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

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

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

We found high inter-plant variability in growth-defining parameters, but strong similarities in response to the local environment. Radial growth starting in spring and early summer exhibited high sensitivity to winter temperatures and prolonged ground freezing, suggesting that the evergreen species remains partly photosynthetically active during winter, which facilitates carbohydrate accumulation for early-season physiological activities. We discovered a phase of radial stem shrinkage during the winter months, which can be attributed to an active cell water reduction to protect the plant from frost damage.

We identified soil moisture availability and winter freezing conditions as the main drivers of radial stem variability, thus forwarding the ongoing debate on the functional mechanisms of greening and browning in arctic and alpine regions.

1 Introduction

Arctic and alpine ecosystems are especially sensitive to recent climate variability, with temperatures increasing thrice as much as the global average in the past decades, caused by a rising concentration of atmospheric CO_2 and accompanied by a substantial lengthening of the growing period (e.g., Stocker, 2013; Post et al., 2019; AMAP, 2021). This trend has favored growth, abundance, and biomass production of numerous shrub species, resulting in a widespread, yet spatially heterogenic,

greening of the affected areas - with potentially global effects (Myers-Smith et al., 2011; Gough et al., 2015; Brodie et al.,
30 2019; Myers-Smith et al., 2020). The observed greening has been verified using remote sensing techniques (e.g., Carlson et al., 2017) and is caused by both evergreen and broadleaved species, although in different ways (Vowles and Björk, 2019; Weijers and Löffler, 2020), with complex relations between carbon assimilation through photosynthesis, environmentally controlled wood formation and associated plant growth, complicating the understanding of underlying processes, as well as predictions of future trends (Fatichi et al., 2019; Peters et al., 2021). In general, shrubs are considered one of the most
35 responsive plant functional groups to climate variability (Elmendorf et al., 2012). Their expanding trend, in turn, has been associated with climatic feedbacks, such as influence on surface albedo and frozen-ground processes (Sturm et al, 2001; Chapin et al., 2005; Blok et al., 2011; Aartsma et al., 2021). Therefore, an understanding of shrub growth-physiology and its environmental controls is of crucial importance.

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

High-resolution data as provided by dendrometer measurements have the potential to bridge this knowledge-gap and to
55 provide valuable insights into fine-scale response mechanisms towards a changing environment, including information on stem water dynamics and carbon fluxes, with higher quality and resolution than previously attainable (Fritts, 1976; De Schepper and Steppe, 2010; Steppe et al., 2015; Zweifel, 2016; González-Rodríguez et al., 2017). In general, stem diameter increase can be described as a result of cambial division and cell enlargement, which is in turn closely linked to temperature and water potential and therefore strongly affected by environmental stressors. Thus, radial stem change is closely related to
60 cambial activity and underlying fine-scale, eco-physiological mechanisms, including water-driven turgor pressure changes in the xylem (Steppe, 2006; Drew and Downes, 2009; Cuny et al., 2014; Chan et al., 2016; Zweifel, 2016; Peters et al., 2021; Körner, 2021). Because cambial activity occurs at time scales ranging from hours to days (Deslauriers et al., 2007; Köcher et al., 2012; Liu et al., 2018), the fine temporal resolution that is gained by dendrometers provides valuable additional insights

compared to traditional methods. These include intra-annual and seasonal growth behavior of shrubs in alpine environments,
thereby bridging existing knowledge gaps regarding plant productivity in remote ecosystems (Le Moullec et al., 2019). In tree physiology and forest sciences, dendrometers have therefore proven useful to monitor tree responses to environmental fluctuations (Breitsprecher and Bethel, 1990; Duchesne et al., 2012; Ježík et al., 2016; Van der Maaten et al., 2018; Smiljanic and Wilmking, 2018), as recent dendrometers can detect radial stem dimensions at hourly or even shorter intervals (Drew and Downes, 2009; Liu et al., 2018). Starting with the early designs, first described in the 1930s and the 1940s (Reineke, 1932; Daubenmire, 1945), dendrometers have been widely used, focusing on long-term monitoring of growth responses to environmental variables (e.g., Duchesne et al., 2012; Liu et al., 2018; Van der Maaten et al., 2018). Recently, a first study using band-dendrometers to monitor radial stem growth of tree-like shrubs was presented (González-Rodríguez et al., 2017). Because current dendrometers are designed to measure at a micrometer scale, they have the potential to be used on shrubs to provide fine-scale, intra-annual, continuous, and highly comparable information (Dobbert et al., 2021a, b).

In this context, we monitored intra- and inter-annual variability of stem radial variations at alpine ridge positions, testing this novel approach using high-precision dendrometer data derived from individual specimens of the shrub species *Empetrum nigrum* ssp. *hermaphroditum* (hereafter *E. hermaphroditum*), an evergreen shrub almost circumpolar in distribution (Bell and Tallis, 1973) and abundant in the Scandes mountain chain. *E. hermaphroditum* has been identified as a niche constructor species with strong direct effects on tundra communities, including a potential slowing of process rates and lowering of biodiversity with *E. hermaphroditum* encroachment (Bråthen et al., 2018). Because of its complex response to variation in snow cover, it is most common at positions with either shallow or relatively deep snow cover (Bienau et al., 2014; Bienau et al., 2016). Additionally, *E. hermaphroditum* has been described as comparatively resistant to low winter temperatures (Stushnoff and Junttila, 1986; Ogren, 2001) and is usually not affected by grazing (Weijers and Löffler, 2020). The species' stem anatomy was described by Carlquist in 1989 and is characterized by a narrow vessel diameter, which can be interpreted as a form of adaptation to drought or physiological drought due to cold, as it impedes embolism formation (Fig. A2). In general, the family of heath-like shrubs is known to match extreme environments by adapting stem anatomy (Carlquist, 1989) and generally occurs in a wide phytogeographic range at various sites along the alpine elevational gradient. We therefore expect to find the monitored specimens highly adapted to their local environment at the exposed ridge positions, possibly independent from larger scale environmental variability associated with the elevational gradient. Thus, we aim to 1) explain major growth patterns and their variation between years and specimens, linking them to on-site measurements of their immediate environmental surroundings, 2) identify the most important environmental drivers controlling these patterns across sites, and 3) gain insights into potential response to environmental change. The main objective of our work is thus to gain detailed understanding of the growth patterns of one common arctic-alpine dwarf shrub (*Empetrum nigrum* ssp. *hermaphroditum)* and their relation to the micro-environment. With this, we hope to bridge the gap between observed large-scale vegetational shifts, and the fine-scale physiological mechanisms driving these complex changes within the highly relevant arctic-alpine ecosystems.

2 Material and Methods

2.1 Study sites

100 We conducted our study in two alpine mountain regions of central Norway. To the west, the Geiranger/Møre og Romsdal region (62°03′N; 7°15′E) is located within the slightly to markedly oceanic climatic section (O1–O2; Moen, 1999) of the inner fjords. It is characterized by humid conditions, with total annual precipitation of 1,500–2,000 mm in the valleys (Aune, 1993) and a mean annual ambient air temperature of 1.9 °C (range: -23.2 °C–17.2 °C) (Löffler, 2003). To the east, the Vågåmo/Innlandet region (61°53′N; 9°15′E) is located within the continental climatic section (C1; Moen, 1999). The total

105 annual precipitation is low, approximately 300–500 mm in the valleys (Kleiven, 1959) and the mean annual ambient air temperature is -1.2 °C (range: -29.2 °C–16.7 °C) (Löffler, 2003). Our own measurements in the alpine parts of the studied regions indicated that the annual liquid precipitation was 900 mm in the west and 375 mm in the east. The additional amount of snow and its water equivalent remains unknown, but snowdrift leads to an uneven distribution of the snowpack within the complex alpine topography (Löffler, 2007).

