

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

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

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

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INTRODUCTION

The change of vegetation within the tundra, the so-called “Arctic greening,” has been identified as one of the clearest examples of the

terrestrial impact of climate change (IPCC 2014). Observed from space over huge expanses of the circumpolar North (Myneni et al. 1997, Jia et al. 2003, Epstein et al. 2012, Berner et al. 2020), undergirded by plot-based evidence (Elmendorf

et al. 2012), and attributed to warming at more than twice the rate of the rest of the planet (Chapin et al. 2005, Serreze and Francis 2006, IPCC 2014, Post et al. 2019), wide-ranging repercussions of this greening on ecosystems and their functioning are to be expected. Effects along a trophic cascade are observed, including declining herbivore populations, altered competition and predation, putting species at risk, and threatening endemic biodiversity (e.g., Fauchald et al. 2017, Ims et al. 2019). Moreover, vegetation trends of this scale are of immense importance to the carbon balance of tundra ecosystems (Joos et al. 2001, Mishra and Riley 2012, Alday et al. 2020), putting their large carbon pool at risk (Schuur et al. 2013, 2015). They also have major impacts on the global water cycle (Zwieback et al. 2019), and they lead, due to changes in the surface albedo, to self-amplifying feedbacks regarding the global climate system (Chae et al. 2015, Zhang et al. 2018, Bjorkman et al. 2020).

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

As such, the actual physiological processes and mechanisms behind the increased shrub growth are still poorly understood (Ackermann et al. 2017, Nielsen et al. 2017).

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

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

MATERIAL AND METHODS

Species and specimens

For this study, we chose two focal dwarf shrub species abundant across arctic-alpine ecosystems, one evergreen (*Empetrum nigrum* ssp. *hermaphroditum*, crowberry, hereafter *E. hermaphroditum*)

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

Study sites

Our study is based on long-term monitored specimens from two study regions located in the alpine mountain region of central Norway, characterized by a steep regional climate gradient (Fig. 1). To the east, the Vågåmo/Innlandet region ($61^{\circ}53' \text{ N}$; $9^{\circ}15' \text{ E}$) is located within the continental climatic section (C1; Moen 1999). With total annual precipitation of approximately 300–500 mm in the valleys, this area experiences the highest aridity found in Norway (Kleiven 1959). In contrast, our second study region to the west, the Geiranger/Møre og Romsdal region ($62^{\circ}03' \text{ N}$; $7^{\circ}15' \text{ E}$), is located within the slightly to markedly oceanic climatic section (O1–O2; Moen 1999) of the inner fjords. It is characterized by humid

conditions, with total annual precipitation of 1500–2000 mm in the valleys (Aune 1993). Measurements within the studied alpine regions indicated annual liquid precipitation of 900 mm in the West and 375 mm in the East. The additional amount of solid precipitation and its snow water equivalent remains unknown, but snowdrift leads to an uneven distribution of the snowpack within the complex alpine topography (Löffler 2005, 2007), leaving the studied plots on elevated ridges with discontinuous snow cover and deeply frozen ground in winter. In regard to temperature, those exposed sites represent the most extreme regimes found in the area where the mean annual ambient air temperature is 1.9°C (range -23.2°C [January] to $+17.2^{\circ}\text{C}$ [July]) in the west and -1.2°C (range -29.2°C [January] to $+16.7^{\circ}\text{C}$ [July]) in the east (e.g., Löffler 2003). The ridge positions used for sampling were stratified-randomly chosen to cover the elevational gradient, following the framework of our long-term alpine ecosystem research project (LTAER; e.g., Löffler and Finch 2005, Hein et al. 2014, Frindte et al. 2019, Beckers et al. 2020). They were placed at elevational levels from the tree line upwards, shifted by approximately 100 height-meters between regions to account for the depression of the elevational zonation toward the west (Löffler et al. 2006, Löffler and Pape 2020, Löffler et al., 2021). In accordance with the elevationally constrained range of the studied two species, we chose ten specimens from the oceanic region (700–1300 m a.s.l.) and 15 specimens from the continental region (900–1510 m a.s.l.) representing our chosen evergreen species, as well as five specimens from the oceanic region (700–1024 m a.s.l.) and ten specimens from the continental region (900–1510 m a.s.l.), representing our chosen deciduous species (Fig. 1). If available, we chose to monitor more than one site per elevational level, and at each site, the specimens were monitored for five full consecutive years (October 1, 2014–December 31, 2019), resulting in a total of 200 ((10 West + 15 East) *E. hermaphroditum* + (5 West + 10 East) *B. nana*) \times 5 yr dendrometer curves, each showing hourly stem diameter changes during the course of one year.

