Received: 13 May 2023 | Accepted: 26 March 2024

DOI: 10.1111/1365-2745.14321

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Complex environmental control of growth in a dominant Mediterranean-alpine shrub species

Eike Corina Albrecht[1] | Svenja Dobbert[1] | Roland Pape[2] | Jörg Löffler[1]

[1]Department of Geography, University of Bonn, Bonn, Germany

[2]Department of Natural Sciences and Environmental Health, University of South-Eastern Norway, Bø, Norway

Correspondence
Jörg Löffler
Email: joerg.loeffler@uni-bonn.de

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

Handling Editor: Susan Schwinning

Abstract

1. Mediterranean-alpine plants are exposed to harsh conditions, forcing them to perform with well-adapted physiological strategies to withstand the dual stressors that arise from winter cold and summer drought. Such growth strategies are not yet fully understood, although they gain importance with regard to the resilience of species in the face of ongoing climate variability.
2. Here, we aimed at understanding shrub growth in a widespread Mediterranean-alpine species, *Cytisus galianoi* Talavera & Gibbs. Using long-term time series of stem diameter change obtained from dendrometer measurements across the species´ range, we were able to characterise its spatiotemporal growth plasticity. Furthermore, separating water-related fluctuations in stem diameter from irreversible stem increment allowed us to disentangle the species´ seasonal growth patterns. Using fine-scale measurements of on-site environmental conditions, we were then able to identify micro-ecological drivers controlling the species´ growth processes by applying correlation analysis and partial least squares regressions.
3. We show the species´ adaptation to the spatial heterogeneity across its range for the first time. Our findings highlight that the combination of bimodality and overall high growth plasticity likely allows the species to cover a wide geographical range across alpine areas and over a wide range of weather conditions. We show the environmental control of bimodal growth in *C. galianoi*, and the importance of pre-growth environmental control, leading to pronounced carry-over effects. These lead to a major advantage in resisting adverse growth conditions and adapting to changing conditions.
4. *Synthesis*: Overall, our findings improve the understanding of the species´ ecological niche and show that preceding photosynthetic activity helps *C. galianoi* to perform even under unfavourable conditions in winter and during the active growth phase, challenging the general assumption on the coupling of growth to specific seasons and suggesting that the species is capable of adapting to future climate variability.

KEYWORDS
adaptation strategies, carry-over effects, *Cytisus galianoi*, dendrometer measurements, ecophysiology, growth plasticity, Sierra Nevada (Spain)

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.
© 2024 The Authors. *Journal of Ecology* published by John Wiley & Sons Ltd on behalf of British Ecological Society.

1 | INTRODUCTION

Climate change scenarios for the Mediterranean suggest warming at a rate about 20% higher than the global average, with summer temperatures likely increasing more than winter temperatures (Lionello & Scarascia, 2018). This will result in substantial drying and warming of the area, especially during the warm season (Giorgi & Lionello, 2008). Specifically for alpine areas of the Mediterranean biome, climate change is expected to reduce annual and especially spring precipitation (Bravo et al., 2008), which may strongly alter growth conditions and limit plant growth during the main growth phase (e.g. Campelo et al., 2021; Touchan et al., 2014). In general, plants are assumed to react immediately to the prevailing environmental influences and require a balance of resources to maintain optimal growth (Chapin III et al., 1987).

Alpine plants are generally exposed to a huge variety of environmental influences, as they are abundant over steep ecological gradients occurring over short distances (Benito et al., 2011; Körner, 2021). In the Mediterranean alpine, plant performance is constraint by both, low-temperature stress, which is rising with elevation, and drought stress that declines with elevation (Magaña Ugarte et al., 2019; Pescador et al., 2015), including severe summer drought in addition to winter frosts (Gutiérrez-Girón & Gavilán, 2013; Morales et al., 2012). However, physiologically effective drought stress and freezing stress are assumed to be rarely fatal in alpine plants (Körner, 2021), with plant performance based on well-adapted physiological strategies to withstand the variety of stressors they are exposed to, helping the species to survive during the two stress periods and allowing for their increased performance under favourable conditions (cf. Mitrakos, 1980). However, these physiological mechanisms are not yet fully understood.