110

Across both regions, we used exposed alpine ridge sites that were - within the framework of our long-term alpine ecosystem research project (LTAER; e.g., Löffler and Finch, 2005; Hein et al., 2014; Frindte et al., 2019; Löffler et al., 2021), stratified-randomly chosen along the elevational gradient, to represent the full elevational range of the focal species within our sampled sites. The elevational gradient was stratified into six elevational bands from the tree line upwards, shifted by

115 100 m between regions to account for slightly different conditions and a diverging position of the tree line. In the oceanic region, we used 900, 1000, 1100, 1200, 1300, and 1400 m a.s.l. (above sea level), in accordance with the tree line in this region, which is located at about 750 to 800 m a.s.l. In the continental region, we used 1000, 1100, 1200, 1300, 1400, and 1500 m a.s.l. Here, the tree line is situated slightly higher, at about 1000 m a.s.l. (Rößler et al., 2008; Rößler and Löffler, 2007). Thus, all of our studied sites were located above the tree line. As study sites, we chose micro-topographical positions

120 at wind-blown ridges, likely representing the most extreme thermal regimes, with discontinuous snow cover and deeply frozen ground during winter. Our study design resulted in a total of two regions × six elevational bands = 12 sites, with one specimen monitored per site (N = 12), resulting in 12 × four years = 48 annual dendrometer curves. A summary of total stem diameter variation and environmental conditions measured at each site is presented in Fig. A1.

2.2 Dendrometric data and monitoring setup

125 Here, we applied a technological approach, commonly used for trees, to our multi-stemmed specimens of *E. hermaphroditum*, taking radial stem measurements using dendrometers. The general idea was to apply well-established methods from dendroecology and tree growth analysis within a novel setting, to assess intra- and inter-annual variation in growth patterns and its environmental controls for a shrub species. We mounted our dendrometers on one major above-ground stem of a randomly chosen specimen per site, horizontal to the ground surface and as close to the assumed root collar

130 as possible. During this process, we removed the dead outer bark (periderm) to place the sensor as close to the living tissue

as possible, following a common practice for dendrometer measurements of trees (Oberhuber et al., 2020; Wang et al., 2020; Grams et al., 2021). This ensures that hygroscopic shrinkage and swelling of dead tissues from the outer bark does not influence the diameter measurements. Such processes have been previously addressed in trees (Zweifel and Häsler, 2000; Gall et al., 2002; Ilek et al., 2016), and comparative studies revealed a complex interplay of xylem as well as phloem growth and pressure induced size changes, which simultaneously affect radial stem change and are thus captured by the dendrometers (Turcotte et al., 2011; Zweifel et al., 2014b; Oberhuber et al., 2020; Knüsel et al., 2021) (Fig. A2). Additionally, we avoided specific micro-positions near stones and depressions, inside the radius of other larger shrub species, and near patches of wind erosion (Fig. A3). Stem diameter data were measured at 1 min intervals using dendrometers (type DRO; Ecomatik, Dachau/Germany). The sensor has a temperature coefficient of <0.2 µm/K. To ensure that the dendrometers produce meaningful data, unaffected by the mounting process and bark removal, we tested the study design for several years, before presenting the final study period here. In order to facilitate the following analysis, we aggregated the measured hourly values to get daily stem diameter variation, defined as the mean stem diameter measured each day, following the "daily mean approach" (Deslauriers et al., 2007). All calculations were made using the R statistical software (R Development Core Team, 2020).

2.3 Analysis of seasonal growth patterns

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

$$y(t) = \alpha \times \exp(-\beta \times \exp(-k \times t)),$$

165   (1)

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

$$GoF = 1 - (\Sigma(f - f2)^2/\Sigma f^2$$

170   (2)

where f is the original and f2 is the modeled stem diameter.

We determined growth initiation (onset) and cessation (offset) from this modeled curve to ensure that the main growth phase was being captured. Both dates were defined as the time when 20% and 90% of the total annual modeled growth occurred, respectively. We chose these thresholds following careful testing and, in accordance with our data, they were slightly higher than the thresholds used in similar studies for trees (e.g., Van der Maaten-Theunissen et al., 2013; Van der Maaten et al., 2018; Drew and Downes, 2018). We calculated these growth-defining parameters for each individual curve to assess the variability between sampled specimens. These values entered into the following statistical analysis individually.

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

2.4 Environmental data collection

To identify the thermal constraints of our species at both, the critical location and time scale of action (cf. Körner and Hiltbrunner, 2018), we measured soil temperatures (°C) at a depth of 15 cm below the ground surface (i.e., within the root zone: hereafter "TRZ") and air temperatures 15 cm above the ground surface (i.e., within the shoot zone: hereafter "TSZ"), 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-002 temperature sensors (±0.2 °C accuracy). For the TSZ measurements, the sensors were equipped with passively ventilated radiation shields. Moreover, to identify the soil moisture constraints in the root zone of our specimens, we measured the volumetric soil water content (m³/m³) 15 cm below the soil surface (hereafter SMRZ) at all sites. The uncalibrated SMRZ was measured at 1 min intervals and recorded as hourly means using ONSET's HOBO type S-SMD-M005 soil moisture sensors (±3% accuracy). Additionally, we measured the shoot zone global radiation (W/m²) at 1 cm above the ground surface in close proximity to the plant (hereafter GRSZ) using ONSET's HOBO type S-LIB-M003

silicon pyranometers (±10 W/m² accuracy). We made sure that those measurements were not affected by the canopy. Our data covered a period of four full calendar years from January 1, 2015, to December 31, 2018. Missing data did not occur at the chosen sites.

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

2.5 Climate-growth relations and potential drivers of radial stem change

To analyze the effect of the on-site environmental conditions on the observed growth patterns, we performed a set of multiple and partial regressions, alongside correlation analyses. All statistical analyses were carried out in R (R Development Core Team, 2020), and site-specific values for each sampled specimen entered into each analysis, to overcome common misconceptions regarding the averaging of environmental data (cf. Körner and Hiltbrunner, 2018; Löffler and Pape, 2020).

First, we tested relations among our previously defined parameters (cf. 2.3 Analysis of seasonal growth patterns) by performing a partial regression analysis (Table 1). Regressions were tested for multicollinearity among the independent variables that would have affected the regression outcome using several measures of collinearity, which are implemented in the mctest package (Imdad and Aslam, 2018). A regression model was discarded if more than two of the six calculated measures indicated collinearity among the independent variables. We then analyzed the environment-growth relationship by correlating the parameters (total annual growth, growth initiation, peak growth, growth cessation, start of the shrinking period, peak shrinking, and day of year (DOY) at which peak shrinking occurred) with potential micro-environmental drivers (Table 3), using Pearson's correlation coefficient. For each group of potential drivers (means, maxima, days at which the maxima were reached for shoot and root zone temperatures, global radiation, and soil moisture), we subsequently performed a multiple regression analysis, predicting each of the parameters from a fitted linear regression model. Finally, we performed a moving window correlation, correlating daily rates of stem diameter change (compared to the previous day) with measured daily environmental values for each of our four environmental parameters (i.e., TRZ, TSZ, GSZ und SMRZ). Here, we chose to include the complete dendrometer series, rather than reducing the data to the main growing season (Deslauriers et al., 2007), to capture seasonal stem shrinking and swelling throughout the year.

Table 1: Results of multiple partial regression analysis for total annual growth (measured cumulative stem diameter increment in comparison to the previous year's maximum stem diameter) and annual peak shrinking (maximum stem water deficit) against growth parameters (growth initiation, growth cessation, and peak growth).