Dendrometric data, monitoring setup, and environmental data collection

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

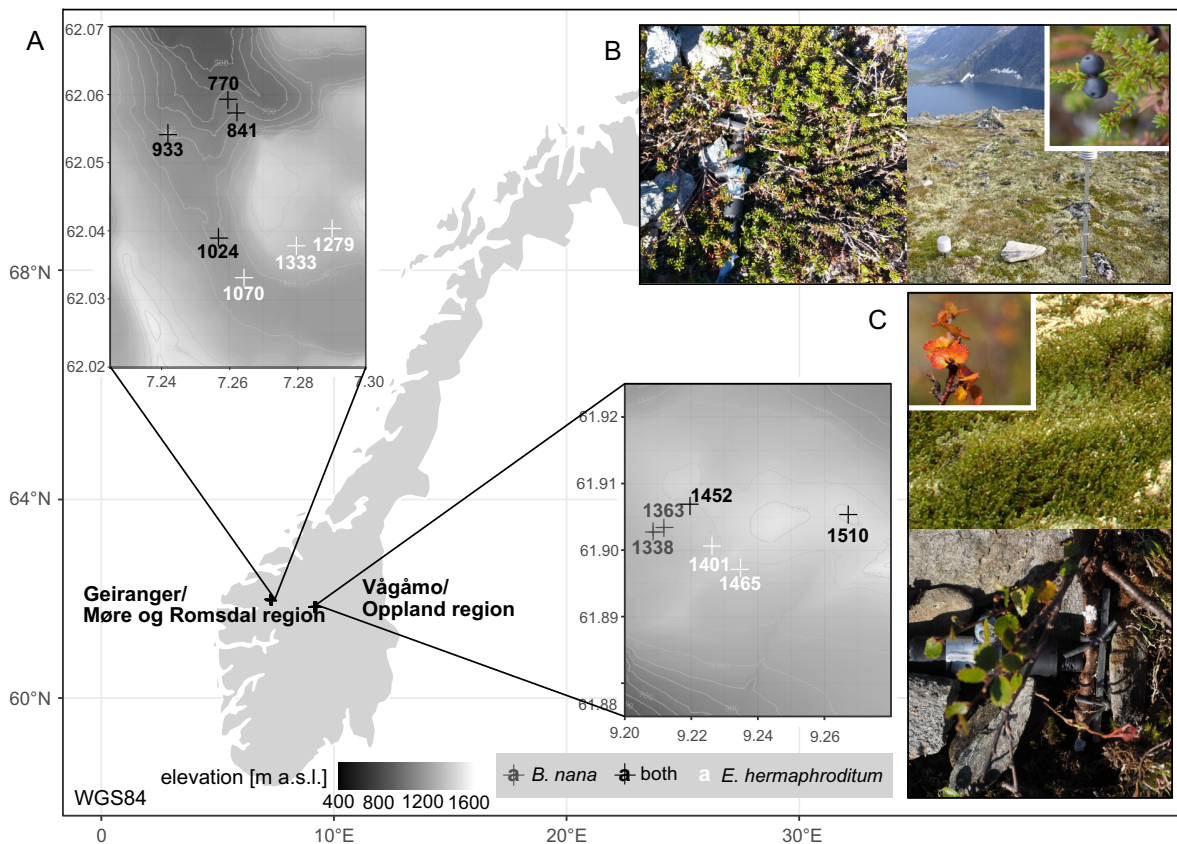


Fig. 1. Study regions in Central Norway and location of the individual study sites (A). At some sites both species were present and monitored (black), at others only one of the two focal species was found (gray, white). The shape file used to create the map was derived from the maps package (Becker et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

Ecomatik, Dachau/Germany) mounted on one major aboveground stem horizontal to the ground surface on randomly chosen specimens, as close to the assumed root collar as possible (approximately 1–5 cm above ground). As addressed by Bär et al. (2006, 2007), this major stem is thought to represent the whole plant at least partly. However, how radial stem changes vary within the individual plant and between multiple stems of the same specimen is still not fully understood and might be a topic for further studies. We tried to account for this variation by sampling a high number of individual specimens. Also, we made sure that the chosen specimens were as representative for the observed local conditions at each site as possible, avoiding positions near stones and small depressions,

inside the radius of other larger shrub species, and near patches of wind erosion. The temperature coefficient of the sensor used was $<0.2 \mu\text{m}$ and measurements were taken at 1-min intervals and aggregated using the daily mean approach, averaging dendrometer data using the dendrometeR package (Van der Maaten et al. 2016), developed for the R statistical software (R Core Team 2020), which was primarily used in our analyses. Additionally, the annual stem diameter curves were normalized through subtraction of the previous year maximum to exclude year-related growth trends and maximize the separation of irreversible growth from water-related swelling and shrinking of the stem. This necessity arises because dendrometers are not measuring the absolute stem diameter, but rather changes in

stem diameter relative to the start of the measurement cycle. Thus, the initial stem diameter, which ranged from 1829.1 to 10023.7 μm for *E. hermaphroditum*, and from 2851.8 to 12095.6 μm for *B. nana*, was removed from the annual curves. Finally, outliers were excluded, by defining cutoff ranges, using the interquartile range (IQR) and the 25th (Q1) and 75th (Q3) percentile ($Q1/Q3 \pm 1.5 \times \text{IQR}$). This led to a total exclusion of approximately 2% of daily measurements per curve.

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

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

Micro-environmental data

Averaged near-surface regimes of TRZ, TSZ, SMRZ, and GRSZ over all monitored sites are illustrated in Appendix S1: Fig. S1 and Fig. S2, as well as in Appendix S1: Table S1. The exposed ridge positions were characterized by extremely low winter temperatures and severe ground freezing, with high exposure to global radiation and only periodic snow cover. Temperatures usually started to increase in April or May.

