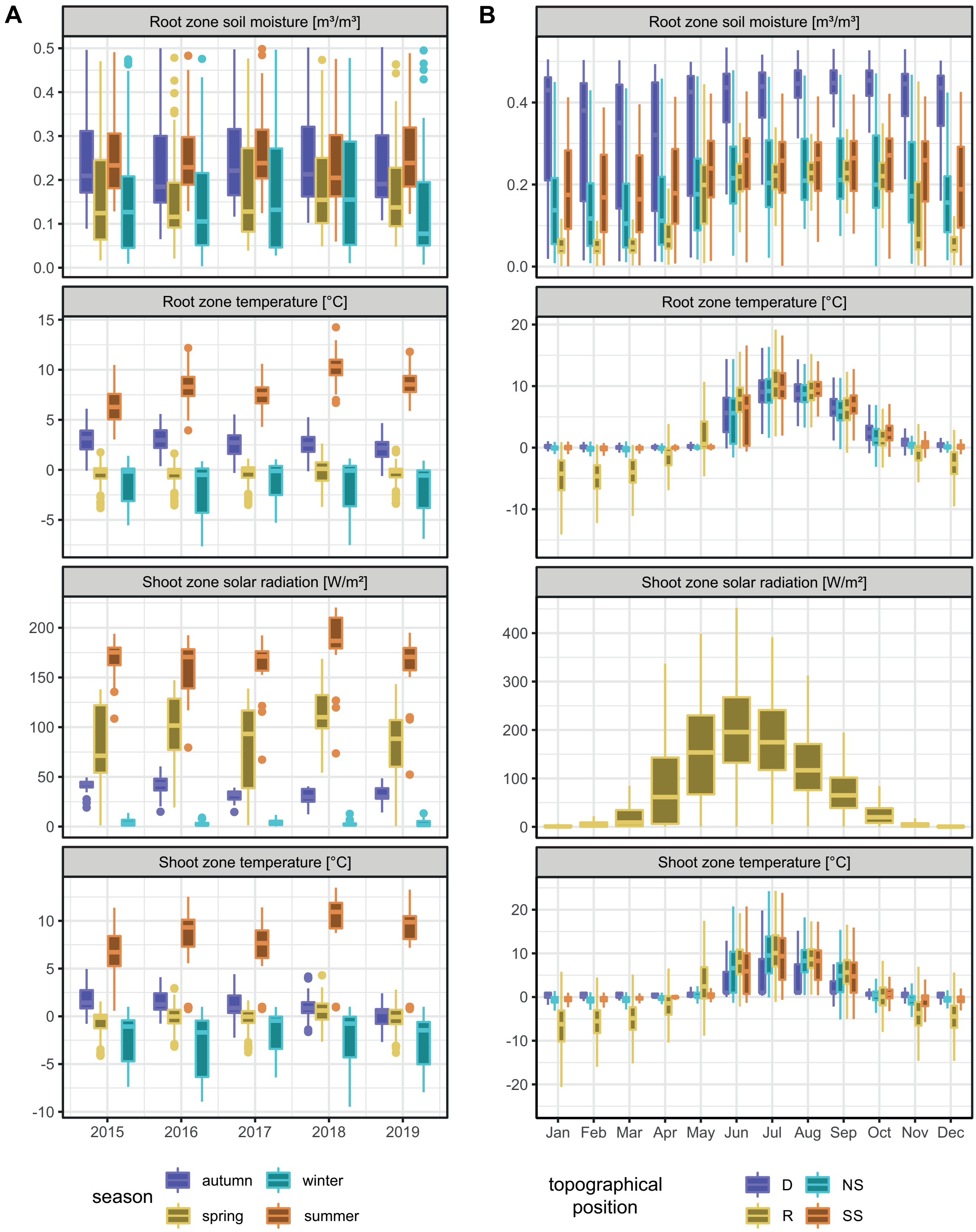

Fig. 9: Seasonally aggregated data and inter-annual variation of measured on-site environmental Parameters (A), and monthly aggregated variability of measured on-site environmental parameters throughout the year, depending on micro-topographic position.

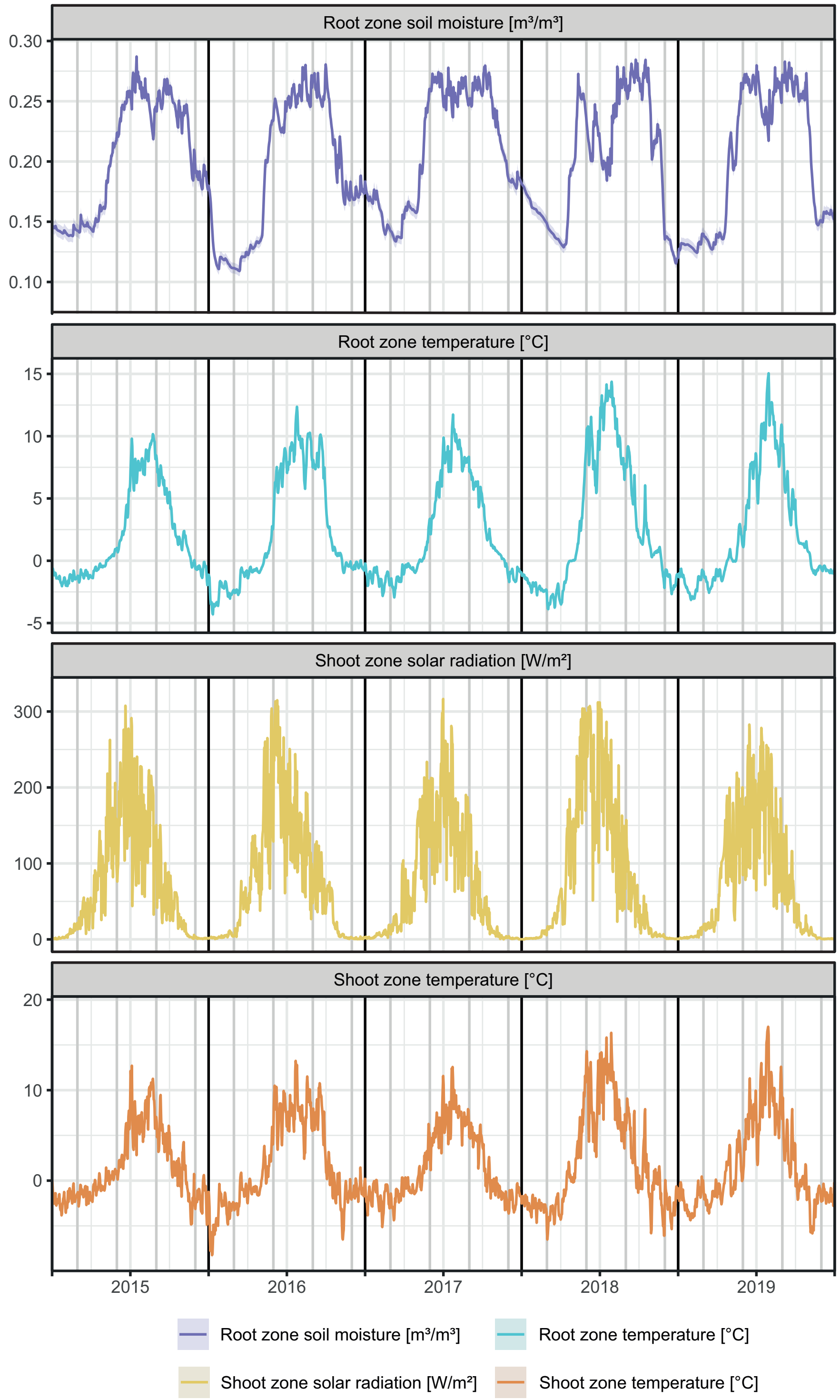

Fig. 10: Intra-annual regimes of measured on-site environmental parameters throughout the study period with standard deviation indicated by shaded areas.

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 subsequently modelled from the aggregated dendrometer measurements using generalized additive models (GAMs, Wood 2006) using 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 & 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 be described as the maximum stem diameter measured during one year minus the maximum stem diameter measured during the previous year. This approach captures 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. 7).

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 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 used to explore the variation in the stem diameter change patterns captured by the dendrometers, as well as the variability within 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 & Bollen 2005).

3 Results and Discussion

Linking the findings of Dobbert et al. (2021a, 2021b, 2022a) 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).

Our dataset allows insights into the physiology and growth mechanism of *E. hermaphroditum* at the exposed ridge positions. It reveals 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. 2022a). 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 on 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*, has become one of the most extensively studied species in high-latitude shrub communities (Bär et al. 2008, Bienau et al. 2014, Angers-Blondin & Boudreau 2017, Hein et al. 2020). In accordance with previous findings defining a wide thermal niche for *E. hermaphroditum* (Löffler & Pape 2020), the species showed the widest range across the studied regions (Fig. 5) 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 (Suppl. I :Fig. S1e). 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 (Suppl. I: Fig. S1a). At the exposed, windblown ridges, for instance, *E. hermaphroditum* showed a distinct and strongly pronounced phase of stem shrinkage during the winter months (Suppl. I: Fig. S1a, S1g). This phase 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 & 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. 9, Fig. 10) (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). This ability allows the species 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 the evergreen species has to sustain water transport to the canopy to some extent. It can thereby remain energetically effective in synthesizing carbohydrates despite limited nutrition and soil moisture availability (Fonti et al. 2010, Gimeno et al. 2012, Wyka & Oleksyn 2014, Löffler & Pape 2020, Dobbert et al. 2021a). These processes are reflected by the high synchrony between short periods of soil thawing in winter and stem diameter fluctuations (Suppl. I: Fig. S1f). Such periods of thawing expose 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 & 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) (Suppl. I: Fig. S1b). 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 (Suppl. I: Fig. S1a, Dobbert et al. 2022b). This limitation was closely linked to exceptionally high summer temperatures (Suppl. I: Fig. S1h), 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 (Post et al. 2019, AMAP 2021, 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. *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 might similarly allow for the development of coping strategies resulting in a highly complex, non-uniform response to warming conditions across *E. hermaphroditum* populations.