Variable	Independent variable	Pearson's correlation coefficient	Partial R²	Semipartial (Part) correlation	Coefficient	Standard Error	T-statistic	p-value
Total annual growth	Growth initiation	-0.169	-0.399	-0.162	-0.349	0.144	-2.423	0.021
	Growth cessation	-0.245	0.448	0.187	0.428	0.153	2.793	0.009
	Peak growth	0.909	0.922	0.890	25.228	1.900	13.278	<0.001
	Total		*0.930*					*<0.001*
Annual peak shrinking	Growth initiation	0.133	0.144	0.129	0.209	0.259	0.808	0.425
	Growth cessation	0.016	-0.037	-0.033	-0.057	0.275	-0.057	0.838
	Peak growth	0.402	0.395	0.383	8.167	3.411	2.394	0.023
	Total		*0.790*					*<0.001*

235 **Table 2**: **Summary of calculated environmental parameters (means). Numbers in parentheses represent inter-site variability (standard deviation, +/- SE).**

Parameter	2015	2016	2017	2018
Shoot zone temperature (T_{SZ})				
Day, when maximum T_{SZ} is reached [DOY]	183	203 (7.41)	203	208
	(5.36)		(0.29)	(0)
First day, at which T_{SZ} >0 [DOY]	100	74 (7.28)	25	104
	(9.24)		(12.41)	(0.56)
Annual T_{SZ} sum [°C]	37.28	47.96	16.21	199.96
	(125.36)	(109.48)	(133.57)	(102.65)
T_{SZ} sum at growth initiation [°C]	-291.87	-421.91	-189.45	-384.76
	(57.03)	(134.73)	(96.27)	(139.80)
Number of days with T_{SZ} >0 (Growing degree days, GDD0) [days]	175	169 (4.48)	165	173
	(6.91)		(5.09)	(5.38)
Number of days with T_{SZ} >5 (Growing degree days, GDD5) [days]	82	117 (3.93)	100	121
	(5.50)		(6.74)	(3.73)
Number of days with T_{SZ} >10 (Growing degree days, GDD10) [days]	21	32 (4.57)	12	57
	(2.53)		(2.80)	(3.27)
Root zone temperature (T_{RZ})				
Day, when maximum T_{RZ} is reached [DOY]	186	206	204	197
	(0.08)	(0)	(0.11)	(1.6)
First day, at which T_{RZ} >1 [DOY]	146	140 (1.73)	139	127
	(3.95)		(1.43)	(1)
Annual T_{RZ} sum [°C]	358.52	351.23	339.15	477.58
	(121.54)	(104.54)	(117.34)	(90.09)
T_{RZ} sum at growth initiation [°C]	-127.05	-326.05	-116.97	-303.43
	(79.27)	(140.50)	(90.72)	(149.08)
Number of days with T_{RZ} >0 (Growing degree days, GDD0) [days]	182	170 (4.19)	176	196
	(8.01)		(5.78)	(5.99)
Number of days with T_{RZ} >5 (Growing degree days, GDD5) [days]	96	124	117	119
	(5.75)	(2.14)	(5.27)	(2.74)
Number of days with T_{RZ} >10 (Growing degree days, GDD10) [days]	7	14	10	57
	(3.70)	(7.48)	(3.68)	(4.10)
Soil moisture				
Day, when maximum soil moisture is reached [DOY]	197	219	193	222
	(21.28)	(17.38)	(18.85)	(22.02)
Day, when minimum soil moisture is reached in autumn [DOY]	351	342 (3.16)	351	353
	(3.25)		(2.32)	(2.88)

Annual soil moisture sum [m³/m³]	54.65	52.78	55.52	54.51
	(4.09)	(3.53)	(3.46)	(3.47)
First day, at which soil moisture >0.15 [DOY]	135	128 (2.53)	126	110
	(3.37)		(6.51)	(3.28)

Global radiation

Day, when maximum global radiation is reached [DOY]	171	156 (1.12)	181	177
	(4.53)		(3.04)	(4.55)
First day, when global radiation >50 W/m² [DOY]	74	75	85	76
	(9.62)	(7.93)	(6.71)	(6.50)
Annual global radiation sum [W/m²]	26686.66	27742.87	25863.3	31229
	(1423.77)	(1133.43)	(1584.93)	(1313.83)
Global radiation sum at growth initiation [W/m²]	16342.47	15435.76	16197.58	15928.75
	(1155.10)	(1678.66)	(1929.40)	(2882.40)

Snow

Number of snow-free days [days]	361	361 (5.53)	358	356
	(4.90)		(13.79)	(9.48)
First autumn frost (T_{RZ} <0°C) [DOY]	320	296 (2.84)	310	301
	(3.60)		(4.58)	(4.70)

3 Results

3.1 Intra-annual growth patterns

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

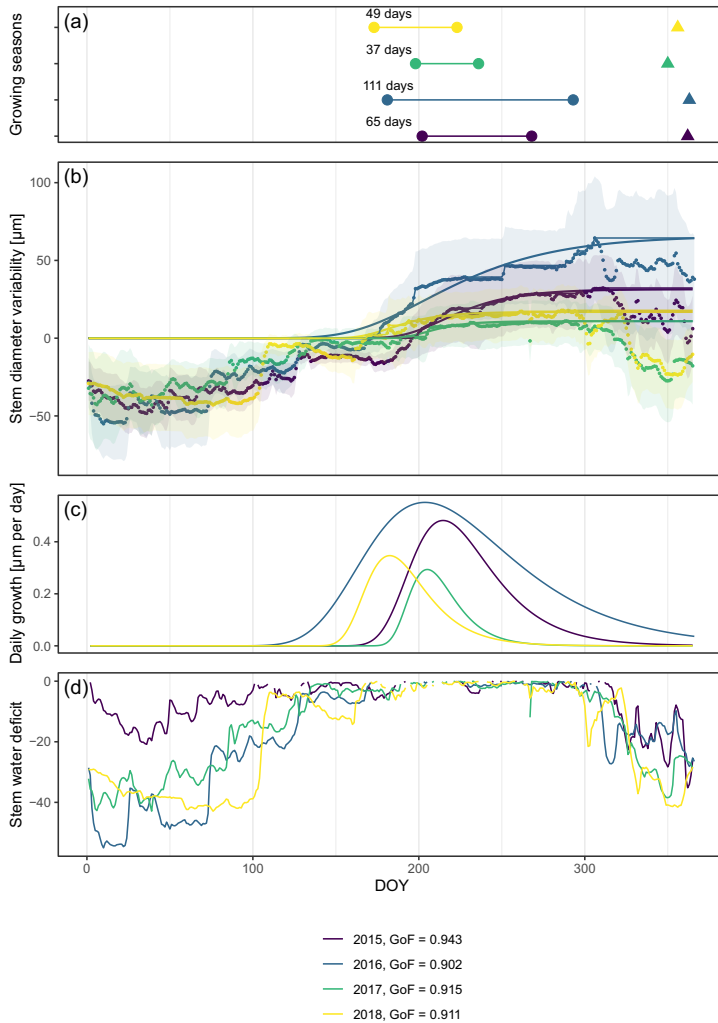



Figure 1: Observed and modelled variability in stem diameter. (a) Growing seasons derived from fitted Gompertz models and timing of peak shrinking defined as the maximum stem water deficit (triangles). (b) Averaged measured daily stem diameter variability and fitted Gompertz models (a goodness-of-fit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

Total annual growth ranged from 11 µm in 2017 to 65 µm in 2016, on average, with the growing season starting in May or June (Table 3 and Fig. 1). Interestingly, year-to-year variability and patterns in total growth were similar in the two studied regions (Fig. A4). Furthermore, while our data showed slight differences in seasonal growth patterns between the two regions, there were no clear overall patterns beyond the high inter-specimen variability observed in the whole dataset (Fig. A5). Our chosen growth parameters, growth initiation, peak growth, and growth cessation, together explained 93% of the variance in total annual growth, with peak growth having by far the greatest influence. For stem contraction (shrinking), the same parameters explained 79% of the variance (Table 1 and Fig. A6), suggesting that the observed winter shrinking in *E. hermaphroditum* might be linked to growth during the growing season.

Table 3: Parameters of stem change (means). Numbers in parentheses represent variability between specimens (standard deviation, +/- SE).