Pronounced climatic seasonality within the Mediterranean alpine promotes two distinct growth peaks separated by summer quiescence, resulting in a bimodal growth pattern, which may be reflected by the anatomical cell structure of woody plants (e.g. Campelo et al., 2021; Tumajer, Shishov, et al., 2021). This pattern has been associated with favourable growth conditions during spring and autumn, when mild temperatures and soil-water availability enhance cambial activity (e.g. Pacheco et al., 2018). However, as cambial reactivation after a dry summer is not always observed, a facultative bimodal growth has been suggested as the best way to characterise growth patterns in the Mediterranean (Battipaglia et al., 2014; Campelo et al., 2018) and also been found in several species, both within the Mediterranean lowland and the Mediterranean alpine (Olano et al., 2013). Since even arctic-alpine shrubs exhibit bimodality (Dobbert, Albrecht, et al., 2022), a facultative bimodal growth might similarly be present in a wide variety of alpine shrub species across biomes. As a growth strategy, it likely enables plants to restrict their growth to phases with favourable environmental conditions (cf. Tumajer, Shishov, et al., 2021). Thus, it is likely to enhance plant performance in the Mediterranean alpine, where winter cold and summer drought are strongly pronounced.

At the same time, future moisture limitations and warming have been found to constrain the physiology of Mediterranean-alpine species under summer drought stress (Giménez-Benavides et al., 2018; Pellizzari et al., 2017). Here, small-stature shrubs, which dominate large parts of the alpine biome, are especially affected (Giménez-Benavides et al., 2018; Pellizzari et al., 2017). On the other hand, the predicted winter warming may enhance shrub growth by reducing thermal constraints and, consequently, lengthening the growing season (Castagneri et al., 2018), associated with positive growth responses and greening of the Mediterranean alpine (Dobbert, Albrecht, et al., 2022). Additionally, earlier studies have shown accelerated growth and high resource use efficiency under higher temperatures, indicating the species´ inherent advanced physiological capacity and their ability to acclimate to a warmer environment (Yang et al., 2011). In this context, it has been noted that the response of alpine plants to climatic variability under simultaneous temperature and drought stress is complex and that models that simply assume an upward shift in distribution as a response to higher temperatures may fail to predict future responses to climate change (Olano et al., 2013).

Further contributing to this complexity is the high adaptation of low-stature alpine shrubs to the microclimate of their immediate surroundings, which allows growth to be decoupled from the free atmosphere (Körner, 2012). During winter, shrub meristems are often protected by snow, limiting the risk of freezing and mechanical damage (Rixen et al., 2010), while the insulating benefits of snowpack to shrub meristems may also be detrimental when late snow melt results in a shortened growing season (Pellizzari et al., 2014, 2017). In complex alpine topography, plant species have been shown to be restricted to their specific ecological niche (e.g. Dobbert et al., 2021a; Löffler & Pape, 2020), and alpine vegetation patterns do reflect these topographical structures (e.g. Gjærevoll, 1956; von Büren & Hiltbrunner, 2022). Thus, growth of alpine shrubs from different biomes has been shown to be not only influenced by the regional climate (e.g. Bär et al., 2008; Gazol & Camarero, 2012a; Li et al., 2013) but also by the local environment which has been addressed as the major driver of shrub growth (Dobbert et al., 2022a; Gazol & Camarero, 2012b). In this context, plastic xylogenesis has been described as a competitive advantage under the Mediterranean climate regime (cf. Camarero et al., 2010). Accordingly, spatiotemporal plasticity of secondary growth has generally been assumed to be of particular importance in cold and dry ecosystems (c.f. Körner, 2012; Pellizzari et al., 2017; Tumajer, Buras, et al., 2021), and high plasticity has been highlighted as the advantage of enabling biogeographically widespread species to colonise large areas (Ghalambor et al., 2007; McLean et al., 2014).

The plasticity of cambial activity and the adjustment of wood formation to fluctuations in climatic conditions can be derived from continuous time-series of stem diameter change, measured using high-resolution dendrometers (Pacheco et al., 2018). Using such time series along alpine elevational gradients, we recently showed that the widespread, green-stemmed Mediterranean-alpine shrub species *Cytisus galianoi* exhibits high ecological plasticity compared

to coexisting species (Albrecht et al., 2023, 2024). This plasticity, combined with a pronounced frost and drought tolerance, allows the species to benefit from additional carbon gain during winter and summer, with pre-growth assimilation leading to carry-over effects, making it competitive even under unfavourable conditions during the active growth phase and under warming climate (Albrecht et al., 2024). Here, our dataset includes continuous time-series of stem diameter change of *C. galianoi* specimens from a variety of different sites colonised by this species along multiple geographical gradients within the Sierra Nevada Mountain range. By separating water-related stem diameter changes from irreversible growth, we aimed to disentangle bimodal growth patterns triggered by frost and drought stress, and to relate these drivers to the timing of growth. This way, we aimed to (a) identify consistent growth patterns across a variety of distinct sites, (b) characterise the species´ spatiotemporal growth plasticity across its range and (c) identify specific environmental drivers that promote both pre-growth assimilation and growth during the active growth phase, in order to explain growth dynamics from a biogeographical perspective.