Lowest annual mean temperatures were measured in 2017 (TSZ = 0.371°C , TRZ = 1.230°C), highest in 2018 (TSZ = 0.912°C , TRZ = 1.614°C) with shoot and root zone conditions following, expectedly, a similar regime throughout the course of our study. The year 2015 stands out because of a comparatively long winter, with lasting low temperatures throughout the meteorological spring and soil moisture rising only gradually, indicating reoccurring freezing conditions. In contrast, the years 2019 and 2018 are characterized by an early rise in spring temperatures, followed by considerable spring cold snaps as evident by drops in the SMRZ regimes, indicating renewed soil freezing. Additionally, the winter 2015/2016 is characterized by the lowest temperatures measured throughout the studied period (Appendix S1: Figs. S1, S2).

Analysis of seasonal growth patterns

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

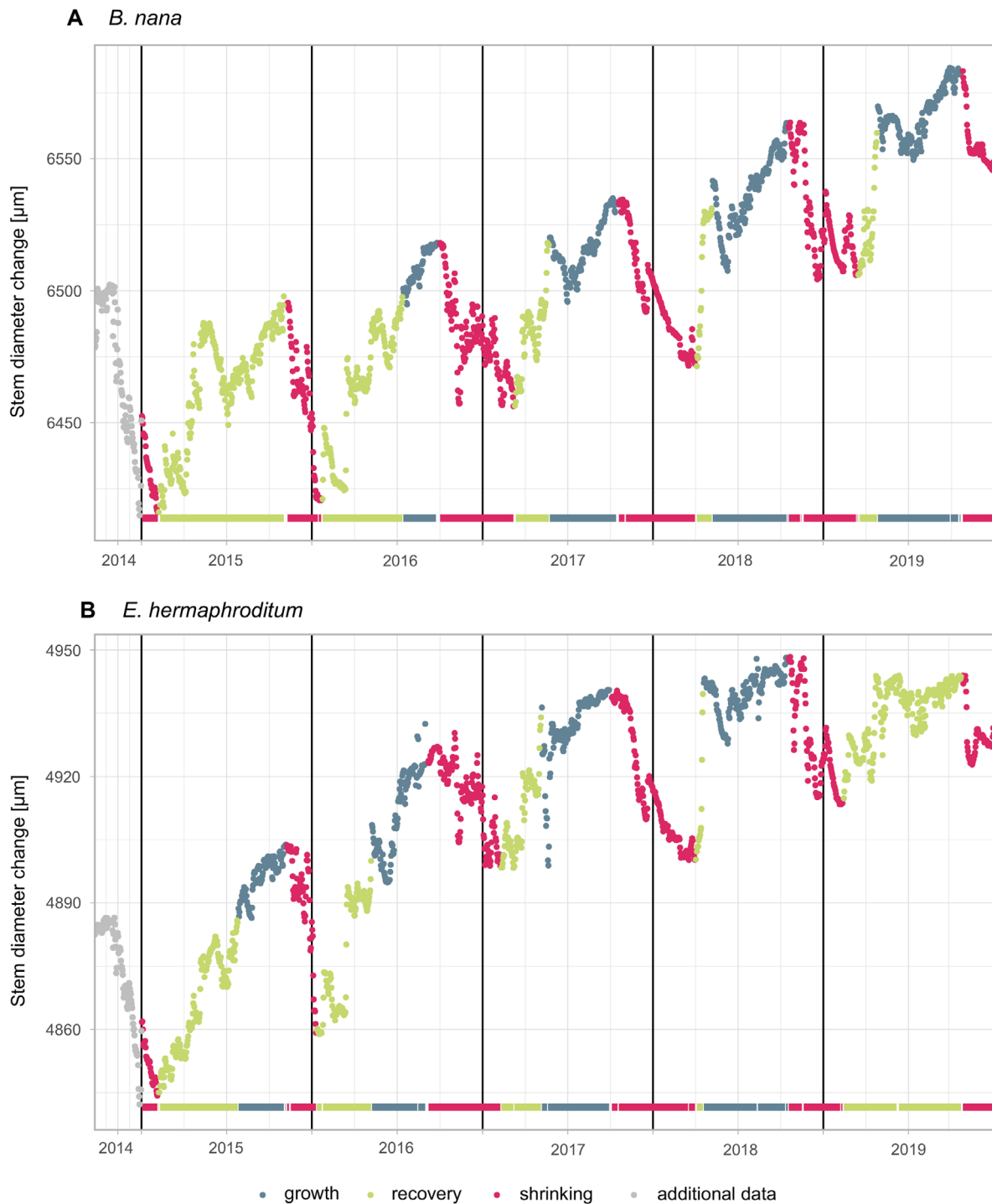


Fig. 2. Stem diameter variations in *B. nana* (A) and *E. hermaphroditum* (B). Measured daily radial stem change averaged over all studied sites (15 for *B. nana* and 25 for *E. hermaphroditum*). Colors represent phases of stem change. Additional relevant data beyond the defined studied period (2015–2019)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

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

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

Correlation and linear mixed-effects analysis

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

To avoid generalizations which might arise from data averaging data measured at the individual sites into mean values, we additionally fitted linear mixed-effects models to our data,

using the lme4 R package (Bates et al. 2015). For these models, we again chose annual irreversible stem growth as response variable, and monthly mean values for all environmental parameters as fixed effect. The individual specimens were included as random effect.