Year	2015	2016	2017	2018
Stem diameter variation (measured variation between start and end of the year) [µm]	31.74 (12.73)	63.86 (11.62)	11.35 (20.79)	19.91 (11.08)
Stem radial growth (growth-induced, irreversible stem increment compared to the previous year) [µm]	31.81 (11.53)	64.66 (21.82)	14.85 (6.27)	17.45 (9.46)
Stem radial shrinking (stem shrinking during the winter months, after the end of the main growing season) [µm]	35.18 (10.35)	28.13 (14.44)	38.45 (12.77)	41.61 (13.47)
Day peak shrinking occurs [DOY]	362 (16.62)	363 (4.38)	350 (17.16)	356 (13.63)
Day shrinking starts [DOY]	311 (26.38)	306 (14.07)	289 (10.35)	287 (12.81)
Growth initiation [DOY]	202 (12.56)	181 (12.12)	198 (8.49)	173 (13.65)
Growth cessation [DOY]	267 (14.06)	292 (14.87)	235 (12.24)	222 (15.47)
Growth duration [days]	65 (7.93)	111 (7.14)	37 (10.70)	49 (9.04)
Peak growth (maximum daily growth rate) [µm]	0.48 (0.40)	0.55 (0.85)	0.29 (0.20)	0.35 (0.50)
Day peak growth occurs [DOY]	215 (13.68)	204 (9.54)	205 (8.24)	182 (13.85)
Mean daily growth [µm]	0.09 (0.03)	0.18 (0.06)	0.03 (0.02)	0.05 (0.03)

3.2 On-site environmental conditions

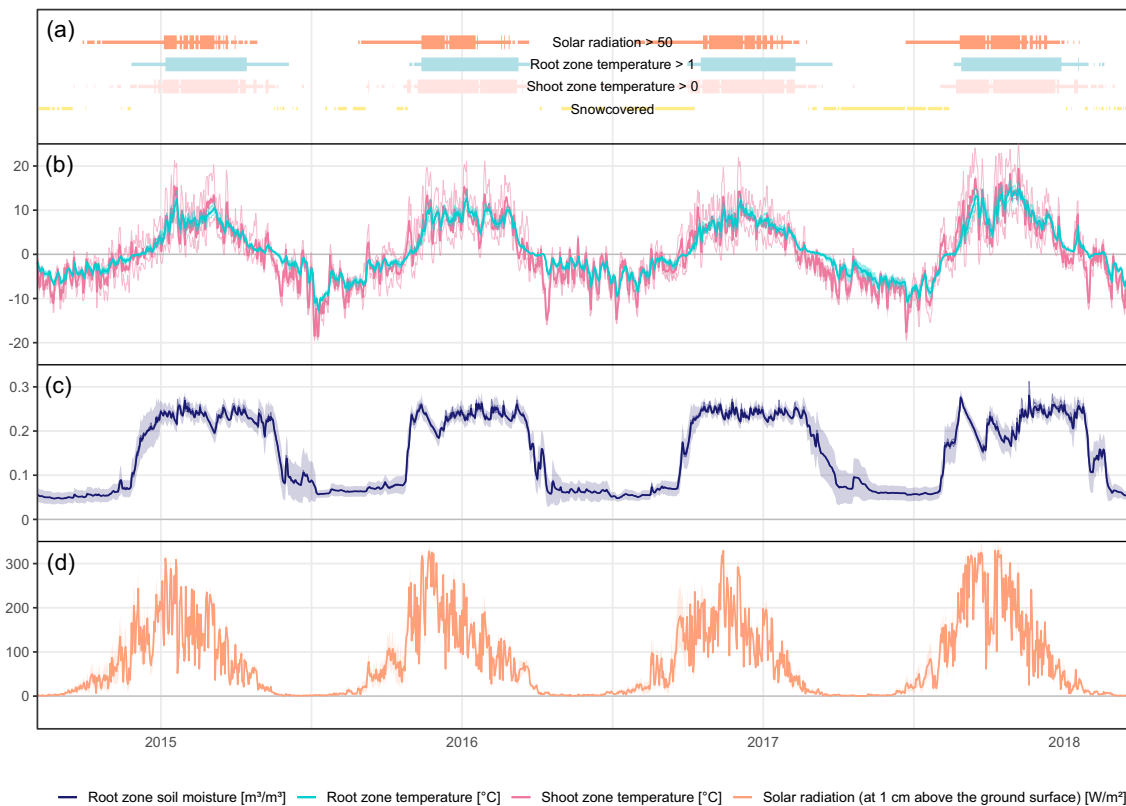
The different near-surface regimes of TRZ, TSZ, SMRZ, and GRSZ at our monitored sites are illustrated in Fig. 2. From these raw data, we calculated a set of variables defining the near-ground environmental conditions experienced by each specimen based on the expected effects on different growth mechanisms. Averaged values for all sites (N=12) are summarized in Table 4.

275

Figure 2: Micro-environmental data. Daily mean values of shoot and root zone temperatures (b), soil moisture (c), and global radiation (d). Measurements were taken at each site individually, but averaged here over all sites for visualization. Shaded areas indicate standard deviations. Bars (a) show time spans for certain environmental conditions, with narrow bars marking the time at which the given condition was present at least at one of the monitored sites, whereas broad bars mark the time for which the given

280 condition was detected at all sites.

Table 4 : Summary of collected environmental data: Annual mean, minimum and maximum values as well as mean values for each meteorological season. Numbers in parentheses represent site variability (standard deviation, +/- SE).

Environmental parameter	Year	Mean	Min	Max	Mean spring	Mean summer	Mean autumn	Mean winter
Shoot zone temperature [°C]	2015	0.10	-13.66	21.24	-2.44	6.95	1.29	-5.50
		(0.34)	(0.70)	(0.59)	(0.34)	(0.36)	(0.37)	(0.43)
	2016	0.13	-19.53	21.10	-1.39	8.40	0.30	-6.86
		(0.30)	(0.74)	(0.46)	(0.33)	(0.33)	(0.30)	(0.34)
	2017	0.04	-15.70	21.97	-1.68	7.28	-0.07	-5.48
		(0.37)	(0.40)	(0.40)	(0.35)	(0.34)	(0.45)	(0.48)
	2018	0.55	-19.373	25.156	-1.071	10.029	0.214	-7.782
		(0.28)	(1.19)	(0.42)	(0.28)	(0.33)	(0.32)	(0.51)
Root zone temperature [°C]	2015	0.98	-7.01	14.27	-1.80	7.04	2.48	-3.88
		(0.33)	(0.56)	(0.33)	(0.31)	(0.39)	(0.32)	(0.37)
	2016	0.96	-13.16	14.37	-1.48	8.76	2.03	-5.52
		(0.29)	(0.58)	(0.42)	(0.31)	(0.34)	(0.24)	(0.36)
	2017	0.93	-9.76	13.57	-1.67	7.71	1.87	-4.30
		(0.32)	(0.52)	(0.43)	(0.28)	(0.31)	(0.32)	(0.49)
	2018	1.31	-11.03	16.79	-1.76	10.45	1.67	-5.27
		(0.25)	(0.65)	(0.48)	(0.25)	(0.34)	(0.23)	(0.47)
Soil moisture [m³/m³]	2015	0.15	0.05	0.28	0.09	0.23	0.15	0.06
		(0.01)	(0.01)	(0.02)	(0.03)	(0.04)	(0.17)	(0.05)
	2016	0.14	0.06	0.27	0.12	0.23	0.12	0.06
		(0.01)	(0.01)	(0.02)	(0.03)	(0.04)	(0.15)	(0.03)
	2017	0.15	0.05	0.27	0.10	0.24	0.14	0.07
		(0.01)	(0.01)	(0.01)	(0.02)	(0.03)	(0.15)	(0.05)
	2018	0.15	0.05	0.312	0.13	0.21	0.14	0.06
		(0.01)	(0.00)	(0.01)	(0.03)	(0.04)	(0.15)	(0.03)
Global radiation [W/m²]	2015	73.11	0	809.34	74.38	169.70	41.82	4.72
		(3.90)		(24.50)	(11.49)	(4.32)	(1.85)	(1.10)
	2016	75.80	0	823.93	93.94	165.04	39.51	3.53
		(3.10)		(28.48)	(9.32)	(5.49)	(2.70)	(0.78)
	2017	70.86	0	791.81	78.45	166.59	32.27	4.26
		(4.34)		(37.21)	(12.55)	(5.38)	(1.30)	(0.94)
	2018	85.57	0	846.38	117.15	190.84	28.59	3.25
		(3.60)		(46.05)	(7.73)	(7.12)	(1.93)	(0.80)

285   In all four monitored years, our sampled specimens experienced the highest temperatures during summer and short periods of shallow snow cover during winter (Fig. 3). The period in which our specimens were snow-covered varied considerably between the monitored winters and between sites. The winter of 2015/2016 had comparatively little snow, whereas 2017/2018 was snow-covered for the longest period. In 2018, the highest mean temperatures were expressed because of exceptionally high summer temperatures (number of days with TSZ > 10, growing degree days, GDD10 = 57), whereas 2015