2 | MATERIALS AND METHODS

2.1 | Focal species

In this study, we focused on the shrub species *Cytisus galianoi* Talavera & Gibbs (Figure S1a; taxonomy and nomenclature after Blanca et al., 2009a), which is a long-living, low-growing (~10–30 cm; Blanca et al., 2009a; Löffler et al., 2022), cushion-forming chamaephyte (Giménez et al., 2004) belonging to the Fabaceae family. It is an N-fixing species (Macek et al., 2016) with an extensive, highly branched root system that extends ~30 cm into the soil (Figure S1b) and forms lateral ramets (Fernández-Santos et al., 2004). During anthesis (May/June), the species produces only a few small leaves (Blanca et al., 2009a) but due to its intensely green stems is potentially able to photosynthesise all year round (cf. Bossard & Rejmanek, 1992). Furthermore, the elasticity of its above-ground biomass suggests high drought resistance (cf. Patakas & Nortsakis, 1999), and its xylem anatomy and hydraulic architecture (Figure S2a) indicate that *C. galianoi* is able to cope with drought and frost (Sperry, 1993; Sperry & Tyree, 1988) and to repair drought-induced embolism (Brodersen & McElrone, 2013), which can occur after severe dehydration (Arbellay et al., 2012). The species is abundant in the Sierra Nevada (Spain) and endemic to the south of the Iberian Peninsula (Giménez et al., 2004).

2.2 | Study sites and specimens

Our focal species colonises a broad spectrum of sites along the alpine elevation gradient up to 3200 m a.s.l. within the Mediterranean biome (Figure S1c). Accordingly, specimens are exposed to the overarching climate signal of the Mediterranean, characterised by hot and dry conditions during summer, and cool and humid conditions in autumn, winter and spring (Anderson et al., 2011; Roberts et al., 2011). The Sierra Nevada reaches its highest peak at 3479 m a.s.l. (Mulhacén) (Herrero & Polo, 2016), encompassing a variety of Mediterranean-alpine ecosystems (Gómez-Ortiz et al., 2019). Here, the growing seasons are comparatively short, and plants are exposed to cold winters, high solar radiation, strong winds and snowfall. In combination with the complex alpine topography (Figure S1d), these conditions affect the spatial distribution of *C. galianoi*, which dominates the vegetation of the middle-alpine environment between 2200 and 2700 m a.s.l. (Löffler et al., 2022) and forms scattered shrub patches at exposed ridges within a matrix of open rocks, debris and *Festuca clementei* Boiss. (Blanca et al., 2009b) remaining the dominant graminaceous species here. Above 2700 m a.s.l., where vegetation is transitioning into a high-alpine environment (Löffler et al., 2022), *C. galianoi* disappears from latest snow beds.

For our monitoring, we selected 29 sites stratified-randomly, following our long-term project on alpine ecosystem research (LTAER-ES; Löffler et al., 2022). These sites represent the spatial variety of different environmental conditions in the area. At each site, we randomly selected shrub specimens of comparable size, leading to a monitoring design consisting of 77 *C. galianoi* (2100–3175 m a.s.l.) specimens (Figure S1c). We recorded stem diameter changes for six full consecutive years (January 1, 2015, to December 31, 2020).

To test whether the annual growth derived from our dendrometer records match the annual growth derived from dendroanatomical measurements of annual ring width, we collected complete *C. galianoi* specimen at 7 of our 29 sites, which we prepared for annual ring-width measurements according to the standardised procedures (Gärtner & Schweingruber, 2013). When collecting, we made sure that the selected specimens grew directly next to the specimens equipped with dendrometers. By cross-cutting the 7 specimens at the shoot, base and root segments (Figure S2b), we obtained 19 thin sections (since one shoot and root segment was broken during cutting), from which we created 19 time series of annual ring-width measurements by averaging the 5 radii we measured per section (for procedure see Figure S3a,b).

2.3 | Dendrometer data and monitoring set-up

To monitor radial stem diameter variations of our species, we used high-precision point dendrometers (type DD-RO; Ecomatik, Dachau/Germany) designed to measure changes in stem diameter of particularly small stems (0–20 mm diameter) and capable of generating data with unprecedented temporal resolution, providing deep insights into seasonal growth patterns and mechanisms of arctic-alpine and Mediterranean-alpine shrubs (Albrecht et al., 2023, 2024; Dobbert et al., 2021a, 2021b; Dobbert, Albrecht, et al., 2022; Dobbert et al., 2022b). The dendrometers had sensors with a temperature coefficient of <0.2 µm/K, recorded data