3.2 *Betula nana*

Similar to *E. hermaphroditum*, *B. nana* 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) (Suppl. I: Fig. S2d). 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 (Suppl. I: Fig. S2g). At the same time, *B. nana* 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 & 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 & 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 (Suppl. I: Fig. S2c, S2e). In addition, lowering temperatures with increasing elevation limited the species' range at the highest study sites (Suppl. I: Fig. S2e). 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). 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 1934). 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 (Suppl. I: Fig. S2a, S2f). 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).

3.3 *Phyllodoce caerulea*

In contrast to both *E. hermaphroditum* and *B. nana*, the dendroecological potential of the evergreen species *P. caerulea* 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 & Coker 1973, Kudo 1991). Accordingly, the species was mostly confined to the north- and south-facing slopes within our studied regions. This indicates 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 (Suppl. I: Fig S3d, S3e), 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 (Suppl. I: Fig. S3e). 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.

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, can be 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. 2022a) 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 belowground 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. 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 microclimatic conditions and therefore in many cases decoupled from governing regional climate signals (Pape & Löffler 2016, Pape & 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. 2022a). 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. 2022a).

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 & 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). 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. All three focal species proved sensitive to exceedingly high summer temperatures (Dobbert et al. 2021a, Dobbert et al. 2022a) 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.

References

Ackerman D, Griffin D, Hobbie SE, Finlay JC (2017) Arctic shrub growth trajectories differ across soil moisture levels. *Global Change Biol*ogy 23: 4294–4302. https://doi.org/10.1111/gcb.13677

Alday JG, Camarero JJ, Revilla J, Resco de Dios V (2020) Similar diurnal, seasonal and annual rhythms in radial root expansion across two coexisting Mediterranean oak species. *Tree Physiol*ogy 40: 956–968. https://doi.org/10.1093/treephys/tpaa041

Aller AE, Eklöf JS, Gullström M, Kloiber U, Linderholm HW, Nordlund LM (2019) Temporal variability of a protected multispecific tropical seagrass meadow in response to environmental change. *Environmental monitoring and assessment* 191: 759–774. https://doi.org/10.1007/s10661-019-7977-z

AMAP (2021) Arctic climate change update 2021: Key trends and impacts. Summary for policy-makers. *Arctic Monitoring and Assessment Programme (AMAP),* Tromsø, Norway.

Andrews JT, Mode WN, Webber PJ, Miller GH, Jacobs JD (1980) Report on the distribution of dwarf birches and present pollen rain, Baffin Island, N.W.T., Canada. *Arctic* 33: 50–58. https://doi.org/10.14430/arctic2547

Angers-Blondin S, Boudreau S (2017) Expansion dynamics and performance of the dwarf shrub *Empetrum hermaphroditum* (Ericaceae) on a subarctic sand sune system, Nunavik (Canada). *Arctic, Antarctic, and Alpine Research* 49: 201–211. https://doi.org/10.1657/AAAR0016-020

Aune B (1993) National atlas of Norway: climate. Hønefoss, Norway.

Bär A, Bräuning A, Löffler J (2006) Dendroecology of dwarf shrubs in the high mountains of Norway – A methodological approach. *Dendrochronologia* 24: 17–27. https://doi.org/10.1016/j.dendro.2006.05.001

Bär A, Bräuning A, Löffler J (2007) Ring-width chronologies of the alpine dwarf shrub *Empetrum hermaphroditum* from Norwegian mountains. *IAWA Journal* 28: 325–338. https://doi.org/10.1163/22941932-90001644

Bär A, Pape R, Bräuning A, Löffler J (2008) Growth-ring variations of dwarf shrubs reflect regional climate signals in alpine environments rather than topoclimatic differences. *Journal of Biogeography* 35: 625–636. https://doi.org/10.1111/j.1365-2699.2007.01804.x

Barry RG (2008) Mountain weather and climate. Cambridge.

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software* 67: 1–51. https://doi.org/10.18637/jss.v067.i01

Bell JNB, Tallis JH (1973) *Empetrum Nigrum* L. *The Journal Ecology* 61: 289–305. https://doi.org/10.2307/2258934

Berner LT, Massey R, Jantz P, Forbes BC, Macias-Fauria M, Myers-Smith I, Kumpula T, Gauthier G, Andreu-Hayles L, Gaglioti BV, Burns P, Zetterberg P, D'Arrigo, R, Goetz SJ (2020) Summer warming explains widespread but not uniform greening in the Arctic tundra biome. *Nature Commun*ications 11: e4621. https://doi.org/10.1038/s41467-020-18479-5

Bhatt U, Walker D, Raynolds M, Bieniek P, Epstein H, Comiso J, Pinzon J, Tucker C, Polyakov I (2013) Recent declines in warming and vegetation greening trends over pan-Arctic tundra. *Remote Sensing* 5: 4229–4254. https://doi.org/10.3390/rs5094229

Bienau MJ, Hattermann D, Kröncke M, Kretz L, Otte A, Eiserhardt WL, Wolf L, Milbau A, Graae BJ, Durka W, Eckstein RL (2014) Snow cover consistently affects growth and reproduction of *Empetrum hermaphroditum* across latitudinal and local climatic gradients. *Alpine Botany* 124: 115–129. https://doi.org/10.1007/s00035-014-0137-8

Bienau MJ, Eckstein RL, Otte A, Durka W (2016) Clonality increases with snow depth in the arctic dwarf shrub Empetrum hermaphroditum. *American Journal of Botany* 103: 2105–2114. https://doi.org/10.3732/ajb.1600229

Bjerke JW, Bokhorst S, Callaghan TV, Phoenix GK (2017) Persistent reduction of segment growth and photosynthesis in a widespread and important sub-Arctic moss species after cessation of three years of experimental winter warming. *Functional Ecology* 31: 127–134. https://doi.org/10.1111/1365-2435.12703

Björk RG, Molau U (2007) Ecology of alpine snowbeds and the impact of global change. *Arctic, Antarctic, and Alpine Research* 39: 34–43. https://doi.org/10.1657/1523-0430(2007)39[34:EOASAT]2.0.CO,2

Bjorkman AD, Myers-Smith IH, Elmendorf SC, Normand S, Rüger N, Beck PSA, Blach-Overgaard A, Blok D, Cornelissen JHC, Forbes BC, Georges D, Goetz SJ, Guay KC, Henry GHR, HilleRisLambers J, Hollister, RD, Karger DN, Kattge J, Manning P, Prevéy JS, Rixen C, Schaepman-Strub G, Thomas HJD, Vellend M, Wilmking M, Wipf S, Carbognani M, Hermanutz L, Lévesque E, Molau U, Petraglia A, Soudzilovskaia NA, Spasojevic MJ, Tomaselli M, Vowles T, Alatalo JM, Alexander HD, Anadon-Rosell A, Angers-Blondin S, te Beest M, Berner L, Björk RG, Buchwal A, Buras A, Christie K, Cooper EJ, Dullinger S, Elberling B, Eskelinen A, Frei ER, Grau O, Grogan P, Hallinger M, Harper KA, Heijmans, MMPD, Hudson J, Hülber K, Iturrate-Garcia M, Iversen CM, Jaroszynska F, Johnstone JF Jørgensen RH, Kaarlejärvi E, Klady R, Kuleza S, Kulonen A, Lamarque LJ, Lantz T, Little CJ, Speed JDM, Michelsen A, Milbau A, Nabe-Nielsen J, Nielsen SS, Ninot JM, Oberbauer SF, Olofsson J, Onipchenko VG, Rumpf SB, Semenchuk P, Shetti R, Collier LS, Street LE, Suding KN, Tape KD, Trant A, Treier UA, Tremblay J-P, Tremblay M, Venn S, Weijers S, Zamin T, Boulanger-Lapointe N, Gould WA, Hik DS, Hofgaard A, Jónsdóttir IS, Jorgenson J, Klein J, Magnusson B, Tweedie C, Wookey PA, Bahn M, Blonder B, van Bodegom PM, Bond-Lamberty B, Campetella G, Cerabolini BEL, Chapin, FSC, William K, Craine J, Dainese M, de Vries FT, Díaz S, Enquist BJ, Green W, Milla R, Niinemets Ü, Onoda Y, Ordoñez JC, Ozinga WA, Penuelas J, Poorter H, Poschlod P, Reich PB, Sandel B, Schamp B, Sheremetev S, Weiher E (2018): Plant functional trait change across a warming tundra biome. *Nature* 562: 57–62. https://doi.org/10.1038/s41586-018-0563-7

Bjorkman AD, Gallois EC (2020) Winter in a warming Arctic. *Nature Climate Change* 10: 1071–1073. https://doi.org/10.1038/s41558-020-0900-3

Blok D, Sass-Klaassen U, Schaepman-Strub G, Heijmans MMPD, Sauren P, Berendse F (2011) What are the main climate drivers for shrub growth in Northeastern Siberian tundra? *Biogeosciences Discussions* 8: 771–799. https://doi.org/10.5194/bgd-8-771-2011