290   and 2017 both experienced shorter periods of high temperatures. Temperatures varied slightly among sites (Table 4 and Fig. A1), with a noticeable but not linear temperature decline with elevation, and a slightly lower difference between the lowest and highest study sites than proposed by the linearly regressed adiabatic lapse rate (Löffler et al. 2006). The reasons are daily variations in the adiabatic lapse rate induced by nocturnal inversions, and variations over specific weather phenomena and seasonality (e.g. Löffler et al. 2006; Pape et al. 2009; Wundram et al. 2010). As expected, the shoot and root zone

295   temperature curves were well coupled. Additionally, we detected slight variability between the two studied regions, but overall similar seasonal temperature patterns on the measured micro-scale (Fig. 3 and A1), which differs from the regional climate signal. This is because these measured temperature signals reflect local, near-ground conditions, which are decoupled from the regional signal. Global radiation showed similar patterns at all sites as well, following the course of the astronomic sun angle, with a mid-summer maximum; however, there were large variations according to cloud coverage. As

300   such, 2018 experienced a short period of temperature and radiation decrease during summer (Fig. 2).

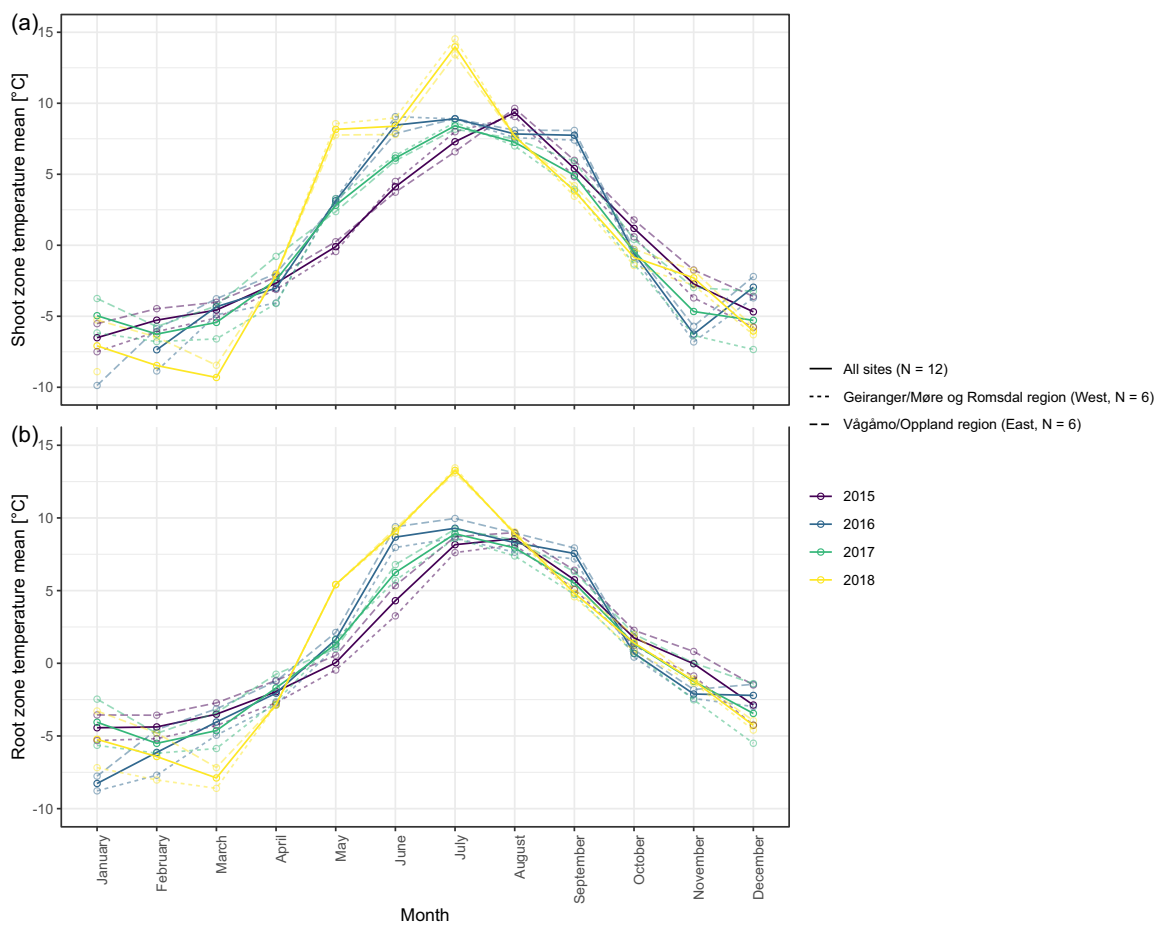



Figure 3: Mean monthly shoot (a) and root (b) zone temperatures from 2015 to 2018, for visualization purposes averaged i), over the measured sites per study region, and ii), over all measured sites.

3.3 Environmental controls of radial stem change

We investigated how the specific on-site environmental conditions were correlated with the parameters described above. A set of 25 chosen environmental parameters (Table 2) was able to explain total annual growth to a very large extent, even though not all parameters contributed significantly. Separate regression models for each environmental variable revealed an overall high explanatory power for global radiation and soil moisture on total annual growth and peak growth, compared to temperatures (Fig. 4). However, moving window correlations revealed a high seasonal variability in climate-growth

relations, with high variation across years. Overall, on-site environmental conditions had comparatively strong explanatory power during spring, when many of the specimens started stem increment. This spring stem increment was positively linked to radiation during cold spring conditions in 2015 and 2017 and showed negative relations to air temperatures in late spring, possibly reflecting late cold snaps (Fig. 2 and Fig. 5).

315

The correlation analysis (Fig. 6) confirmed the lack of uniformity, indicating that a multitude of environmental drivers influenced growth, yet, to a very low degree and with high inter-annual variation. Maximum soil moisture was significantly correlated with total annual growth (r = 0.47). Minimum soil moisture was positively correlated with growth cessation (r = 0.56), as were annual mean soil moisture (r = 0.40) and soil moisture sum (r = 0.39), indicating a strong overall influence of

320   soil moisture on growth processes throughout all four seasons. Growth initiation, on the other hand, was linked to spring radiation (r = -0.37) and winter temperatures (r = 0.40). Furthermore, growth cessation was negatively correlated with maximum shoot zone temperatures (r = -0.46), mean summer temperatures (r = -0.40), and GDD5 (r = -0.40).