at 1-min intervals and were mounted on a T-shaped aluminium bar that we carefully attached to the main stem of the selected specimens horizontally above the ground surface. To minimise the influence of hygroscopic swelling and shrinking of the bark (Zweifel & Häsler, 2001), we removed the outermost layers of dead periderm (0.5 mm) at the contact point of the dendrometer (cf. Dobbert et al., 2022b). We took care to place dendrometers as close as possible to the specimens' root collar, which is thought to integrate the growth of the whole plant (Bär et al., 2007; Ropars et al., 2017), although the extent to which changes in radial stem diameter vary within individual specimens and between multiple stems of the same specimen has not been fully explored (Dobbert et al., 2021b). To account for this variation, we monitored a large number of specimens and ensured that selected specimens were representative of the conditions observed at each site. To obtain daily mean values from the raw dataset, the dendrometer data were averaged (Deslauriers et al., 2007). Because dendrometers measure changes in stem diameter relative to the start of the measurement and not the absolute stem diameter, we normalised the annual stem diameter curves by removing the initial stem diameter (2358.96–10300.84 µm) from the annual curves. Finally, we checked the data for outliers, defining the interquartile range (IQR) and the 25th (Q1) and 75th (Q3) percentile (Q1/Q3 ± 1.5*IQR) as cut-off ranges. As there were no outliers, all daily values were retained.

2.4 | Environmental conditions

To assess the drivers of radial stem diameter variations, we additionally measured environmental variables at each site and for each specimen separately, using thermistors and soil moisture probes at 10 cm soil depth within the specimen's root zone (c.f. Dobbert et al., 2021b; Löffler & Pape, 2020). Root zone temperatures (T_{RZ}) were recorded at 1-min intervals and stored as hourly averages using ONSET's HOBO loggers (type H21-002) and thermistors (type S-TMB-002) with ±0.2°C accuracy. Soil moisture conditions within the specimen's root zone (SM_{RZ}) were measured as volumetric soil water content (m^3/m^3) at 1-min intervals, again recorded as hourly averages, using soil moisture probes (type S-SMD-M005) with ±3% accuracy. All environmental data were collected for the period 1 January 2015 to 31 December 2020, with additional data from 2014 used when needed. There were no missing data.

The mean below-ground regimes of T_{RZ} and SM_{RZ} for all monitored specimens are shown in Figure S4 (see also Löffler et al., 2022). Consistent with the typical bimodality of the Mediterranean climate (e.g. Camarero et al., 2012; Mitrakos, 1980), conditions were characterised by comparatively mild and humid conditions in spring and autumn, intermitted by harsh, cold winters with occasionally occurring frosts and periodic snow cover, and hot and dry summers with overall high incoming solar radiation (Figure S4).

2.5 | Analysis of seasonal growth patterns

Aiming to discern the species´ seasonal growth patterns from our dendrometer curves, we defined two growth phases, one during the first half of the year (January–June) and one during the second half of the year (July–December; Figure S5). Since these phases were intermitted by phases of stem contraction during summer and winter, the subdivision of intra-annual growth reflects the species' seasonal growth patterns and accounts for the bimodal rhythm of the Mediterranean climate (Mitrakos, 1980), which is known to produce bimodal growth patterns in several Mediterranean lowland plants (Camarero et al., 2010) and possibly also in Mediterranean-alpine species (Olano et al., 2013). Accordingly, growth-induced irreversible stem expansion (hereafter growth) was calculated semi-annually by subtracting the maximum stem diameter in the current six-month period from the last maximum in the previous study period. Thus, growth was defined as cumulative stem increment during the respective period compared to previously achieved stem growth. In this way, we identified a first and a second growth phase, with total annual growth calculated as the sum of growth in both phases (Figure S5). Although applied to semi-annual rather than daily data, this definition of growth parallels that of the "zero-growth approach" where growth is defined as equivalent to an incremental increase in stem radius when the measured radius is greater than at any point in the past (Zweifel, 2016; Zweifel et al., 2021). Accordingly, growth can only take on positive values, but does not necessarily take place in every growth phase or in every year, which is why we refer to phases or years without growth as dormant phases or years. For each half-year period, we calculated both, the change in stem diameter, and the temporal duration of the growth phase, defined as the period from the first day growth occurred till the last day growth occurred during the respective period (Figure S5) for all specimens and years. Additionally, we calculated stem water deficit, defined as periods of stem contraction, by subtracting the measured stem diameter changes from a cumulative growth curve (Zweifel, 2016).

To validate our dendrometer measurements and relate the observed changes in stem diameter to traditional assessments of growth based on annual rings, we compared the annual growth curves derived from our dendrometer curves by summing the growth of both growth phases for each year with the averaged time series derived from our annual ring width measurements of 7 collected neighbouring samples. In addition, we calculated the Spearman's correlation coefficient between our annual dendrometer curves and the averaged time series to provide statistical support for the visually observed synchronicity of the growth patterns derived from the two different methods (Figures S6 and S7). We found pronounced variance between curves from different sites and between the different intra-plant segments (shoot, base, root) in both the dendrometer curves and the annual anatomy-based time series. At the same time, however, the dendrometer curves and the annual time series from the same sites showed pronounced synchronicity (for more details see Figures S6 and S7).