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

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

Partial least squares regression

To complement the correlation analysis, we additionally analyzed the relation between annual growth and micro-environmental parameters applying partial least squares regression (PLSR; Wold 1975), also known as projection on latent structures (Abdi 2010). Our aim in

applying this statistical approach was solely to use variable selection methods to assess the relative importance of certain micro-environmental conditions in promoting or hindering growth, and to define a subset of relevant conditions. Primarily intended for multidisciplinary problems (Wold 1980), PLSR has found application in ecological studies during the past decade (Carrascal et al. 2009, Frindte et al. 2019, Löffler and Pape 2020). Main advantages include that it works without distributional assumptions (Wold 1980, Dijkstra 1983, Vinzi et al. 2010) and deals efficiently with unreliability and heteroscedasticity issues (Martens and Næs 1989, Frindte et al. 2019). Moreover, the method is not limited, if the number of predictors exceeds the number of observations or if the predictors are highly correlated, as is the case with our data. This distinguishes PLSR from classical methods, like multiple linear regression and principal component regression, and makes it highly suitable for our purposes (Geladi and Kowalski 1986, Carrascal et al. 2009, Frindte et al. 2019). Following the approach successfully applied by Löffler and Pape (2020) to determine species thermal niches, we aggregated our (hourly) environmental data, rounding to 0.5°C for temperatures and 0.01 m³/m³ for soil moisture values. Subsequently, we counted and totaled the frequency of each value occurring within the rounded time-series. These calculations were performed for each meteorological season separately, resulting in sets of 35–124 predictor variables, which were subsequently scaled and centered. Previously calculated annual growth (which was found to be almost normally distributed, see Appendix S1: Fig. S4) served as the associated response variable. For final single response model estimation, we used the SIMPLS algorithm (de Jong 1993), implemented in the R package *mdatools* (Kucheryavskiy 2020). The optimal number of components in the PLSR model was found using Wold's R criterion (Wold 1978), and tenfold cross-validation was used to assess the explained variance during model calibration and validation. To assess the relevance of each independent variable from the created models, there are numerous methods available (reviewed by Mehmood et al. 2012). Based on assessments by Farrés et al. (2015) and Frindte et al. (2019), we considered the selectivity ratio (SR, defined as the ratio of explained to

residual (unexplained) variance for each variable in the target projection vector), most appropriate for our data. From the SR, we derived the explained variance (SR/abs(SR + 1)) for more contrastable results. In the resulting plots (Appendix S1: Figs. S5, S6), the variables with highest values represent the most important explanatory variables (Rajalahti et al. 2009). Finally, we increased the interpretability of these results by multiplying the SR of each variable by the sign of its corresponding regression coefficient, making it easy to identify which variables were positively or negatively related to the dependent variable (Rajalahti et al. 2009, Löffler and Pape 2020). Thus, we were able to clearly identify those environmental conditions that were significantly related to annually realized growth.

RESULTS

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

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

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

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

On the contrary, our correlation analysis revealed a negative growth response of *B. nana* to high late summer temperatures and radiation (Figs. 4 and 5), evident in the years 2018 and 2019, which were characterized by comparatively warm summers. In contrast, in 2015, in which we measured the lowest summer temperatures, we found a more positive temperature-growth relation for both species, and, in the intermediate years 2016 and 2017, *B. nana* showed no clear dependency on summer and

spring temperatures, responding positively to wet conditions characterized by high soil moisture and low radiation input instead (Appendix S1: Fig. S11). This indicates that raising summer temperatures and increasing summer radiation might affect *B. nana* negatively (Appendix S1: Fig. S11). PLSR results (Figs. 6 and 7) support those findings, indicating a negative influence of high summer soil temperatures, with *B. nana* being negatively affected by root zone temperatures exceeding 10°C. For *E. hermaphroditum*, we were able to identify a significant optimum range of root zone temperatures (7°–8°C), but higher temperatures (11°–12°C) had a negative effect as well.