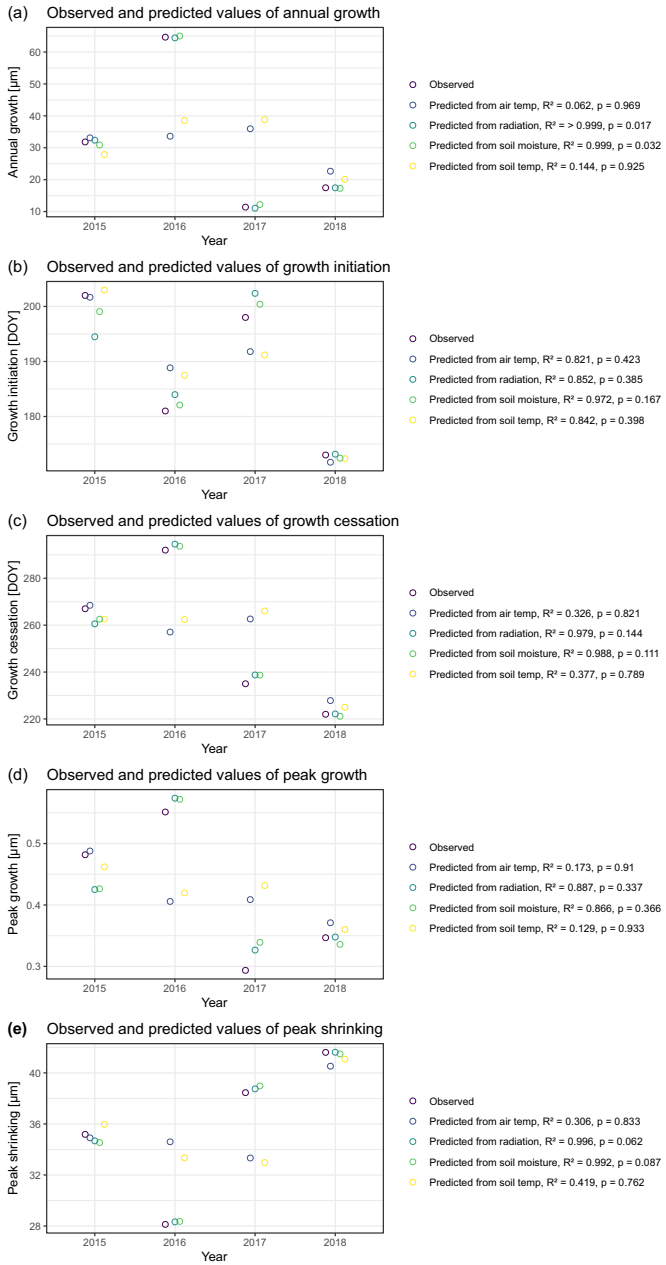
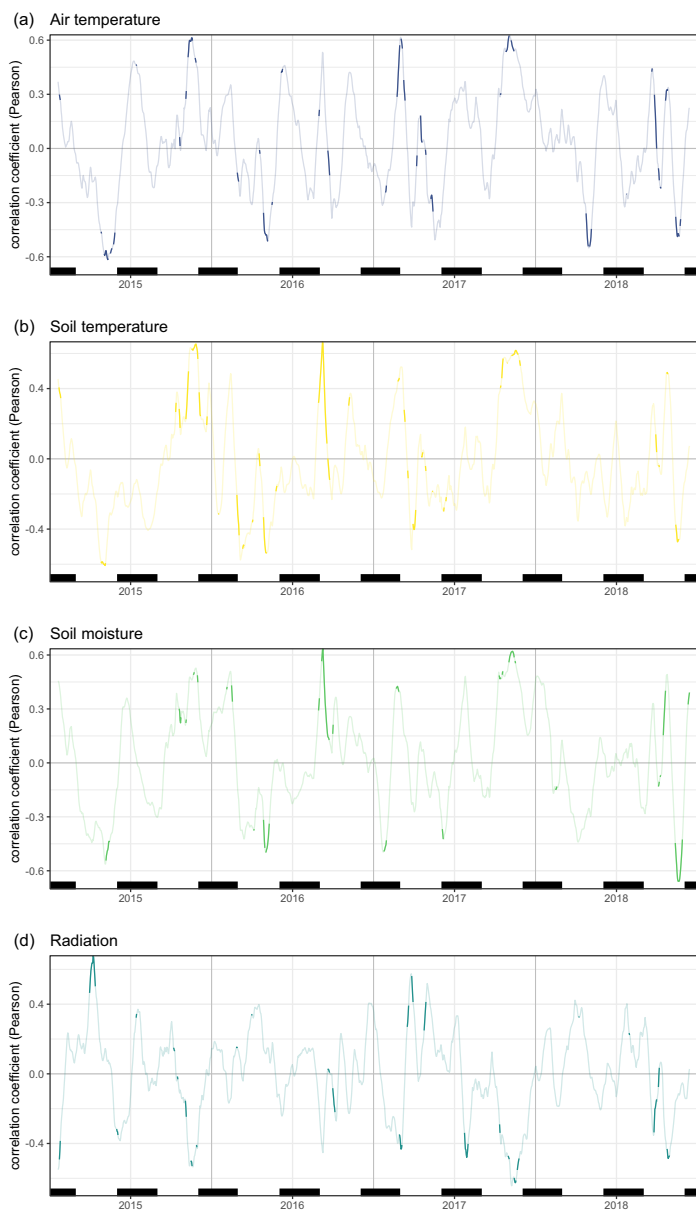



Figure 4: Observed and predicted values of total annual growth, defined as growth-induced, irreversible stem increment compared to the previous year, timing of growth (growth initiation and cessation), peak growth, defined as t he maximum daily growth rate, and peak shrinking, defined as the maximum stem shrinking during the winter months. Predictions were obtained from the respective mean of four micro-environmental drivers and the Julian day at which their maximum occurred.

330 **Figure 5:** Moving pearson's correlation coefficients for daily rates of radial stem diameter change against measured daily values of on-site environmental parameters (TSZ, TRZ, SMRZ, GRSZ). Non-significance (p > 0.05) is indicated by transparency and black bars show meteorological seasons. All individual specimens entered into the analysis separately.

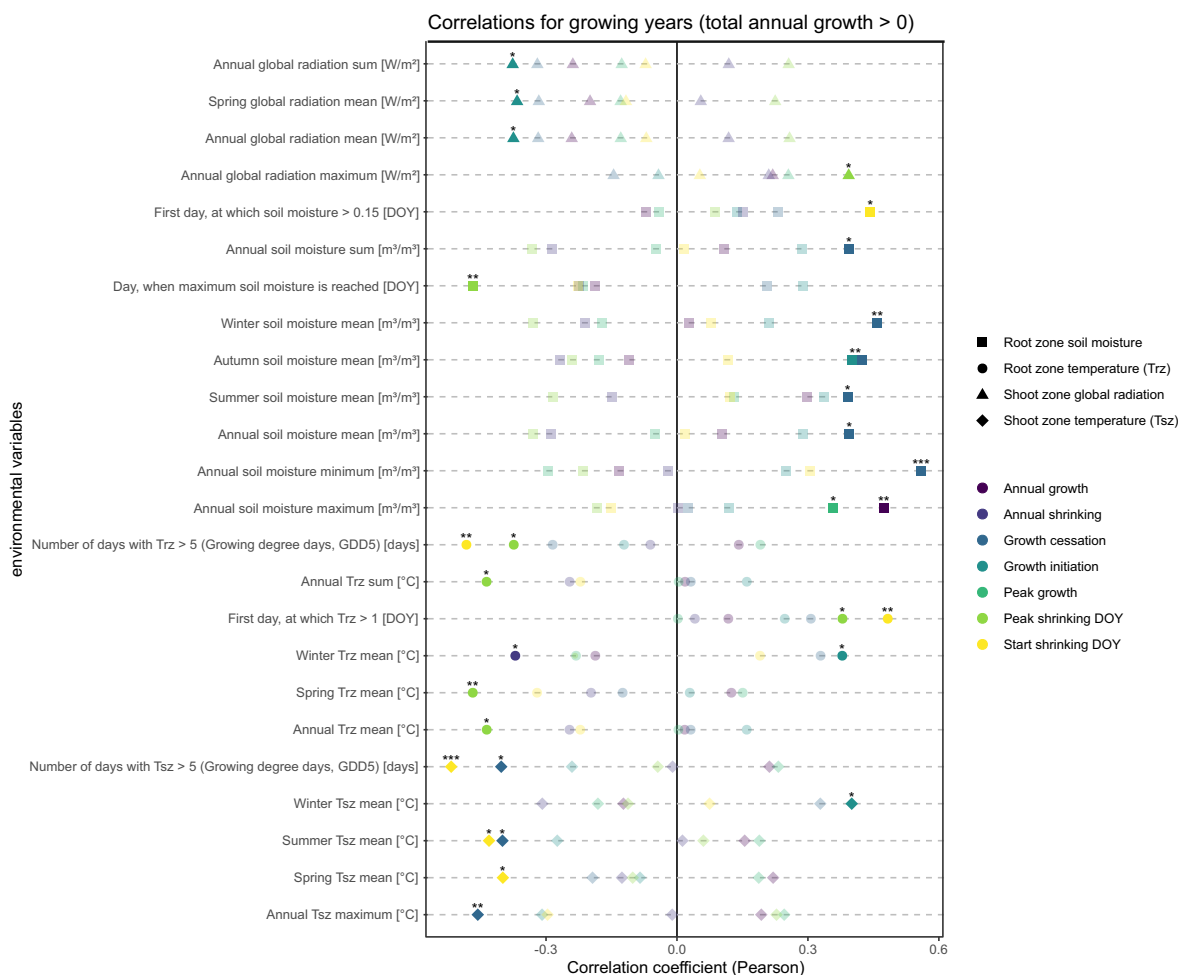



Figure 6: Pearson's correlation coefficients for previously defined parameters of stem change **with key environmental parameters, characterizing on-site environmental conditions (for years with a total annual growth > 0). The parameters included: a) Total annual growth, defined as irreversible stem increment in comparison to the previous year, b) Total annual shrinking, defined as stem shrinking during the winter months, after the end of the growing season, c) Timing of the main growing season (start and end), d) Peak growth, defined as the maximum daily growth rate, e) Timing of the winter shrinking phase, including the start of stem shrinking (usually cooccurring with the maximum annual stem diameter) and peak shrinking, or the day when minimum winter stem diameter is reached. All dates were given as day of the year (DOY). Only those environmental parameters that correlated significantly with at least one growth parameter are included in the plot. Nontransparent colors indicate significance (*** = p-value < 0.001, ** = p-value < 0.01, * = p-value < 0.05).**