2.6 | Statistical analysis

Aiming to explore the spatial and temporal variation in stem diameter change patterns, we used a modelling approach to decompose the variability within the grouped, complex data (Dobbert et al., 2021a; Firn et al., 2019; Henn et al., 2018). We developed linear mixed-effect models for total annual growth, as well as for growth in both previously defined growth phases, which entered as response variables alongside annual stem increment (maximum stem diameter–minimum stem diameter) and the total number of growing days per year. We then grouped our data by a set of characteristics, that is, topographical position, year, site and the initial stem diameter at the beginning of the year, rounded to the nearest decimal. These grouping factors were included as random effects into the models. In order to meet the model requirements, sites were grouped into eight groups, according to elevation and study region (Figure S1c; Group 1: <2360 m a.s.l., Group 2: 2360–2630 m a.s.l., Group 3: 2630–2900 m a.s.l., Group 4: >2900 m a.s.l., for our two study regions, respectively). Subsequently, we investigated the percentage of variance explained by each factor, which was derived from the models using the VarCorr R function (Bates et al., 2015). To represent the study design, we nested topographical position within the site variable. The final models thus had the form growth variable ~ (1|Site/Topographical position) + (1|Year) + (1|Initial stem diameter) as implemented into the lmer function of the lme4 R package (Bates et al., 2015).

To uncover the relations between on-site environmental conditions and species' growth patterns, we examined the influence of microclimate on shrub growth through correlation analysis and linear mixed-effects models. Using the statistical software R (R Core Team, 2020), we calculated Pearson's correlation coefficients between semi-annual irreversible stem growth and daily mean values for each month and for each of our environmental variables T_{RZ} and SM_{RZ}. To account for possible effects of previous-year conditions on current-year growth, we included data from the previous year in our analyses (e.g. Bär et al., 2008; Weijers et al., 2018), including additional measurements from before the start of our study period (2014). To account for the variability between the observed specimens, we additionally fitted linear mixed-effects models to our data, using the lme4 R package (Bates et al., 2015). For these models, we chose semi-annual growth as response variable, and monthly mean values for all environmental variables as fixed effects. The individual specimens were included as random effects.

To complement the correlation analysis, we applied partial least squares regression (PLSR; Wold, 1975), using variable selection methods to define a subset of relevant environmental conditions promoting or limiting growth. PLSR works for data where the number of predictors exceeds the number of observations or the predictors are highly correlated (Frindte et al., 2019). It is therefore frequently implemented in ecological studies (Carrascal et al., 2009; Dobbert et al., 2021a; Frindte et al., 2019; Löffler & Pape, 2020). Here, we aggregated our environmental data by rounding them to 0.5°C for T_{RZ} and 0.01 m^3/m^3 for SM_{RZ} values. We then counted and summed the frequency of each value occurring within the rounded time series (Löffler & Pape, 2020) for each meteorological season, that is winter, spring, summer and autumn (Table S1; for definition see Trenberth, 1983). In this way, we obtained scaled and centred sets of predictor variables with the previously calculated growth values as associated response variables. For the final estimation of the single-response models, we used the SIMPLS algorithm (de Jong, 1993) implemented in the R package mdatools (Kucheryavskiy, 2020). We determined the optimal number of variables in the PLSR model using Wold's R criterion (Wold, 1978), and assessed the explained variance during model calibration and validation by tenfold cross-validation. We then used the selectivity ratio (SR) to assess the relevance of each independent variable (Farrés et al., 2015). The SR is defined as the ratio of explained to remaining (unexplained) variance for each variable in the target projection vector. In order to achieve better contrastable results, the explained variance (SR/abs (SR +1)) was derived from the SR. Multiplying the SR of each variable by the sign of the corresponding regression coefficient we determined which variables were positively or negatively associated with the dependent variable (Löffler & Pape, 2020; Rajalahti et al., 2009). In this way, we were able to identify those environmental conditions significantly related to growth.

3 | RESULTS

3.1 | Spatiotemporal patterns

Decomposing the variance within our dataset using linear mixed-effect models revealed the relative effect of spatiotemporal variability between sites, topographical positions and years on growth, with these variables, together with the initial stem diameter, accounting for up to 51.3% of the overall variation within our data (Figure 1). Despite of the highly complex topography found in the studied area, differences in topographical position only partially explained the observed differences in growth. Instead, variation in climate and environmental variation associated with elevation, as well as the overall regional climate signal reflected in the site variable, had somewhat higher explanatory power. The initial stem diameter at the start of the study period played a significant role for all growth variables, especially the first growth phase. Inter-annual variation had overall low explanatory power (Figure 1). At the same time, relatively low explanatory power of microsite environmental variation for growth during the first growth phase was contrasted by high explanatory power for overall (annual) growth (Figure 1).