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

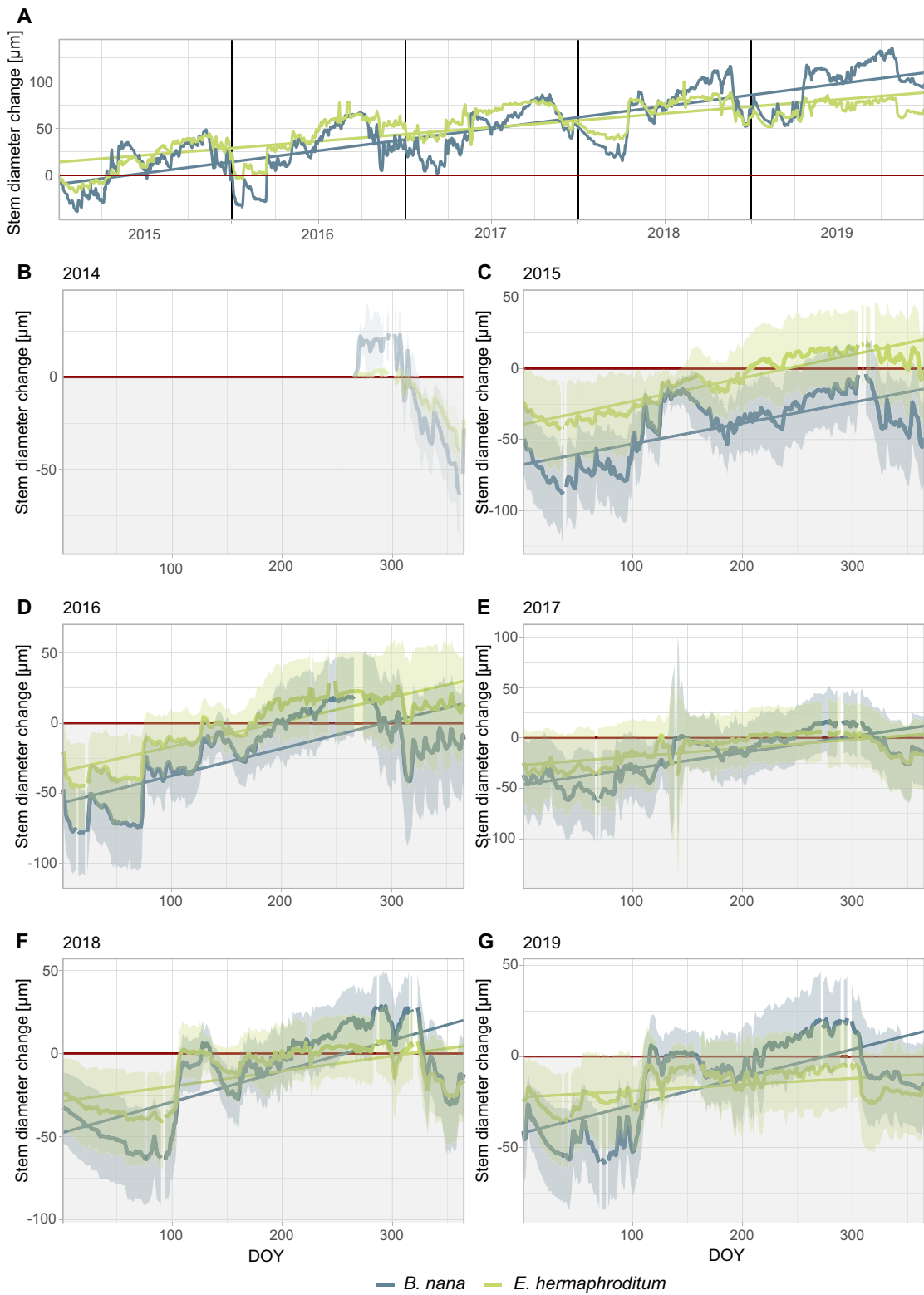


Fig. 3. Averaged annual stem diameter variations (± 1 SE) relative to previous years maximum (B–G) and

(Fig. 3. Continued)

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

DISCUSSION

Dendroecological meaningful aboveground stem diameter curves can successfully be derived from both *B. nana* and *E. hermaphroditum* using high-precision dendrometers. In addition to annual growth characteristics measured by traditional methods (e.g., Bär et al. 2006, 2007, Macias-Fauria et al. 2012, Shetti et al. 2018, Le Moulllec et al. 2019), we were thus able to directly track stem diameter changes on a daily time-scale. Net stem diameter change in woody plants is thought to represent the sum of

expansion/shrinkage of living cells due to changes in turgor pressure and expansion/shrinking of xylem due to changes in xylem water tension (Lintunen et al. 2016, Lindfors et al. 2019). In most years, our focal species presented a phase of irreversible stem increment (usually associated with cambial activity, including cell enlargement and cell division, Rossi et al. 2008, Drew et al. 2010, Steppe et al. 2015, Zweifel 2016) during the summer months. This phase was missing in individual specimens, indicating reduced or inhibited cambial activity during those years, most likely caused by the extreme