Blok D, Weijers S, Welker JM, Cooper EJ, Michelsen A, Löffler J, Elberling B (2015) Deepened winter snow increases stem growth and alters stem δ13 C and δ15 N in evergreen dwarf shrub *Cassiope tetragona* in high-arctic Svalbard tundra. *Environmental Research Letters* 10: e44008. https://doi.org/10.1088/1748-9326/10/4/044008

Bokhorst S, Bjerke JW, Davey MP, Taulavuori K, Taulavuori E, Laine K, Callaghan TV, Phoenix GK (2009) Impacts of extreme winter warming events on plant physiology in a sub-Arctic heath community. *Physiologia plantarum* 140: 128–140. https://doi.org/10.1111/j.1399-3054.2010.01386.x

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology and Evolution* 24: 127–135. https://doi.org/10.1016/j.tree.2008.10.008

Bowling, D. R., Logan, B. A., Hufkens, K., Aubrecht, D. M., Richardson, A. D., Burns SP, Anderegg WRL, Blanken PD, Eiriksson DP (2018) Limitations to winter and spring photosynthesis of a Rocky Mountain subalpine forest. *Agricultural and Forest Meteorology* 252: 241–255. https://doi.org/10.1016/j.agrformet.2018.01.025

Bråthen KA, Gonzalez VT, Yoccoz NG (2018) Gatekeepers to the effects of climate warming? Niche construction restricts plant community changes along a temperature gradient. *Perspectives in Plant Ecology, Evolution and Systematics* 30: 71–81. https://doi.org/10.1016/j.ppees.2017.06.005

Breitsprecher A, Bethel JS (1990) Stem-growth periodicity of trees in a tropical wet forest of Costa Rica. *Ecology* 71: 1156–1164. https://doi.org/10.2307/1937383

Bret-Harte MS, Shaver GR, Zoerner JP, Johnstone JF, Wagner JL, Chavez AS, Gunkelman RF, Lippert SC, Laundre JA (2001): Developmental plasticity allows Betula nana to dominate tundra subjected to an altered environment. *Ecol*ogy 82: 18–32. https://doi.org/10.1890/0012-9658(2001)082[0018:DPABNT]2.0.CO;2

Brodie JF, Roland CA, Stehn SE, Smirnova E (2019) Variability in the expansion of trees and shrubs in boreal Alaska. *Ecology* 100: e02660. https://doi.org/10.1002/ecy.2660

Büntgen U, Hellmann L, Tegel W, Normand S, Myers-Smith I, Kirdyanov AV, Nievergelt D, Schweingruber FH (2015) Temperature-induced recruitment pulses of Arctic dwarf shrub communities. *The Journal of Ecology* 103: 489–501. https://doi.org/10.1111/1365-2745.12361

Cabon A, Peters RL, Fonti P, Martínez-Vilalta J, de Cáceres M (2020) Temperature and water potential co-limit stem cambial activity along a steep elevational gradient. *The New Phytologist* 226: 1325–1340. https://doi.org/10.1111/nph.16456

Cahoon SMP, Sullivan PF, Post E (2016) Greater abundance of *Betula nana* and early onset of the growing season increase ecosystem CO2 uptake in West Greenland. *Ecosystems* 19: 1149–1163. https://doi.org/10.1007/s10021-016-9997-7

Callaghan TV, Cazzolla GR, Phoenix G (2021) The need to understand the stability of arctic vegetation during rapid climate change: An assessment of imbalance in the literature. *Ambio* 51: 1034–1044. https://doi.org/10.1007/s13280-021-01607-w

Callaway RM, Pennings SC, Richards CL (2003) Phenotypic plasticity and interactions among plants. *Ecology* 84: 1115–1128. https://doi.org/10.1890/0012-9658(2003)084[1115:PPAIAP]2.0.CO;2

Carlquist S, Zona S (1988) Wood anatomy of *Papaveraceae*, with comments on vessel restriction patterns. *IAWA Journal* 9: 253–267. https://doi.org/10.1163/22941932-90001073

Carlson BZ, Corona MC, Dentant C, Bonet R, Thuiller W, Choler P (2016) Observed long-term greening of alpine vegetation - a case study in the French Alps. *Environmental Research Letters* 12: e114006. https://doi.org/10.1088/1748-9326/aa84bd

Chae Y, Kang SM, Jeong SJ, Kim B, Frierson DMW (2015) Arctic greening can cause earlier seasonality of Arctic amplification. *Geophysical Research Letters* 42: 536–541. https://doi.org/10.1002/2014GL061841

Chan T, Hölttä T, Berninger F, Mäkinen H, Nöjd P, Mencuccini M, Nikinmaa E (2016) Separating water-potential induced swelling and shrinking from measured radial stem variations reveals a cambial growth and osmotic concentration signal. *Plant, Cell & Environment* 39: 233–244. https://doi.org/10.1111/pce.12541

Chevin L-M, Lande R, Mace GM (2010) Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. *PLOS Biol* 8 (4), e1000357. https://doi.org/10.1371/journal.pbio.1000357

Coker PD, Coker AM (1973): *Phyllodoce Caerulea* (L.) Bab. *The Journal of Ecology* 61: 901–913. https://doi.org/10.2307/2258657

Collins, C. G., Elmendorf, S. C., Hollister, R. D., Henry, G. H. R., Clark, K., Bjorkman, A. D, Myers-Smith IH, Prevéy JS, Ashton IW, Assmann JJ, Alatalo JM, Carbognani M, Chisholm C, Cooper EJ, Forrester C, Jónsdóttir, IS, Klanderud K, Kopp CW, Livensperger C, Mauritz M, May JL, Molau U, Oberbauer SF, Ogburn E, Panchen ZA, Petraglia A, Post E, Rixen C, Rodenhizer H, Schuur EAG, Semenchuk P, Smith JG, Steltzer H, Totland Ø, Walker MD, Welker JM, Suding KN (2021) Experimental warming differentially affects vegetative and reproductive phenology of tundra plants. *Nature Communications* 12: 3442. https://doi.org/10.1038/s41467-021-23841-2

Crawford RMM (2008): Cold climate plants in a warmer world. *Plant Ecology & Diversity* 1: 285–297. https://doi.org/10.1080/17550870802407332

Cruz-García R, Balzano A, Čufar K, Scharnweber T, Smiljanić M, Wilmking M (2019) Combining Dendrometer Series and Xylogenesis Imagery - DevX, a simple visualization tool to explore plant secondary growth phenology. *Frontiers in Forests and Global Change* 2: 60. https://doi.org/10.3389/ffgc.2019.00060

Cuerrier A, Brunet ND, Gérin-Lajoie J, Downing A, Lévesque E (2015) The study of Inuit knowledge of climate change in Nunavik, Quebec: A mixed methods approach. *Human Ecology* 43: 379–394. https://doi.org/10.1007/s10745-015-9750-4

Cuny HE, Rathgeber CBK., Frank D, Fonti P, Mäkinen H, Prislan P, Rossi S, Del Castillo EM, Campelo F, Vavrčík H, Camarero JJ, Bryukhanova MV, Jyske T, Gričar J, Gryc V, de Luis M, Vieira J, Čufar K, Kirdyanov AV, Oberhuber W, Treml V, Huang J-G, Li X, Swidrak I, Deslauriers A, Liang E, Nöjd P, Gruber A, Nabais C, Morin H, Krause C, King G, Fournier M (2015) Woody biomass production lags stem-girth increase by over one month in coniferous forests. *Nature Plants* 1: 15160. https://doi.org/10.1038/nplants.2015.160

Dahl E (1986) Zonation in arctic and alpine tundra and fellfield ecobiomes. Polunin N (ed): *Ecosystem theory and application*: 35–62. Chichester.

Daubenmire RF (1945) An improved type of precision dendrometer. *Ecology* 26: 97–98. https://doi.org/10.2307/1931920

Descals A, Verger A, Filella I, Baldocchi D, Janssens IA, Fu YH, Piao S, Peaucelle M, Ciais P, Peelas J (2020) Soil thawing regulates the spring growth onset in tundra and alpine biomes. *The Science of the Total Environment* 742: 140637. https://doi.org/10.1016/j.scitotenv.2020.140637

Deslauriers A, Rossi S, Anfodillo T (2007) Dendrometer and intra-annual tree growth: What kind of information can be inferred? *Dendrochronologia* 25: 113–124. https://doi.org/10.1016/j.dendro.2007.05.003

Deslippe JR, Simard SW (2011) Below-ground carbon transfer among Betula nana may increase with warming in Arctic tundra. *The New Phytologist* 192: 689–698. https://doi.org/10.1111/j.1469-8137.2011.03835.x

Dierssen K (1996) Vegetation Nordeuropas. Stuttgart.