3.2 | Seasonal patterns

Stem diameter changes in *C. galianoi* followed a distinct bimodal pattern with high intra-annual and inter-annual variability and high

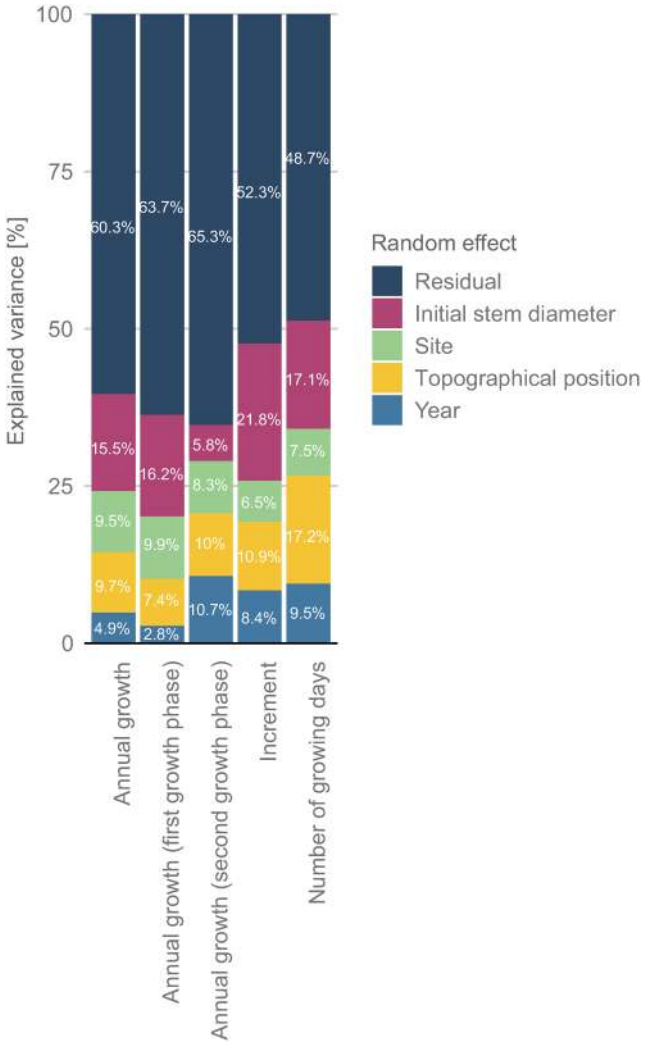


FIGURE 1 Variance explained as derived from linear mixed-effect models. Partitioned variance in growth variables explained by variation in spatial and temporal grouping variables. A model was fitted for each growth variable (annual growth, growth in first growth phase, growth in second growth phase, stem increment, number of growing days). The models had the form Growth ~ (1|Site/Topographical position) + (1|Year) + (1|Initial stem diameter).

variability between the individual specimens (Figure 2a,b, Figure S8). Overall, patterns closely matched the seasonal SM_{RZ} conditions, resulting in (a) periods of stem contraction during winter and summer when SM_{RZ} content was low due to frost in winter and drought in summer, respectively, and (b) periods of stem expansion during spring and autumn when SM_{RZ} content was high due to thaw, snowmelt and precipitation in spring and rainfall in autumn, respectively (Figure 2a,b, Figure S4).

The close match between the patterns and the seasonal SM_{RZ} conditions was best expressed in the high synchronicity between the stem water deficit, indicating stem contraction, and the SM_{RZ} curves throughout the year (Figure 3). Here, it became clear that deeply frozen ground during winter led to low available SM_{RZ}, which was accompanied by stem contraction, and even single freeze–thaw cycles were visible in the stem water deficit curve. Likewise, during mild winters (2015/2016, 2019/2020) frost-independent winter droughts co-occurred with a high stem water deficit. During periods of intense summer drought, the stem water deficit continuously rose to its maximum (at the end of August), followed by shorter drought spells which were accompanied by less severe but well pronounced stem water deficit peaks, frequently interrupted by single precipitation events (2019). As an exception from the rule, maximum stem water deficit was not followed by shorter drought spells in 2018, so that stem water deficit remained low during autumn. Overall, stem water deficit was low during the generally humid winters, but high during periods of intense summer drought.