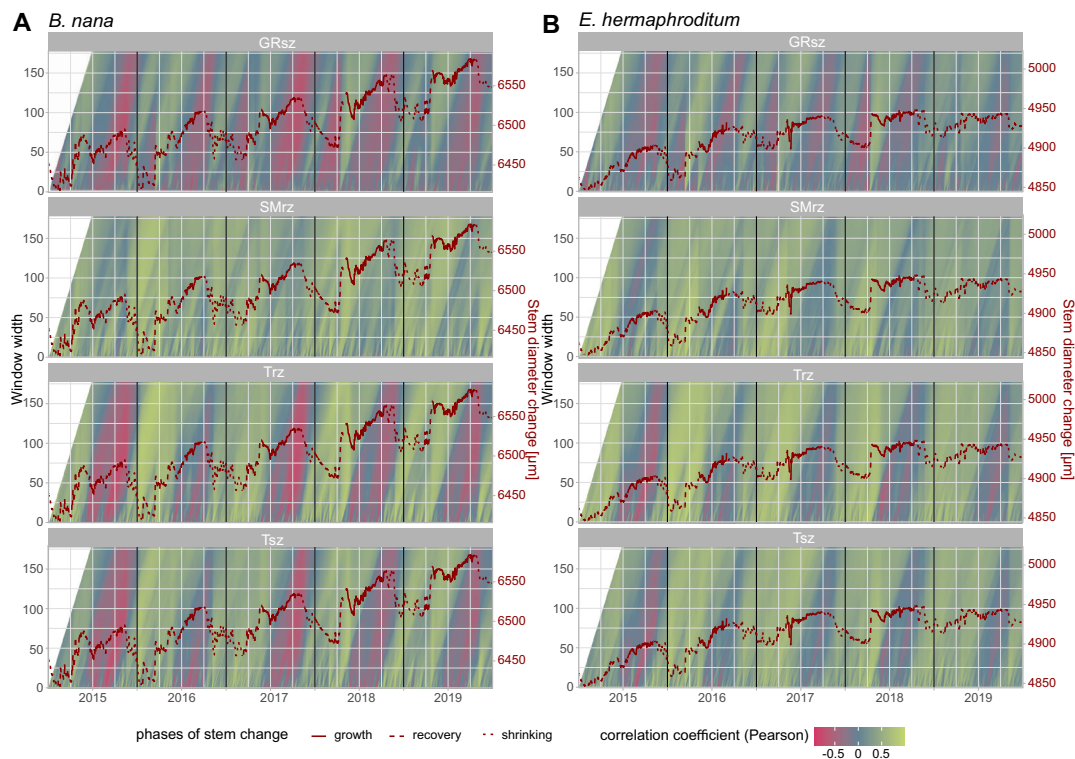


Fig. 4. Moving window correlations for daily stem diameter change as shown in Fig. 2 and daily measurements of environmental data. Moving window correlations were performed for window widths ranging from 3 to 180 days (right-aligned), revealing temporal patterns of radial stem change and microenvironment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