Dobbert S, Albrecht E C, Pape R, Löffler J (2022b) Alpine shrub growth follows bimodal seasonal patterns across biomes - unexpected environmental controls. *Communications Biology* 5: 793. https://doi.org/10.1038/s42003-022-03741-x

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

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

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

Drew DM, Downes GM (2009) The use of precision dendrometers in research on daily stem size and wood property variation: A review. *Dendrochronologia* 27: 159–172. https://doi.org/10.1016/j.dendro.2009.06.008

Duchesne L, Houle D, D'Orangeville L (2012) Influence of climate on seasonal patterns of stem increment of balsam fir in a boreal forest of Québec, Canada. *Agricultural and Forest Meteorology* 162/163: 108–114. https://doi.org/10.1016/j.agrformet.2012.04.016

Duputié A, Rutschmann A, Ronce O, Chuine I (2015) Phenological plasticity will not help all species adapt to climate change. *Global Change Biology* 21: 3062–3073. https://doi.org/10.1111/gcb.12914

Eidesen PB, Ehrich D, Bakkestuen V, Alsos IG, Gilg O, Taberlet P, Brochmann C (2013) Genetic roadmap of the Arctic: plant dispersal highways, traffic barriers and capitals of diversity. *The New Phytologist* 200: 898–910. https://doi.org/10.1111/nph.12412

Elmendorf SC, Henry GHR, Hollister RD, Björk RG, Boulanger-Lapointe N, Cooper EJ, Cornelissen JHC, Day TA, Dorrepaal E, Elumeeva TG, Gill M, Gould WA, Harte J, Hik DS, Hofgaard A, Johnson DR, Johnstone JF, Jónsdóttir IS, Jorgenson JC, Klanderud K, Klein JA, Koh S, Kudo G, Lara M, Lévesque E, Magnússon B, May JL, Mercado-Di´az JA, Michelsen A, Molau U, Myers-Smith IH, Oberbauer SF, Onipchenko VG, Rixen C, Martin Schmidt N, Shaver GR, Spasojevic MJ, Þórhallsdóttir ÞE, Tolvanen A, Troxler T, Tweedie CE, Villareal S, Wahren C-H, Walker X, Webber PJ, Welker JM, Wipf S (2012) Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change* 2: 453–457. https://doi.org/10.1038/nclimate1465

Engler R, Randin CF, Vittoz P, Czáka T, Beniston M, Zimmermann NE, Guisan A (2009) Predicting future distributions of mountain plants under climate change: does dispersal capacity matter? *Ecography* 32: 34–45. https://doi.org/10.1111/j.1600-0587.2009.05789.x

Epstein HE, Raynolds MK, Walker DA, Bhatt US, Tucker CJ, Pinzon, JE (2012) Dynamics of aboveground phytomass of the circumpolar Arctic tundra during the past three decades. *Environmental Research Letters* 7: 015506. https://doi.org/10.1088/1748-9326/7/1/015506

Epstein HE, Bhatt U, Raynolds M, Walker D, Forbes B, Horstkotte T et al. (2021) Tundra greenness. *Arctic Report Card, NOOA*. https://doi.org/10.25923/8n78-wp73

Firn J, Nguyen H, Schütz M, Risch AC (2019) Leaf trait variability between and within subalpine grassland species differs depending on site conditions and herbivory. *Proceedings of the Royal Society B: Biological Sciences* 286: 20190429. https://doi.org/10.1098/rspb.2019.0429

Fonti P, von Arx G, García-González I, Eilmann B, Sass-Klaassen U, Gärtner H, Eckstein D (2010) Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. *The New Phytologist* 185: 42–53. https://doi.org/10.1111/j.1469-8137.2009.03030.x

Forbes BC, Macias-Fauria M, Zetterberg P (2010) Russian Arctic warming and 'greening' are closely tracked by tundra shrub willows. *Global Change Biologist* 16: 1542–1554. https://doi.org/10.1111/j.1365-2486.2009.02047.x

Francon L, Corona C, Till-Bottraud I, Choler P, Carlson BZ, Charrier G, Améglio T, Morin S, Eckert N, Roussel E, Lopez-Saez J, Stoffel, M (2020a) Assessing the effects of earlier snow melt-out on alpine shrub growth: The sooner the better? *Ecological Indicators* 115, 106455. https://doi.org/10.1016/j.ecolind.2020.106455

Francon L, Corona C, Till-Bottraud I, Carlson BZ, Stoffel M (2020b) Some (do not) like it hot: shrub growth is hampered by heat and drought at the alpine treeline in recent decades. *American Journal of Botany* 107: 607–617. https://doi.org/10.1002/ajb2.1459

Fraser RH, Lantz TC, Olthof I, Kokelj SV, Sims RA (2014) Warming-induced shrub expansion and lichen decline in the western Canadian Arctic. *Ecosystems* 17: 1151–1168. https://doi.org/10.1007/s10021-014-9783-3

Gall R, Landolt W, Schleppi P, Michellod V, Bucher JB (2002) Water content and bark thickness of Norway spruce (*Picea abies*) stems: phloem water capacitance and xylem sap flow. *Tree Physiology* 22: 613–623. https://doi.org/10.1093/treephys/22.9.613

Gamm CM, Sullivan PF, Buchwal A, Dial RJ, Young AB, Watts DA, Cahoon SMP, Welker JM, Post E (2018) Declining growth of deciduous shrubs in the warming climate of continental western Greenland. *The Journal of Ecology* 106: 640–654. https://doi.org/10.1111/1365-2745.12882

Gimeno TE, Camarero JJ, Granda E, Pías B, Valladares F (2012) Enhanced growth of *Juniperus thurifera* under a warmer climate is explained by a positive carbon gain under cold and drought. *Tree Physiology* 32: 326–336. https://doi.org/10.1093/treephys/tps011

Gorsuch DM, Oberbauer SF, Fisher JB (2001) Comparative vessel anatomy of arctic deciduous and evergreen dicots. *American Journal of Botany* 88: 1643–1649. https://doi.org/10.2307/3558409

Gottfried M, Pauli H, Futschik A, Akhalkatsi M, Barančok P, Benito A, José L, Coldea G, Dick J, Erschbamer B, Fernández Calzado MR, Kazakis G, Krajči J, Larsson P, Mallaun M, Michelsen O, Moiseev D, Moiseev P, Molau U, Merzouki A, Nagy L, Nakhutsrishvili G, Pedersen B, Pelino G, Puscas M, Rossi G, Stanisci A, Theurillat J-P, Tomaselli M, Villar L, Vittoz P, Vogiatzakis I, Grabherr G (2012) Continent-wide response of mountain vegetation to climate change. *Nature Climate Change* 2: 111–115. https://doi.org/10.1038/nclimate1329

Graae BJ, Vandvik V, Armbruster WS, Eiserhardt WL, Svenning J-C, Hylander K, Ehrlén J, Speed JDM, Klanderud K, Bråthen, KA, Milbau A, Opedal ØH, Alsos IG, Ejrnæs R, Bruun HH, Birks H, John B, Westergaard, KB, Birks HH, Lenoir J (2018) Stay or go – how topographic complexity influences alpine plant population and community responses to climate change. *Perspectives in Plant Ecology, Evolution and Systematics* 30: 41–50. https://doi.org/10.1016/j.ppees.2017.09.008

Grace JB, Bollen KA (2005) Interpreting the results from multiple regression and structural equation models. *Bulletin of the Ecological Society of America* 86: 283–295. https://doi.org/10.1890/0012-9623(2005)86[283:ITRFMR]2.0.CO;2

Grams TEE, Hesse BD, Gebhardt T, Weikl F, Rötzer T, Kovacs B, Hikino K, Hafner BD, Brunn M, Bauerle T, Häberle K-H, Pretzsch H, Pritsch K (2021) The Kroof experiment: Realization and efficacy of a recurrent drought experiment plus recovery in a beech/spruce forest. *Ecosphere* 12: e03399. https://doi.org/10.1002/ecs2.3399

Gricar J, Zupancic M, Cufar K, Koch G, Schmitt U, Oven P (2006) Effect of local heating and cooling on cambial activity and cell differentiation in the stem of Norway spruce (*Picea abies*). *Annals of Botany* 97: 943–951. https://doi.org/10.1093/aob/mcl050

de Groot WJ, Thomas PA, Wein RW (1997) *Betula nana* L. and *Betula glandulosa* Michx. *The Journal of Ecology* 85: 241–264. https://doi.org/10.2307/2960655

Grytnes J-A, Kapfer J, Jurasinski G, Birks HH, Henriksen H, Klanderud K, Odland A, Ohlson M, Wipf S, Birks HJB (2014) Identifying the driving factors behind observed elevational range shifts on European mountains. *Global Ecology and Biogeography* 23: 876–884. https://doi.org/10.1111/geb.12170

González-Rodríguez ÁM, Brito P, Lorenzo JR, Gruber A, Oberhuber W, Wieser G (2017) Seasonal cycles of sap flow and stem radius variation of *Spartocytisus supranubius* in the alpine zone of Tenerife, Canary Islands. *Alpine Botany* 127: 97–108. https://doi.org/10.1007/s00035-017-0189-7

Hagedorn F, Shiyatov SG, Mazepa VS, Devi NM, Grigor'ev AA, Bartysh AA, Hagedorn F, Shiyatov SG, Mazepa VS, Devi NM, Grigor'ev AA, Bartysh AA, Fomin VV, Kapralov DS, Terent'ev M, Bugman H, Rigling A, Moiseev PA (2014) Treeline advances along the Urals mountain range - driven by improved winter conditions? *Global Change Biology* 20: 3530–3543. https://doi.org/10.1111/gcb.12613

Hallinger M, Manthey M, Wilmking M (2010) Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *The New Phytologist* 186: 890–899. https://doi.org/10.1111/j.1469-8137.2010.03223.x

Hein N, Merkelbach J, Zech K, Weijers S (2020) Drought sensitivity of *Empetrum nigrum* shrub growth at the species' southern lowland distribution range margin. *Plant Ecology* 222: 305–321 https://doi.org/10.1007/s11258-020-01107-z

Henn JJ, Buzzard V, Enquist BJ, Halbritter AH, Klanderud K, Maitner BS, Michaletz ST, Pötsch C, Seltzer L, Telford RJ, Yang Y, Zhang L, Vandvik V (2018) Intraspecific trait variation and phenotypic plasticity mediate alpine plant species response to climate change. *Frontiers in Plant Science* 9: 1548. https://doi.org/10.3389/fpls.2018.01548

Körner C, Hiltbrunner E (2018) The 90 ways to describe plant temperature. *Perspectives in Plant Ecology, Evolution and Systematics* 30: 16–21. https://doi.org/10.1016/j.ppees.2017.04.004

Hoffmann AA, Sgrò CM (2011) Climate change and evolutionary adaptation. *Nature* 470: 479–485. https://doi.org/10.1038/nature09670

Hollesen J, Buchwal A, Rachlewicz G, Hansen BU, Hansen MO, Stecher O, Elberling B (2015) Winter warming as an important co-driver for *Betula nana* growth in western Greenland during the past century. *Global Change Biology* 21: 2410–2423. https://doi.org/10.1111/gcb.12913

Holtedahl H (1967) Notes on the formation of fjords and fjord-valleys. *Geografiska Annaler: Series A, Physical Geography* 49: 88–203. https://doi.org/10.1080/04353676.1967.11879749

Hultén E (1968) Flora of Alaska and neighboring territories. A manual of the vascular plants. Redwood City

Ilek A, Kucza J, Morkisz K (2017) Hygroscopicity of the bark of selected forest tree species. *Iforest* 10: 220–226. https://doi.org/10.3832/ifor1979-009

IPCC (2021) Climate Change 2021: The physical science basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. Geneva.