4 Discussion

In this study, we demonstrated that our focal species *Empetrum hermaphroditum* displayed distinct annual patterns of stem
diameter change in response to near-ground environmental drivers and in close accordance with distinct conditions caused
by the local topographical characteristics of the studied wind-blown ridge positions. These unique environmental conditions
are a feature of the heterogeneous topography that characterizes alpine terrain (Scherrer and Körner, 2011) and are thus
distinctly different from the immediate surroundings. They include high exposure to global radiation and very little,
temporary snow cover during the winter months, associated with very low temperatures (Wundram et al., 2010). Moreover, a
layer of lichens limits water transport from the soil to the atmosphere, reducing evaporative loss to a minimum and, as such,
reducing the danger of summer drought (Löffler, 2005). These conditions varied comparatively little between the study
regions (Fig. 2 and Fig. A1) as well as along the elevational gradient. Consequently, they led to very similar seasonal growth
patterns and timing of growth (Fig. A5), suggesting that their influence on growth conditions was stronger than the
governing regional environmental signal, which was not clearly reflected in our growth data, as suggested by Bär et al.
(2008). Here, future studies using a higher number of samples along the elevational gradient might confirm, if the observed
growth patterns develop independently of elevational constraints, with possibly important implications for shrub distribution
and growth limitation with elevation in alpine ecosystems (Körner, 2021).

In contrast to the high synchrony between seasonal growth patterns, our study showed high inter-plant and interannual
variability in total annual growth (Fig. A1 and Fig. A4), which has been previously described in *E. hermaphroditum* (Bär et
al., 2008) and could be a result of internal growth variability within the multi-stemmed plant itself (Bär et al., 2007). Some
specimens (31% of the dendrometer curves) experienced zero growth in more than one year and we linked these dormant
years to comparatively long periods of snow cover during the previous winter, which might prevent *E. hermaphroditum* from
photosynthetic activity and resource accumulation, and thus, may limit a crucial precondition of growth success. This
assumption was supported by a highly negative correlation between stem diameter variation and the number of snow-free
days (R = -0.60, p = 0.024, Fig. A9) during these years. In accordance with Buchwal et al. (2013), we assumed that during
years of no apparent radial growth, dwarf shrubs might prioritize growth in the more protected and long-living below ground
segments, instead of investing in the more vulnerable shoots. This ability to reduce cambial activity to a minimum and cease
above-ground wood formation is a trait common among woody plants (Wilmking et al., 2012).

The effects of winter snow cover on shrub growth are a critical topic in arctic and alpine ecology, with findings ranging from
positive (Blok et al., 2015; Addis and Bret-Harte, 2019) to negative (Schmidt et al., 2010) growth responses, depending on
snow depth and vegetation type. Our results highlight the importance of winter conditions for early growth, indicating that
for our sampled evergreen species the degree to which photosynthetic activity was effective in synthesizing carbohydrates
during the winter months was especially important. Such continued photosynthetic activity was found in *E. hermaphroditum*,
as well as several other evergreen shrub species before (e.g. Bienau et al., 2014; Wyka and Oleksyn, 2014; Blok et al., 2015).

It is forced by the exposure of the plant to high incoming solar radiation, which typically occurs at ridge positions that lack snow cover (Saccone et al., 2017). Accordingly, we concluded that growth initiation might be driven by the constantly increasing radiation with the astronomic rise of the angle of the sun. At this time of the year, energy transfer from global radiation into thermal heat was low, but radiation was high enough for photosynthetic activity, which might explain the decoupling of thermal and radiation drivers of growth initiation. Under snow free conditions, it is likely that, in our study design, global radiation is directly linked to soil thawing close to the soil surface, which was previously linked to growth onset (Descals et al., 2020). Furthermore, we found growth initiation in *E. hermaphroditum* was positively linked to winter temperatures (Fig. 6), indicating that low winter temperatures were correlated with an early start of the growing season, in contrast to common assumptions relating high temperatures during late winter to an early growth start (Dolezal et al., 2020). This highlights the influence of high radiation on energy storage during periods of an absent snow cover, which is usually accompanied by low temperatures, whereas mild winters are often associated with cloudy, humid weather, and snow cover on the ridges.

However, forced photosynthetic activity during winter causes continued water transport under extreme temperatures, increasing the risk of cavitation (Tyree and Sperry, 1989; Venn and Green, 2018), while long and severe ground frosts might limit access to soil moisture, and frost-triggered droughts might thus result in tissue damage caused by an internal water deficit (Mayr et al., 2006). Yet, *E. hermaphroditum* at our studied sites proved mostly frost hardy, drought tolerant and highly adapted to these conditions (Carlquist, 1989; Hacke et al., 2001), with winter stem diameter change closely linked to soil moisture availability and singular thawing events, suggesting that the sampled specimens were able to utilize available liquid water even under extreme conditions (Fig. A7). In this context, we assume that *E. hermaphroditum* uses cell dehydration to actively protect living cells from the consequences of freezing (e.g., ice nucleation), causing the radial stem contraction during phases of extreme subzero temperatures evident in our data. In trees, radial stem shrinkage has been related to sap flow and tree water content (Winget and Kozlowski, 1964; Zweifel and Häsler, 2000; Zweifel et al., 2006; Tian et al., 2019). When temperatures sink below approximately −5 ∘C, extra-cellular water begins to freeze, inducing the osmotic withdrawal of intra-cellular water and, thus, cell and ultimately stem shrinkage (Zweifel et al., 2000; King et al., 2013). As such, stem shrinkage could be interpreted as a result of freezing processes causing living cell shrinkage because of water losses, as well as a strategy to avoid frost damage, especially where the protective effects of snow cover are missing (Kuprian et al., 2014; Neuner, 2014; Charra-Vaskou et al., 2016). We concluded that surviving during extreme winters was the main principle governing *E. hermaphroditum* growth when existing at alpine ridge positions, causing unique adaptations to local micro-site conditions.

During these extreme conditions, low temperatures prevented cell production and differentiation, resulting in a carbon overflow (Körner, 2015; Saccone et al., 2017), which gives *E. hermaphroditum* the ability to start growth activity as soon as liquid water is available in the root zone (Starr and Oberbauer, 2003). In general, carbon assimilation may be greater or lower than the demand for plant functions, resulting in periods of carbon surplus and deficit, respectively (e.g. Martínez-

Vilalta et al., 2016). Though there is never a critical depletion of carbohydrates in alpine plants, resources at or shortly after snowmelt and, thus, at the onset of the growing season, are still diminished - due to respiratory consumption during winter (Körner 2021). Any surplus of carbohydrates, gained by photosynthetic activity in late winter/spring due to high solar irradiance is, thus, likely to be beneficial for growth throughout the growing period. The ability to use additional photosynthetic opportunities throughout the year is similar to mechanisms found in *Juniper thurifera* (Gimeno et al., 2012) and, for high latitude vascular plants and shrubs, photosynthetic activity was previously observed under extreme thermal conditions (Semikhatova et al., 1992; Lundell et al., 2008). If confirmed, the ability to preserve resources produced during the winter months would give *E. hermaphroditum* a local advantage compared to broadleaved species at the same sites. However, it is most likely a unique feature of the snow free ridge positions and thus not present at other micro-topographic positions, where energy budget and water balance is strongly altered (Dahl, 1956; Fritts, 1976; Löffler et al., 2006; Pape et al., 2009).