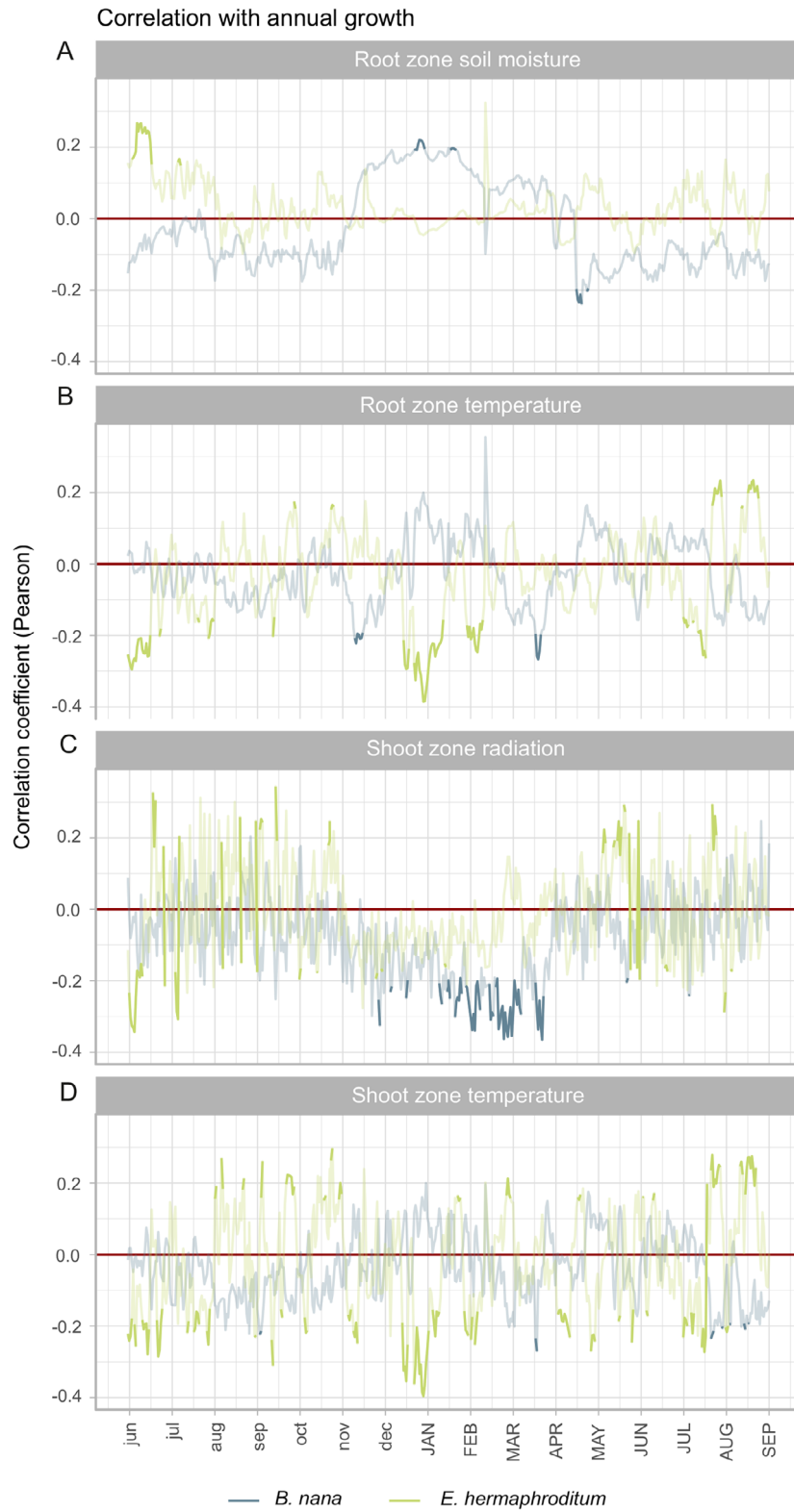


Fig. 5. Pearson's correlation coefficients calculated between total annual growth as derived from the

(Fig. 5. *Continued*)

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

growing conditions and cold stress experienced at the studied sites (Wilmking et al. 2012). Throughout the rest of the year, most of our specimens showed very strongly pronounced reversible expansion/shrinkage, which can be attributed to underlying changes in water relations

(distribution of water and water potential gradients between different compartments and parts of the plant, Lindfors et al. 2019). In this context, both *B. nana* and *E. hermaphroditum* showed short-term variations in stem radius, directly linked to fluctuations in soil moisture and

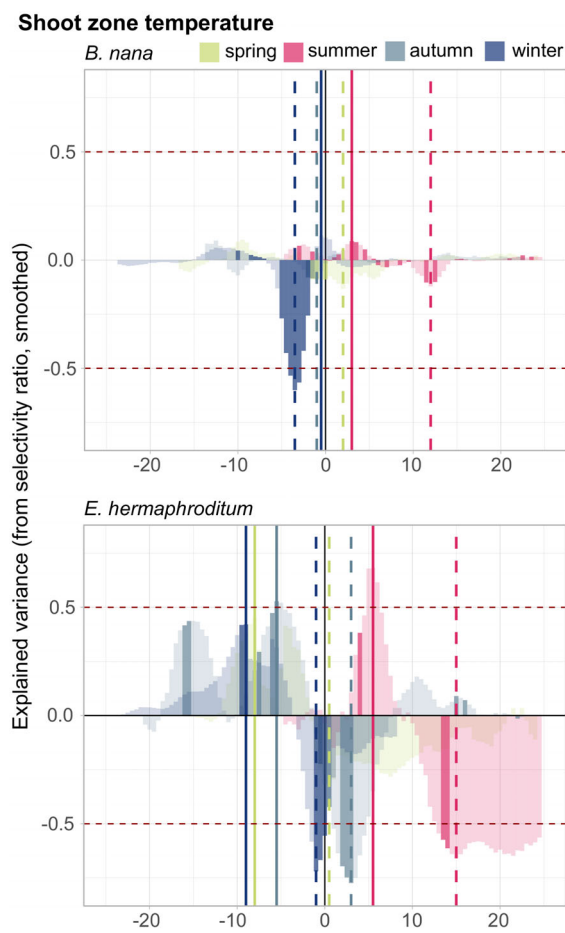


Fig. 6. Pearson's correlation coefficients calculated between total annual growth as derived from the dendrometer curves and daily environmental data, measured at the individual sites. Transparency indicates non significance. Abbreviations of months from the previous year are in lowercase letters and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

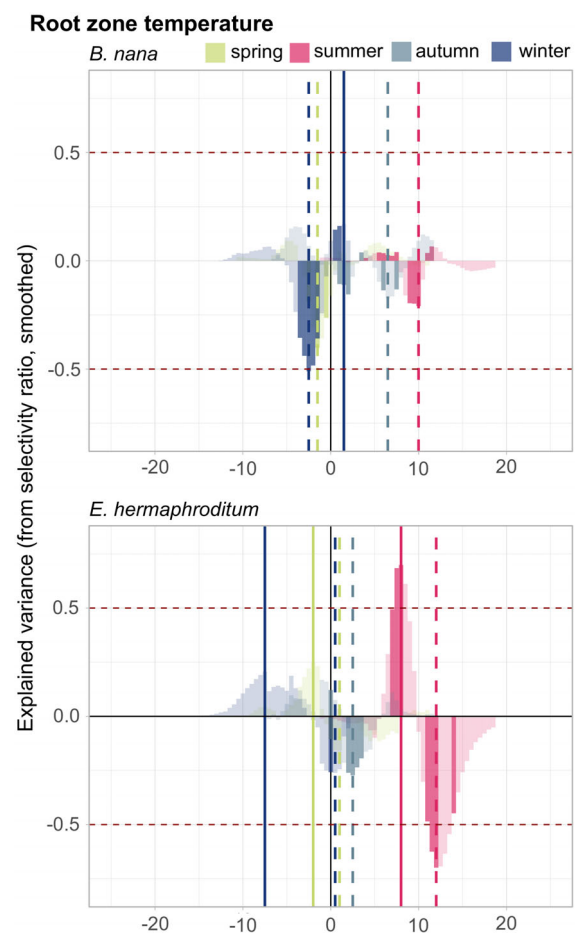


Fig. 7. Smoothed variance explained derived from selectivity ratio multiplied with the sign of its corresponding regression coefficient for shoot zone temperature (T_{sz} , independent variables) and total annual growth (dependent variable), derived from PLSR analysis. Shaded areas represent values rendered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