Ježík M, Blaženec M, Kučera J, Strelcová K, Ditmarová L (2016) The response of intra-annual stem circumference increase of young European beech provenances to 2012-2014 weather variability. *Iforest* 9: 960–969. https://doi.org/10.3832/ifor1829-009

Jia GJ, Epstein HE, Walker DA (2003) Greening of arctic Alaska, 1981–2001. *Geophysical Research Letters* 30: 2067. https://doi.org/10.1029/2003GL018268

Jonasson S (1981) Plant communities and species distribution of low alpine *Betula nana* heaths in northernmost Sweden. *Plant Ecology* 44: 51–64. https://doi.org/10.1007/BF00119804

Joos F, Prentice IC, Sitch S, Meyer R, Hooss G, Plattner G-K, Gerber S, Hasselmann K (2001): Global warming feedbacks on terrestrial carbon uptake under the Intergovernmental Panel on Climate Change (IPCC) emission scenarios. *Global Biogeochemical Cycles* 15: 891–907. https://doi.org/10.1029/2000GB001375

Kameyama Y, Kasagi T, Kudo G (2008) A hybrid zone dominated by fertile F1s of two alpine shrub species, *Phyllodoce caerulea* and *Phyllodoce aleutica*, along a snowmelt gradient. *Journal of evolutionary biology* 21: 588–597. https://doi.org/10.1111/j.1420-9101.2007.01476.x

Kleiven M (1959) Studies on the xerophile vegetation in northern Gudbrandsdalen, Norway. *Nytt magasin for botanikk* 7: 1–60.

Knüsel S, Peters RL, Haeni M, Wilhelm M, Zweifel R (2021) Processing and extraction of seasonal tree physiological parameters from stem radius time series. *Forests* 12: 765. https://doi.org/10.3390/f12060765

Köcher P, Horna V, Leuschner C (2012) Environmental control of daily stem growth patterns in five temperate broad-leaved tree species. *Tree Physiology* 32: 1021–1032. https://doi.org/10.1093/treephys/tps049

Körner C (2012) Treelines will be understood once the functional difference between a tree and a shrub is. *Ambio* 41 Suppl 3: 197–206. https://doi.org/10.1007/s13280-012-0313-2

Körner C (2015) Paradigm shift in plant growth control. *Current opinion in plant biology* 25: 107–114. https://doi.org/10.1016/j.pbi.2015.05.003

Körner C, Hiltbrunner E (2018) The 90 ways to describe plant temperature. *Perspectives in Plant Ecology, Evolution and Systematics* 30: 16–21. https://doi.org/10.1016/j.ppees.2017.04.004

Körner C (2021) Alpine plant life. Berlin, Heidelberg.

Krab EJ, Roennefarth J, Becher M, Blume-Werry G, Keuper F, Klaminder J, Kreyling J, Makoto K, Milbau A, Dorrepaal E (2017) Winter warming effects on tundra shrub performance are species-specific and dependent on spring conditions. *The Journal of Ecology* 106: 599–612. https://doi.org/10.1111/1365-2745.12872

Kudo G (1991) Effects of snow-free period on the phenology of alpine plants inhabiting snow patches. *Arctic, Antarctic, and Alpine Research* 23: 436–443. https://doi.org/10.1080/00040851.1991.12002863

Lamacque L, Charrier G, dos Santos FF, Lemaire B, Améglio T, Herbette S (2019) Drought-induced mortality: stem diameter variation reveals a point of no return in lavender species. *Journal of Environmental Sciences* 1: 1–25. https://doi.org/10.1101/848879

Lara MJ, Nitze I, Grosse G, Martin P, McGuire AD (2018) Reduced arctic tundra productivity linked with landform and climate change interactions. *Scientific Reports* 8: 2345. https://doi.org/10.1038/s41598-018-20692-8

Le Moullec M, Buchwal A, Wal R, Sandal L, Hansen BB (2019) Annual ring growth of a widespread high arctic shrub reflects past fluctuations in community-level plant biomass. *The Journal of Ecology* 107: 436–451. https://doi.org/10.1111/1365-2745.13036

Li B, Heijmans MMPD, Berendse F, Blok D, Maximov T, Sass-Klaassen U (2016) The role of summer precipitation and summer temperature in establishment and growth of dwarf shrub *Betula nana* in northeast Siberian tundra. *Polar Biology* 39: 1245–1255. https://doi.org/10.1007/s00300-015-1847-0

Liang E, Lu X, Ren P, Li, X, Zhu L, Eckstein D (2012) Annual increments of juniper dwarf shrubs above the tree line on the central Tibetan Plateau: a useful climatic proxy. *Annals of Botany* 109 721–728. https://doi.org/10.1093/aob/mcr315

Lindfors L, Atherton J, Riikonen A, Hölttä T (2019) A mechanistic model of winter stem diameter dynamics reveals the time constant of diameter changes and the elastic modulus across tissues and species. *Agricultural and Forest Meteorology* 272/273: 20–29. https://doi.org/10.1016/j.agrformet.2019.03.016

Lintunen A, Paljakka T, Jyske T, Peltoniemi M, Sterck F, von Arx G, Cochard H, Copini P, Caldeira MC, Delzon S, Gebauer R, Grönlund L, Kiorapostolou N, Lechthaler S, Lobo-do-Vale R, Peters RL, Petit G, Prendin AL, Salmon Y, Steppe K, Urban J, Roig JS, Robert EMR, Hölttä T (2016) Osmolality and non-structural carbohydrate composition in the secondary phloem of trees across a latitudinal gradient in Europe. *Frontiers in Plant Science* 7: 726. https://doi.org/10.3389/fpls.2016.00726

Liu X, Nie Y, Wen F (2018) Seasonal dynamics of stem radial increment of *Pinus taiwanensis* Hayata and its response to environmental factors in the Lushan Mountains, southeastern China. *Forests* 9: 387. https://doi.org/10.3390/f9070387

Liu X, Wang C, Zhao J (2019) Seasonal drought effects on intra-annual stem growth of Taiwan pine along an elevational gradient in subtropical China. *Forests* 10: 1128. https://doi.org/10.3390/f10121128

Lockhart JA (1965) An analysis of irreversible plant cell elongation. *Journal of Theoretical Biology* 8: 264–275. https://doi.org/10.1016/0022-5193(65)90077-9

Löffler J (2003) Micro-climatic determination of vegetation patterns along topographical, altitudinal, and oceanic-continental gradients in the high mountains of Norway. *Erdkunde* 57: 232–249. https://doi.org/10.3112/erdkunde.2003.03.05

Löffler J (2005) Snow cover dynamics, soil moisture variability and vegetation ecology in high mountain catchments of central Norway. *Hydrological Processes* 19: 2385–2405. https://doi.org/10.1002/hyp.5891

Löffler J, Albrecht E C, Dobbert S, Pape R, Wundram, D (2022) Dendrometer measurements of Mediterranean-alpine dwarf shrubs and micro-environmental drivers of plant growth – Dataset from long-term alpine ecosystem research in the Sierra Nevada, Spain (LTAER-ES). Erdkunde 76: DP311202. https://doi.org/10.3112/erdkunde.2022.dp.01

Löffler J, Dobbert S, Pape R, Wundram D (2021) Dendrometer measurements of arctic-alpine dwarf shrubs and micro-environmental drivers of plant growth - Dataset from long-term alpine ecosystem research in central Norway. *Erdkunde* 75: DP311201. https://doi.org/10.3112/erdkunde.2021.dp.01

Löffler J, Pape R (2020) Thermal niche predictors of alpine plant species. *Ecology* 101: e02891. https://doi.org/10.1002/ecy.2891

Löffler J, Pape R, Wundram D (2006) The climatologic significance of topography, altitude and region in high mountains – A survey of oceanic-continental differentiations of the Scandes. *Erdkunde* 60: 16–24. https://doi.org/10.3112/erdkunde.2006.01.02

Lu X, Liang E, Wang Y, Babst F, Camarero JJ (2021) Mountain treelines climb slowly despite rapid climate warming. *Global Ecology and Biogeography* 30: 305–315. https://doi.org/10.1111/geb.13214

Lu X, Liang E, Babst F, Camarero JJ, Büntgen U (2022) Warming-induced tipping points of Arctic and alpine shrub recruitment. *Proceedings of the National Academy of Sciences of the United States of America* 119: e2118120119. https://doi.org/10.1073/pnas.2118120119

Macias-Fauria M, Forbes BC, Zetterberg P, Kumpula T (2012) Eurasian Arctic greening reveals teleconnections and the potential for structurally novel ecosystems. *Nature Climate Chang*e 2: 613–618. https://doi.org/10.1038/NCLIMATE1558

Macias-Fauria M, Jepson P, Zimov N, Malhi Y (2020) Pleistocene Arctic megafaunal ecological engineering as a natural climate solution? *Philosophical transactions of the Royal Society of London. Series B, Biological sciences* 375: 20190122. https://doi.org/10.1098/rstb.2019.0122

Martin AC, Jeffers ES, Petrokofsky G, Myers-Smith I, Macias-Fauria M (2017) Shrub growth and expansion in the Arctic tundra: an assessment of controlling factors using an evidence-based approach. *Environmental Research Letters* 12: 85007. https://doi.org/10.1088/1748-9326/aa7989

Miller TW, Stangler DF, Larysch E, Honer H, Seifert T, Kahle H-P (2022) A methodological framework to optimize models predicting critical dates of xylem phenology based on dendrometer data. *Dendrochronologia* 72: 125940. https://doi.org/10.1016/j.dendro.2022.125940

Mishra U, Riley WJ (2012) Alaskan soil carbon stocks: spatial variability and dependence on environmental factors. *Biogeosciences* 9: 3637–3645. https://doi.org/10.5194/bg-9-3637-2012

Moen A, Lillethun A (1999) National atlas of Norway: vegetation. Hønefoss.