In general, stem contraction and, accordingly, stem water deficit during winter was comparatively low (Figure 4a,b). The average onset of growth was in February/March (~ DOY 56–81; Table S2; Figures S9 and S10) in conjunction with rising T_{RZ} (Figure S4). However, as visible in the cumulative curve of stem diameter change (Figure 4c), initial growth sometimes occurred as early as January/February in years with early soil thawing and comparatively mild winter T_{RZ} (between 2°C and 5°C) (Figure S4). Following this initial growth during winter, main growth occurred in spring with the phase of greatest stem expansion starting in mid-April (~ DOY 100), when stem water deficit was still low (Figure 4a–c), enabling the species to achieve highest growth rates from April to June (Figure 4c). The diurnal pattern of stem diameter change in spring showed low variations (with the largest increase occurring from ~4 PM to ~9 AM the next morning, when the stems begin to shrink again until ~4 PM; Figure S11). Towards the end of June (~ DOY 144–156; Table S2) growth ceased in close accordance with decreasing SM_{RZ} content (Figure 4c, Figure S4). The subsequent period of stem contraction during summer was pronounced and associated with continuously increasing stem water deficit (Figure 4a,b). The increasing drought was reflected in a pronounced amplitude of the diurnal pattern of stem diameter change (Figure S11), with daily stem contraction peaking at ~5 PM and followed by a strong stem expansion that lasted all night and peaked at ~9 AM. The period of summer drought was usually terminated by the first autumn rains, which induced a period of pronounced stem expansion that continued throughout the entire autumn season (Figure 4a, Figure S4). However, growth resumption usually occurred well after the first autumn rains in August (~ DOY 217–250; Table S2, Figure S9) and was delayed by severe drought spells in autumn in combination with a long summer drought (e.g. 2019) (Figures S4 and S9). In contrast, immediate growth resumption occurred after short summer drought combined with an early onset of humid conditions in August (e.g. 2018) (Figures S4 and S9). Here, the pronounced stem expansion following summer stem contraction was not matched by irreversible stem increment represented by the cumulative curve of stem diameter change (Figure 4a,c), and accordingly, growth rates achieved in autumn were comparatively low. Overall, spring growth was, thus, usually highest, while autumn growth was of minor importance in most years (Figure S12).