Furthermore, we found total annual growth was largely determined by peak growth, the maximum daily growth rate, indicating that the overall duration of the growth phase was less important for overall growth than the daily growth rate. Thus, we cannot confirm a clear relation of growing season length and overall growth (Rammig et al., 2010; Blok et al., 2011; Prislan et al., 2019). The predominant role of peak growth in controlling total growth suggested that the shrubs were usually able to invest in new cells following the cell water level rise caused by thawing conditions, most likely affected by prior carbohydrate storage (see above). At the same time, an early growth start after favourable winter conditions may not be efficient in terms of total growth, if conditions in early summer prevent the survival of the formed cells. For most snow-free ridges, budburst and flowering are not influenced by snowmelt and can, therefore, occur early on, causing high vulnerability to late frost events (Weijers et al., 2018b). This is in accordance with the findings of Choler (2018) and Weijers et al. (2018a), who suggested a strong influence of sub-zero temperatures in spring, counteracting improved conditions during summer. In our data, we found strong evidence of this relation in inter-annual comparison, with low growth rates in 2018, despite favourable summer conditions after an early growth start followed by a short cold snap and ground frost. In contrast, we found high summer growth rates in 2016. During this year, we measured the highest number of days with soil temperatures above 5 °C, with temperatures rising quickly and steadily to that threshold without reaching continuously higher values during the summer (Fig. 2). This could indicate that optimum growth conditions lie within a soil temperature span of 5 to 10 °C, which is in accordance with previously reported temperature thresholds for alpine plant distribution (Körner and Paulsen, 2004; Rossi et al., 2008; Steppe et al., 2015). On the other hand, our regression analysis indicated no direct relationship between total growth and near-surface temperatures and no clear thermal growth limit, suggesting more complex connections, probably influenced by the evident temperature extremes at our chosen sites, as well as complex interconnections with soil water availability (Körner and Hiltbrunner, 2018). Overall, our results highlight the overall importance of the root zone soil moisture as the key driver of growth in *E. hermaphroditum*. This was evident in the strong contraction and expansion patterns of the stems, most likely controlled by active or passive water level variability within the plant, linked to the extreme thawing and freezing processes prominent at our study sites. To fully explore these processes

and possible links to transpiration dynamics and carbon fluxes, on-site measurements of vapour pressure deficit, as a measure of atmospheric water demand, might yield additional insights in future studies (Novick et al., 2016; Peters et al., 2021; Zweifel et al., 2021).

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Shoot zone temperatures played a role in determining when xylogenesis ceased, but a critical temperature threshold, as present in many trees (Rossi et al., 2007; Rossi et al., 2008; Deslauriers et al., 2008) and found for xylem growth of alpine rhododendron shrubs (Li et al., 2016), could not be determined for *E. hermaphroditum*. In trees, the timing of maximum growth and growth cessation in cold environments has been linked to day length (Heide, 1985; Rossi et al., 2006; Duchesne

455 et al., 2012). This cannot be confirmed for our monitored shrubs because of the high variability observed between specimens. Therefore, timing of these critical parameters is most likely controlled by other factors in shrubs than those assumed for trees. Growth cessation was linked to summer temperatures, suggesting that high peak temperatures during the summer might delay growth cessation by the thermal promotion of carbohydrate storage, enabling growth continuity even under unfavorable thermal constraints during autumn (Fig. 6). Additionally, we identified soil moisture as the main driver for

460 the end of the growing season. Yet, we could not determine a minimum soil moisture threshold, which would lead to growth cessation. A contrasting pattern was shown in 2016, with a prolonged growing phase after dry conditions during early summer. Thus, we concluded that *E. hermaphroditum* growth was strongly dependent on the availability of water, which is why dry conditions during spring and early summer were less crucial and did not lead to immediate growth cessation, because evaporation was not fully active at these times of the year leaving enough exploitable moisture available. This

465 accounts for the species dependency on a damp climate and high rainfall (Bell and Tallis, 1973).

Overall, our findings confirmed the positive effects of temperatures on shoot growth in *E. hermaphroditum* to some extent (Chapin and Shaver, 1985; Shevtsova et al., 1997; Hollesen et al., 2015; Ackerman et al., 2017; Bråthen et al., 2018), yet, a clear link between near-surface thermal conditions and growth was lacking. Yet, previous studies commonly used free

470 atmospheric air temperature measured at 2 m above ground, in combination with ring width measurements (e.g. Bär et al. 2007 and 2008; Hollesen et al., 2015; Weijers et al., 2018a). While a direct comparison of annual growth derived from our dendrometer measurements and such ring width measurements at the studied sites revealed high synchrony (Fig. A8), dendrometer measurements have the potential to reveal much deeper insights into complex functional aspects of growth, and, in combination with on-site environmental data, might help rethinking climate growth relations. For example, while a phase

475 of winter stem shrinking has been described in trees (Winget and Kozlowski, 1964; Zweifel and Häsler, 2000), the distinct and strongly pronounced phase we found in our sampled specimens might be described as a unique feature of shrub growth, which we documented for the first time in this study. The reason why this phase has not been described earlier might be attributable to the methods for shrub growth measurements used in the past, which were insufficient to document intra-annual variability at the appropriate time scale. High-precision dendrometers can reveal these patterns in growth variability,

480 demonstrating the large amount of additional information gained from this method compared to traditional measuring methods (Knüsel et al., 2021). For our focal species *Empetrum hermaphroditum,* dendrometer measurements yielded several

novel insights into phenology and growth physiology. However, further studies are necessary to fully explore how dendrometer measurements compare to traditional measurement methods and which additional information can be gained. Still, the comparative data presented in Fig. A8 clearly shows that both have the potential to reveal important aspects of stem variability and growth.

The fine-scale data provided by dendrometer measurements proved highly important, since they allowed for a detailed growth analysis, revealing a growth mechanism that is highly adapted to the local micro-environmental conditions at our studied exposed ridge positions. The ability of continuing photosynthetic activity throughout the year and to thus aggregate resources for use in early cell formation, as observed in other evergreen plants (Wyka and Oleksyn, 2014) might provide a competitive advantage of the evergreen species over deciduous species in the same habitat, limiting the risk of losing resources through competition. To sustain the continued metabolism throughout the year, we found that *E. hermaphroditum* was highly dependent on available moisture, and thus, highly adapted to local microsite conditions. Accordingly, the overall growth mechanism was mainly defined by moisture, as well as solar radiation. Hence, temperatures mainly played a role in freezing and thawing processes, on an intra-annual scale. We can thus confirm that while there is a link between shrub growth and warming conditions, it is most likely not uniform and highly variable over spatial and temporal scales (Elemendorf et al., 2012). The high local adaptation explains the wide distribution and competitive ability of the species at these sites (Bienau et al., 2014; Bienau et al., 2016; Löffler and Pape, 2020) and highlights the prominent role of on-site near-ground environmental conditions in controlling growth processes (Zellweger et al., 2020). In a changing climatic regime, this dependency on specific winter radiation conditions and soil moisture availability might become a disadvantage, complicating the adaptation to warming winters and longer snow-covered periods, coupled with prolonged dry periods during summer (Hollesen et al., 2015; Weijers, Pape et al., 2018), which might cause early growth cessation. Thus, we conclude that changing winter conditions and altered snow regimes represented one of the most serious threats to evergreen shrub growth in tundra ecosystems and *E. hermaphroditum* will not be able to persist at exposed positions in a changing climate or respond with longer periods of dormancy to warming conditions. This will potentially promote the spread of competing deciduous species and thus contribute to the arctic-alpine greening trend.

Data availability

All underlying data pertinent to the results presented in this publication are publicly available in a data publication in "ERDKUNDE---Archive for Scientific Geography" (https://www.erdkunde.uni-bonn.de). DOI: 10.3112/erdkunde.2021.dp.01.

Author contribution

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

Competing interests

515 The authors declare that they have no conflict of interest.

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