Morgner E, Elberling B, Strebel D, Cooper EJ (2010) The importance of winter in annual ecosystem respiration in the High Arctic: effects of snow depth in two vegetation types. *Polar Research* 29: 58–74. https://doi.org/10.1111/j.1751-8369.2010.00151.x

Myers-Smith IH, Forbes BC, Wilmking M, Hallinger M, Lantz T, Blok D, Myers-Smith IH, Forbes BC, Wilmking M, Hallinger M, Lantz T, Blok D, Tape KD, Macias-Fauria M, Sass-Klaassen U, Lévesque E, Boudreau S, Ropars P, Hermanutz L, Trant A, Collier LS, Weijers S, Rozema J, Rayback SA, Schmidt N, Schaepman-Strub G, Wipf S, Rixen C, Ménard CB, Venn S, Goetz S, Andreu-Hayles L, Elmendorf S, Ravolainen V, Welker J, Grogan P, Epstein HE, Hik DS (2011): Shrub expansion in tundra ecosystems: Dynamics, impacts and research priorities. *Environmental Research Letters* 6: 45509. https://doi.org/10.1088/1748-9326/6/4/045509

Myers-Smith IH, Elmendorf SC, Beck PSA, Wilmking M, Hallinger M, Blok D, Myers-Smith IH, Elmendorf SC, Beck, PSA, Wilmking M, Hallinger M, Blok D, Tape KD, Rayback SA, Macias-Fauria M, Forbes BC, Speed JDM, Boulanger-Lapointe N, Rixen C, Lévesque E, Schmidt N, Baittinger C, Trant AJ, Hermanutz L, Collier LS, Dawes MA, Lantz TC, Weijers S, Jørgensen RH, Buchwal A, Buras A, Naito AT, Ravolainen V, Schaepman-Strub G, Wheeler JA, Wipf S, Guay KC, Hik DS, Vellend M (2015) Climate sensitivity of shrub growth across the tundra biome. *Nature Climate Change* 5: 887–891. https://doi.org/10.1038/nclimate2697

Myers-Smith IH, Kerby JT, Phoenix GK, Bjerke JW, Epstein HE, Assmann JJ, John C, Andreu-Hayles L, Angers-Blondin S, Beck PSA, Berner LT, Bhatt US, Bjorkman AD, Blok D, Bryn, A, Christiansen CT, Cornelissen JHC, Cunliffe AM, Elmendorf SC, Forbes BC, Goetz SJ, Hollister RD, de Jong R, Loranty MM, Macias-Fauria M, Maseyk K, Normand S, Olofsson J, Parker TC, Parmentier F-JW, Post E, Schaepman-Strub G, Stordal F, Sullivan PF, Thomas HJD, Tømmervik H, Treharne R, Tweedie CE, Walker DA, Wilmking M, Wipf S (2020) Complexity revealed in the greening of the Arctic. *Nature Climate Change* 10: 106–117. https://doi.org/10.1038/s41558-019-0688-1

Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* 386: 698–702. https://doi.org/10.1038/386698a0

Nauta AL, Heijmans MMPD, Blok D, Limpens J, Elberling B, Gallagher A, Li B, Petrov RE, Maximov TC, van Huissteden J, Berendse F (2015) Permafrost collapse after shrub removal shifts tundra ecosystem to a methane source. *Nature Climate Change* 5: 67–70. https://doi.org/10.1038/nclimate2446

Nielsen SS, von Arx G, Damgaard CF, Abermann J, Buchwal A, Büntgen U, Treier UA, Barfod AS, Normand S (2017) Xylem anatomical trait variability provides insight on the climate-growth relationship of *Betula nana* in western Greenland. *Arctic, Antarctic, and Alpine Research* 49: 359–371. https://doi.org/10.1657/AAAR0016-041

Oberhuber W, Sehrt M, Kitz F (2020) Hygroscopic properties of thin dead outer bark layers strongly influence stem diameter variations on short and long time scales in Scots pine (*Pinus sylvestris* L.). *Agricultural and Forest Meteorology* 290: 108026. https://doi.org/10.1016/j.agrformet.2020.108026

Odland A, Munkejord HK (2008) Plants as indicators of snow layer duration in southern Norwegian mountains. *Ecological Indicators* 8: 57–68. https://doi.org/10.1016/j.ecolind.2006.12.005

Ögren E (2001) Effects of climatic warming on cold hardiness of some northern woody plants assessed from simulation experiments. *Physiologia plantarum* 112: 71–77. https://doi.org/10.1034/j.1399-3054.2001.1120110.x

Pape R, Löffler J (2016) Spatial patterns of alpine phytomass, primary productivity, and related calorific resources. *Ecosphere* 7: e01347. https://doi.org/10.1002/ecs2.1347

Pape R, Löffler J (2017) Determinants of arctic-alpine pasture resources: the need for a spatially and functionally fine-scaled perspective. *Geografiska Annaler: Series A, Physical Geography* 99: 353–370. https://doi.org/10.1080/04353676.2017.1368833

Pape R, Wundram D, Löffler J (2009) Modelling near-surface temperature conditions in high mountain environments: an appraisal. *Climate Research* 39: 99–109. https://doi.org/10.3354/cr00795

Pappas C, Peters RL, Fonti P (2020) Linking variability of tree water use and growth with species resilience to environmental changes. *Ecography* 43: 1386–1399. https://doi.org/10.1111/ecog.04968

Pérez-Ramos IM, Matías L, Gómez-Aparicio L, Godoy Ó (2019) Functional traits and phenotypic plasticity modulate species coexistence across contrasting climatic conditions. *Nature Communications* 10: 2555. https://doi.org/10.1038/s41467-019-10453-0

Peters RL, Steppe K, Cuny HE, de Pauw DJW, Frank DC, Schaub M, Rathgeber CBK, Cabon A, Fonti P (2021) Turgor - a limiting factor for radial growth in mature conifers along an elevational gradient. *The New Phytologist* 229: 213–229. https://doi.org/10.1111/nph.16872

Pfennigwerth AA, Bailey JK, Schweitzer JA (2017) Trait variation along elevation gradients in a dominant woody shrub is population-specific and driven by plasticity. *AoB PLANTS* 9: plx027. https://doi.org/10.1093/aobpla/plx027

Phoenix GK, Bjerke JW (2016) Arctic browning: extreme events and trends reversing arctic greening. *Global Change Biology* 22: 2960–2962. https://doi.org/10.1111/gcb.13261

Post E, Alley RB, Christensen TR, Macias-Fauria M, Forbes BC, Gooseff MN, Iler A, Kerby JT, Laidre KL, Mann ME, Olofsson J, Stroeve JC, Ulmer F, Virginia RA, Wang M (2019) The polar regions in a 2°C warmer world. *Science Advances* 5: eaaw9883. https://doi.org/10.1126/sciadv.aaw9883

Price MF, Barry RG (1997) Climate change. Messerli B, Ives JD (eds) *Mountains of the world. A global priority:* 409–445. New York.

R Core Team (2021) R: A language and environment for statistical computing. *R Foundation for Statistical Computing*. https://www.R-project.org/

Randin CF, Paulsen J, Vitasse Y, Kollas C, Wohlgemuth T, Zimmermann NE, Körner C (2013) Do the elevational limits of deciduous tree species match their thermal latitudinal limits? *Global Ecology and Biogeography* 22: 913–923. https://doi.org/10.1111/geb.12040

Raunkiær C (1934) Life forms of plants and statistical plant geography. Oxford.

Rathgeber CBK, Cuny HE, Fonti P (2016) Biological basis of tree-ring formation: A crash course. *Frontiers in Plant Science* 7: 734. https://doi.org/10.3389/fpls.2016.00734

Reineke LH (1932) A precision dendrometer. *Journal of Forestry* 30: 692–697.