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

In general, the importance of the adaptive mechanisms described above is highlighted by the fact that the observed winter shrinking was missing in individual specimens, causing them to cease radial growth in the following years indicating a direct inhibiting influence on cambial activity (Wilmking et al. 2012). Overall, the growth and response patterns observed at the

sampled ridge positions confirm that both *E. hermaphroditum* and *B. nana* might be able to adjust key xylem anatomical traits to annual fluctuations in micro-climatic conditions in order to optimize their total radial stem growth rate and avoid negative effects of extreme winter conditions.

However, even though the importance of unfavorable winter conditions is highlighted by our findings, their effects on total realized growth have shown to be highly contrasting in our focal species. In the context of future climate change, this is particularly important as temperature increase at high latitudes is expected to be higher during winter, and there are more extreme events expected during winters, including unseasonal warm periods, ground ice formation, and loss of snow cover (Post et al. 2009, Seneviratne et al. 2012, Vikhamar-Schuler et al. 2016). At our studied wind-blown ridge positions, characterized by shallow snow cover and consequent low winter temperatures, pronounced temperature amplitudes, and high year-to-year variability in winter, future changes in (micro-)environmental conditions might differ and are hard to predict (Löffler et al. 2006, Wundram et al. 2010). In recent years, there have been several studies recognizing the importance of winter warming on dwarf shrub development in addition to growing season conditions, which have long been the focus. Though there is no consensus regarding direction and magnitude of the effects, they generally agree that the response is highly species-specific (Bokhorst et al. 2010, Cooper 2014, Blok et al. 2015, Hollesen et al. 2015, Krab et al. 2018, González et al. 2019). In our focal species, this is evident by the highly contrasting response to winter conditions. Both *B. nana* and *E. hermaphroditum* are able to mitigate the effects of extreme negative temperatures, but only *E. hermaphroditum* shows a strong positive response to those conditions, benefiting from prolonged snow-free periods. This suggests that in contrast to deciduous species, *E. hermaphroditum* is able to continue photosynthetic activity and remain energetically effective in synthesizing carbohydrates during at least parts of the winter months (Gimeno et al. 2012, Wyka and Oleksyn 2014, Löffler and Pape 2020). While nutrition uptake and soil moisture access are extremely limited during those times, high global radiation can lead

to additional photosynthetic opportunities (Körner 2015, Saccone et al. 2017). However, this implies that *E. hermaphroditum* has to sustain water transport to the canopy to some extent, risking cavitation in the xylem (Sperry 2003, Fonti et al. 2010, Bowling et al. 2018). Thus, we suggest that the negative relation found between winter shrinkage in *E. hermaphroditum* and temperatures is caused by this need for water transport in order to remain photosynthetically active in cold winters with high global radiation and little snow cover, consequently risking frost damage, evident in the high rate of dormant years. With this highly localized advantage over deciduous species such as *B. nana*, *E. hermaphroditum* is able to start growth activity as soon as liquid water is available in the root zone, and to acquire nitrogen early in the season (Bråthen et al. 2018), leading to a slightly earlier growth start. However, this phase of early growth is highly critical (Fonti et al. 2007, 2010), and Venn and Green (2018) found evergreen alpine shrub species strongly affected by freezing events very early in spring, before they become frost-hardened after snowmelt. This could explain the low growth rates found in *E. hermaphroditum* in 2019, a year characterized by such spring conditions. In contrast, *B. nana* might benefit from warmer winters, with increased nutrition availability (Sturm et al. 2005, Hagedorn et al. 2014) and high soil moisture content, indicating pronounced snow cover, and early snowmelt that allows the soils to drain and warm quicker and the flowering and leaf-forming processes to start earlier (Pop et al. 2000, Hollesen et al. 2015). Therefore, we found *B. nana* highly sensitive to prolonged snow cover and late temperature rise as was the case in 2015. Early snowmelt, evident in high soil moisture content during spring, on the contrary had a positive effect on *B. nana* growth. Such links between snow cover and shrub growth have been suggested before (Hallinger et al. 2010, Blok et al. 2015).

While the effects of winter conditions on shrub growth have only recently been addressed, summer conditions have long been recognized as a driver of radial growth, with most studies reporting positive effects (Bär et al. 2008, Elmendorf et al. 2012, Myers-Smith et al. 2015, Young et al. 2016, Weijers et al. 2018), and negative effects found in a few areas only (Myers-Smith et al. 2015, Young et al. 2016, Gamm et al. 2018),

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

CONCLUSION

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

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

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DATA AVAILABILITY STATEMENT

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

SUPPORTING INFORMATION

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