Ropars P, Lévesque E, Boudreau S (2015) How do climate and topography influence the greening of the forest-tundra ecotone in northern Québec? A dendrochronological analysis of *Betula glandulosa*. *The Journal of Ecology* 103: 679–690. https://doi.org/10.1111/1365-2745.12394

Ropars P, Angers-Blondin S, Gagnon M, Myers-Smith IH, Lévesque E, Boudreau S (2017) Different parts, different stories: climate sensitivity of growth is stronger in root collars vs. stems in tundra shrubs. *Global Change Biology* 23: 3281–3291. https://doi.org/10.1111/gcb.13631

Rossi S, Deslauriers A, Morin H (2003) Application of the Gompertz equation for the study of xylem cell development. *Dendrochronologia* 21: 33–39. https://doi.org/10.1078/1125-7865-00034

Rossi S, Deslauriers A, Anfodillo T, Morin H, Saracino A, Motta R, Borghetti M (2006) Conifers in cold environments synchronize maximum growth rate of tree-ring formation with day length. *The New Phytologist* 170: 301–310. https://doi.org/10.1111/j.1469-8137.2006.01660.x

Rossi S, Deslauriers A, Griçar J, Seo J-W, Rathgeber CBK, Anfodillo T, Morin H, Levanic T, Oven P, Jalkanen R (2008) Critical temperatures for xylogenesis in conifers of cold climates. *Global Ecology and Biogeography* 17: 696–707. https://doi.org/10.1111/j.1466-8238.2008.00417.x

Rossi S, Anfodillo T, Čufar K, Cuny HE, Deslauriers A, Fonti P, Frank D, Gričar J, Gruber A, Huang J-G, Jyske T, Kašpar J, King G, Krause C, Liang E, Mäkinen H, Morin H, Nöjd P, Oberhuber W, Prislan P, Rathgeber CBK, Saracino A, Swidrak I, Treml V (2016) Pattern of xylem phenology in conifers of cold ecosystems at the Northern Hemisphere. *Global Change Biology* 22: 3804–3813. https://doi.org/10.1111/gcb.13317

Sabater AM, Ward HC, Hill TC, Gornall JL, Wade TJ, Evans JG, Prieto-Blanco A, Disney M, Phoenix GK, Williams M, Huntley B, Baxter R, Mencuccini M, Poyatos R (2019) Transpiration from subarctic deciduous woodlands: environmental controls and contribution to ecosystem evapotranspiration. *Ecohydrology* 13: e2190. https://doi.org/10.1002/ECO.2190

Saccone P, Hoikka K, Virtanen R (2017) What if plant functional types conceal species-specific responses to environment? Study on arctic shrub communities. *Ecology* 98: 1600–1612. https://doi.org/10.1002/ecy.1817

Saetersdal M, Birks HJB (1997) A comparative ecological study of Norwegian mountain plants in relation to possible future climatic change. *Journal of Biogeography* 24: 127–152. https://doi.org/10.1046/j.1365-2699.1997.00096.x

Scherrer D, Körner C (2011) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography* 38: 406–416. https://doi.org/10.1111/j.1365-2699.2010.02407.x

Schott RT, Roth-Nebelsick A (2018) Ice nucleation in stems of trees and shrubs with different frost resistance. *IAWA Journal* 39: 177–190. https://doi.org/10.1163/22941932-20180201

Schuur EAG, Abbott BW, Bowden WB, Brovkin V, Camill P, Canadell JG, Chanton JP, Chapin FS, Christensen TR, Ciais P, Crosby BT, Czimczik CI, Grosse G, Harden J, Hayes DJ, Hugelius G, Jastrow JD, Jones JB, Kleinen T, Koven CD, Krinner G, Kuhry P, Lawrence DM, McGuire AD, Natali SM, O'Donnell JA, Ping CL, Riley WJ, Rinke A, Romanovsky VE, Sannel ABK, Schädel C, Schaefer K, Sky J, Subin ZM, Tarnocai C, Turetsky MR, Waldrop MP, Walter Anthony KM, Wickland KP, Wilson CJ, Zimov SA (2013) Expert assessment of vulnerability of permafrost carbon to climate change. *Climate Change* 119: 359–374. https://doi.org/10.1007/s10584-013-0730-7

Schuur, EAG, McGuire AD, Schädel C, Grosse G, Harden JW, Hayes DJ, Hugelius G, Koven CD, Kuhry P, Lawrence DM, Natali SM, Olefeldt D, Romanovsky VE, Schaefer K, Turetsky MR, Treat CC, Vonk JE (2015) Climate change and the permafrost carbon feedback. *Nature* 520: 171–179. https://doi.org/10.1038/nature14338

Seebacher F, White CR, Franklin CE (2015) Physiological plasticity increases resilience of ectothermic animals to climate change. *Nature Climate Change* 5: 61–66. https://doi.org/10.1038/NCLIMATE2457

Smiljanić M, Wilmking M (2018) Drivers of stem radial variation and its pattern in peatland Scots pines: A pilot study. *Dendrochronologia* 47: 30–37. https://doi.org/10.1016/j.dendro.2017.12.001

Sperry JS (2003) Evolution of Water Transport and Xylem Structure. *International Journal of Plant Sciences* 164: 115-127. https://doi.org/10.1086/368398

Steppe K, de Pauw DJW, Lemeur R, Vanrolleghem PA (2006) A mathematical model linking tree sap flow dynamics to daily stem diameter fluctuations and radial stem growth. *Tree Physiology* 26: 257–273. https://doi.org/10.1093/treephys/26.3.257

Steppe K, Sterck F, Deslauriers A (2015) Diel growth dynamics in tree stems: linking anatomy and ecophysiology. *Trends in Plant Science* 20: 335–343. https://doi.org/10.1016/j.tplants.2015.03.015

Sturm M, Schimel J, Michaelson G, Welker JM, Oberbauer SF, Liston GE, Fahnestock J, Romanovsky VE (2005) Winter biological processes could help convert arctic Tundra to shrubland. *BioScience* 55: 17–26. https://doi.org/10.1641/0006-3568(2005)055[0017:WBPCHC]2.0.CO;2

Stushnoff C, Junttila O (1986) Seasonal development of cold stress resistance in several plant species at a coastal and a continental location in North Norway. *Polar Biology* 5: 129–133. https://doi.org/10.1007/BF00441691

Turcotte A, Rossi S, Deslauriers A, Krause C, Morin H (2011) Dynamics of depletion and replenishment of water storage in stem and roots of black spruce measured by dendrometers. *Frontiers in Plant Science* 2: 2–21. https://doi.org/10.3389/fpls.2011.00021

Turcotte MM, Levine JM (2016) Phenotypic plasticity and species coexistence. *Trends in Ecology & Evolution* 3: 803–813. https://doi.org/10.1016/j.tree.2016.07.013

van der Maaten, E., Pape, J., van der Maaten-Theunissen, M., Scharnweber, T., Smiljanic, M., Cruz-García, R., Wilmking, M. (2018): Distinct growth phenology but similar daily stem dynamics in three co-occurring broadleaved tree species. *Tree Physiology* 38: 1820–1828. https://doi.org/10.1093/treephys/tpy042

Venn SE, Green K (2018) Evergreen alpine shrubs have high freezing resistance in spring, irrespective of snowmelt timing and exposure to frost: an investigation from the Snowy Mountains, Australia. *Plant Ecology* 219: 209–216. https://doi.org/10.1007/s11258-017-0789-8

Wahren C-HA, Walker MD, Bret-Harte MS (2005) Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology* 11: 537–552. https://doi.org/10.1111/j.1365-2486.2005.00927.x

Wang Y, Wang Y, Li Z, Yu P, Han X (2020) Interannual variation of transpiration and its modeling of a larch plantation in semiarid northwest China. *Forests* 11: 1303. https://doi.org/10.3390/f11121303

Wang S, Callaway RM (2021) Plasticity in response to plant-plant interactions and water availability. *Ecology* 102: e03361. https://doi.org/10.1002/ecy.3361

Weijers S, Broekman R, Rozema J (2010) Dendrochronology in the High Arctic: July air temperatures reconstructed from annual shoot length growth of the circumarctic dwarf shrub *Cassiope tetragona*. *Quaternary Science Reviews* 29: 3831–3842. https://doi.org/10.1016/j.quascirev.2010.09.003

Weijers S, Buchwal A, Blok D, Löffler J, Elberling B (2017) High Arctic summer warming tracked by increased Cassiope tetragona growth in the world's northernmost polar desert. *Global Change Biology* 23: 5006–5020. https://doi.org/10.1111/gcb.13747

Weijers S, Beckers N, Löffler J (2018a) Recent spring warming limits near-treeline deciduous and evergreen alpine dwarf shrub growth. *Ecosphere* 9: e02328. https://doi.org/10.1002/ecs2.2328

Weijers S, Pape R, Löffler J, Myers-Smith IH (2018b) Contrasting shrub species respond to early summer temperatures leading to correspondence of shrub growth patterns. *Environmental Research Letters* 13: 34005. https://doi.org/10.1088/1748-9326/aaa5b8

Wipf S (2010) Phenology, growth, and fecundity of eight subarctic tundra species in response to snowmelt manipulations. *Plant Ecology* 207: 53–66. https://doi.org/10.1007/s11258-009-9653-9

Wood SN (2006) Generalized additive models. An introduction with R. Boca Raton.

Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 73: 3–36. https://doi.org/10.1111/j.1467-9868.2010.00749.x

Wundram D, Löffler J (2008) High-resolution spatial analysis of mountain landscapes using a low-altitude remote sensing approach. *International Journal of Remote Sensing* 29: 961–974. https://doi.org/10.1080/01431160701352113

Wundram D, Pape R, Löffler J (2010) Alpine soil temperature variability at multiple scales. *Arctic, Antarctic, and Alpine Research* 42: 117-128. https://doi.org/10.1657/1938-4246-42.1.117

Wyka TP, Oleksyn J (2014) Photosynthetic ecophysiology of evergreen leaves in the woody angiosperms – a review. *Dendrobiology* 72: 3–27. https://doi.org/10.12657/denbio.072.001

Xu L, Myneni RB, Chapin III FS, Callaghan TV, Pinzon JE, Tucker CJ, Zhu Z, Bi J, Ciais P, Tømmervik H, Euskirchen ES, Forbes BC, Piao SL, Anderson BT, Ganguly S, Nemani RR, Goetz SJ, Beck PSA, Bunn AG, Cao C, Stroeve JC (2013) Temperature and vegetation seasonality diminishment over northern lands. *Nature Climate Change* 3: 581–586. https://doi.org/10.1038/nclimate1836

Yee TW, Mitchell ND (1991) Generalized additive models in plant ecology. *Journal of Vegetation Science* 2: 587–602. https://doi.org/10.2307/3236170

Young AB, Watts DA, Taylor AH, Post E (2016) Species and site differences influence climate-shrub growth responses in West Greenland. *Dendrochronologia* 37: 69–78. https://doi.org/10.1016/j.dendro.2015.12.007

Zhang W, Miller PA, Jansson C, Samuelsson P, Mao J, Smith B (2018) Self-amplifying feedbacks accelerate greening and warming of the Arctic. *Geophysical Research Letters* 45: 7102–7111. https://doi.org/10.1029/2018GL077830

Zweifel R, Häsler R (2000) Frost-induced reversible shrinkage of bark of mature subalpine conifers. *Agricultural and Forest Meteorology* 102: 213–222. https://doi.org/10.1016/S0168-1923(00)00135-0

Zweifel R, Zimmermann L, Newbery DM (2005) Modeling tree water deficit from microclimate: an approach to quantifying drought stress. *Tree Physiology* 25: 147–156. https://doi.org/10.1093/treephys/25.2.147

Zweifel R, Zimmermann L, Zeugin F, Newbery DM (2006) Intra-annual radial growth and water relations of trees: implications towards a growth mechanism. *Journal of Experimental Botany* 57: 1445–1459. https://doi.org/10.1093/jxb/erj125

Zweifel R, Drew DM, Schweingruber F, Downes GM (2014) Xylem as the main origin of stem radius changes in Eucalyptus. *Functional Plant Biology* 41: 520–534. https://doi.org/10.1071/FP13240

Zweifel R, Haeni M, Buchmann N, Eugster W (2016) Are trees able to grow in periods of stem shrinkage? *The New Phytologist* 211: 839–849. https://doi.org/10.1111/nph.13995

Zweifel R, Sterck F, Braun S, Buchmann N, Eugster W, Gessler A, Häni M, Peters RL, Walthert L, Wilhelm M, Ziemińska K, Etzold S (2021): Why trees grow at night. *The New Phytologist* 231: 2174-2185. https://doi.org/10.1111/nph.17552

Zwieback S, Chang Q, Marsh P, Berg A (2019) Shrub tundra ecohydrology: rainfall interception is a major component of the water balance. *Environmental Research Letters* 14: 55005. https://doi.org/10.1088/1748-9326/ab1049

Authors

Svenja Dobbert
ORCID: 0000-0001-6231-4572
sdobbert@uni-bonn.de
Prof. Dr. Jörg Löffler
ORCID: 0000-0002-9320-6168
joerg.loeffler@uni-bonn.de
Department of Geography
University of Bonn
Meckenheimer Allee 166
53115 Bonn
Germany

Prof. Dr. Roland Pape
ORCID: 0000-0002-7955-1918
Roland.Pape@usn.no
Department of Natural Sciences and
Environmental Health
University of South-Eastern Norway
Gullbringvegen 36
3800 Bø
Norway

Growth patterns and climate-growth relations for the three focal species

Fig. S1: *Empetrum nigrum* ssp. *hermaphroditum*

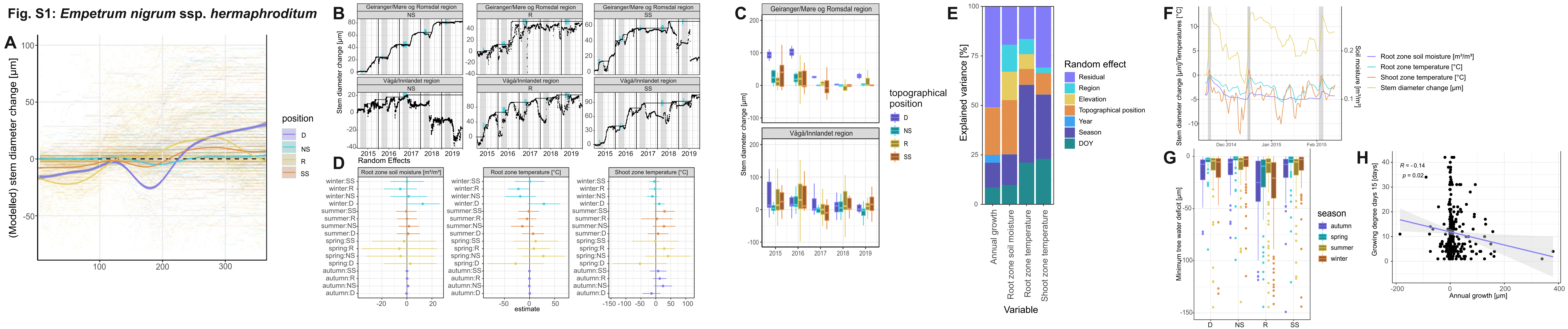

Fig. S1: Growth patterns and climate-growth relations of *E. hermaphroditum*. (A) Intra-annual stem diameter change predicted by generalized additive models (GAMs). Transparent, dotted curves show daily means of measured stem diameter change in relation to the start of the year for all individual dendrometers. 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)

Fig. S2: *Betula nana*

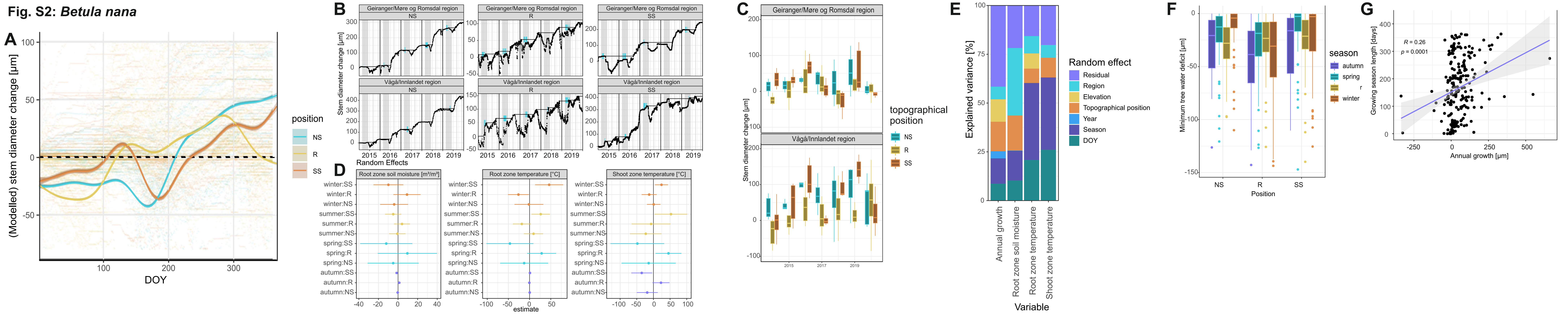

Fig. S2: Growth patterns and climate-growth relations of *B. nana*. (A) Intra-annual stem diameter change predicted by generalized additive models (GAMs). Transparent, dotted curves show daily means of measured stem diameter change in relation to the start of the year for all individual dendrometers. 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.

Fig. S3: *Phyllodoce caerulea*

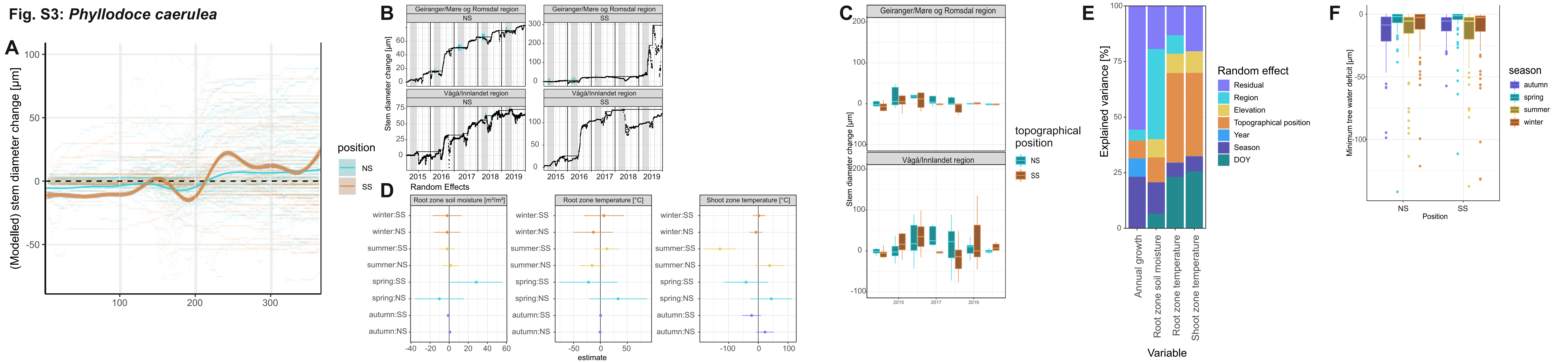

Fig. S3: Growth patterns and climate-growth relations of *P. caerulea*. (A) Intra-annual stem diameter change predicted by generalized additive models (GAMs). Transparent, dotted curves show daily means of measured stem diameter change in relation to the start of the year for all individual dendrometers. 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).