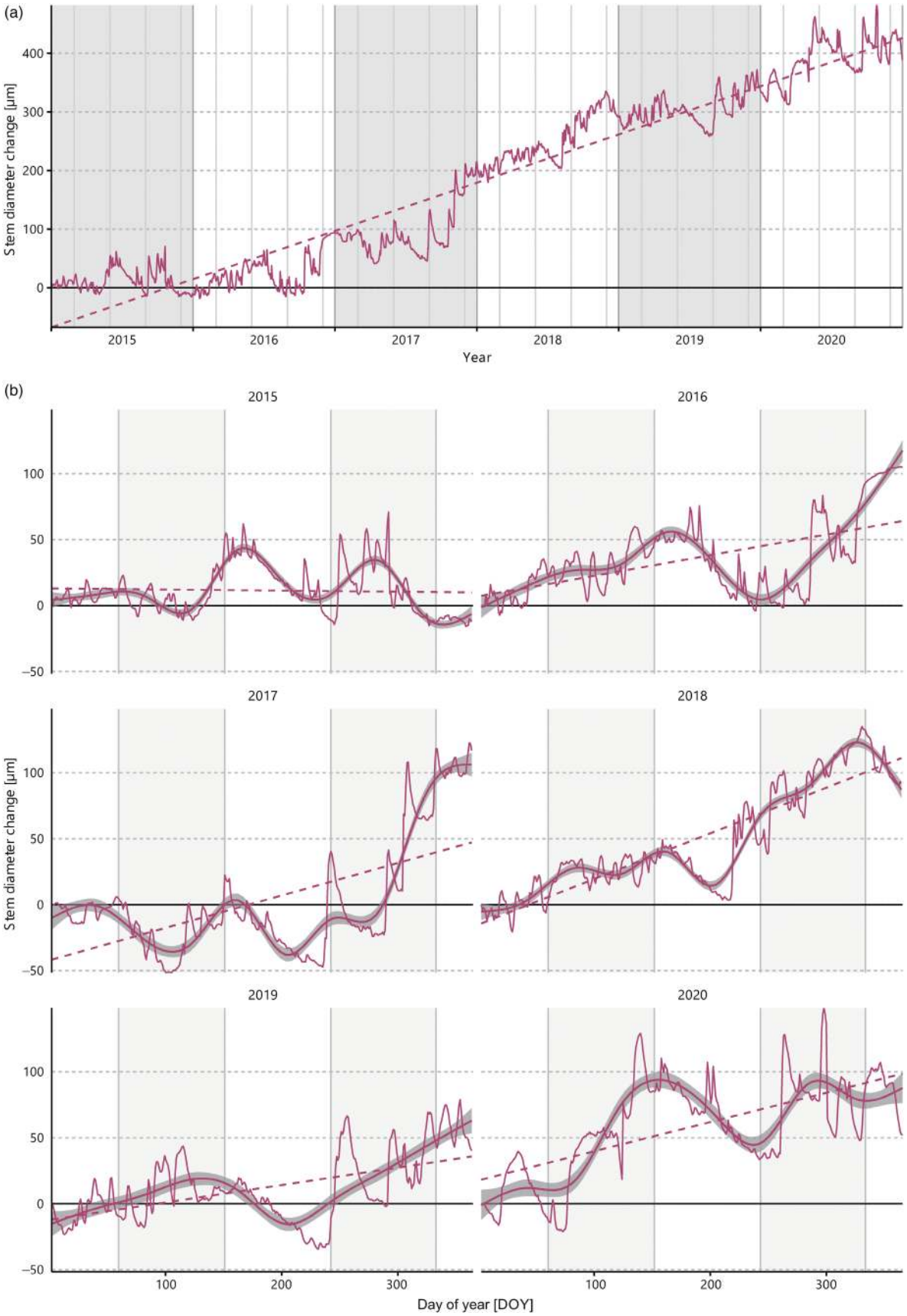


FIGURE 2 (a) Stem diameter change of *Cytisus galianoi* pooled for all positions relative to the start of the measuring period and (b) averaged annual stem diameter change relative to the previous year's maximum, represented by generalised additive models (bold) and linear trends (dashed). In (a), vertical grey lines indicate meteorological seasons (see Table S1) and alternating grey and white background markers highlight the years. In (b), alternating grey and white background markers highlight the meteorological seasons.

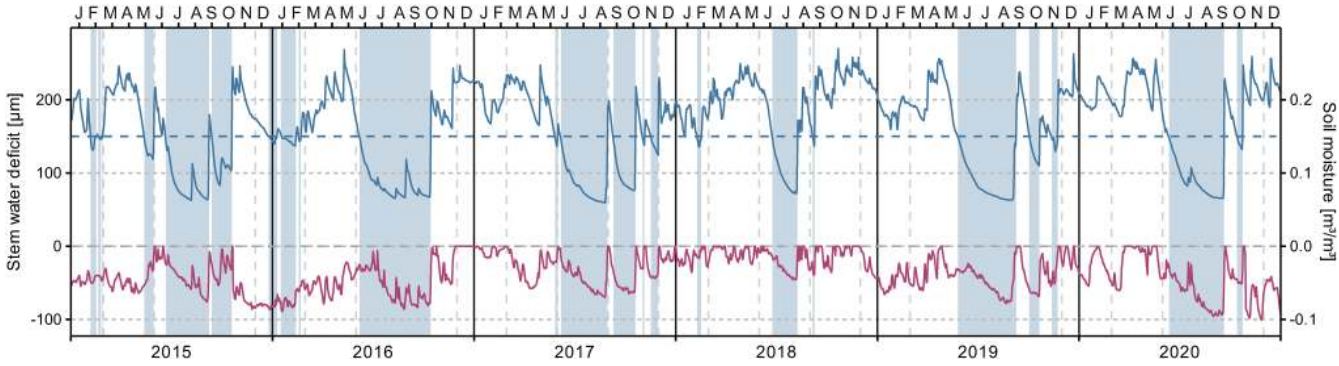


FIGURE 3 Seasonal pattern of averaged stem water deficit over all positions (lower red curve below the horizontal dashed grey line marking $SM_{RZ} < 0.0\,m^3/m^3$) related to minimum, average, and maximum soil moisture (upper blue curve). Summer and winter drought periods were defined as $SM_{RZ} < 0.15\,m^3/m^3$ (horizontal dashed blue line indicates this threshold) and are highlighted by vertical light blue bands. Dashed vertical lines indicate the meteorological seasons (see Table S1) and vertical black lines the years.

3.3 | Environmental control

Overall, growth during both, the first growth phase in spring, and the second growth phase in autumn, was closely linked to the environmental conditions during actual growth and before the onset of growth, highlighting the importance of pre-growth conditions for growth in *C. galianoi* (Figure 5, Figures S8 and S9). For the first growth phase, the correlation analysis revealed growth promotion by overall high T_{RZ} during the previous year including the pre-growth winter, but low T_{RZ} during February and March, followed by warm and dry conditions in April but mild and humid conditions in May/June (Figures S8 and S9). Correlation results for pre-growth winter and current spring were supported by the PLSR results, showing that the species benefited from pre-growth winter T_{RZ} of 2.5°C and T_{RZ} of ~6–14°C during the actual growth phase in spring (Figure 5). For the second growth phase, the correlation analysis and linear mixed effects models revealed that the species preferred high T_{RZ} during previous year November, but low T_{RZ} during spring and summer prior to growth (Figures S13 and S14). Here, PLSR results revealed that the species benefited from pre-growth winter T_{RZ} of 5°C, but comparatively mild pre-growth summer conditions with T_{RZ} of 10–18°C. Moreover, during actual growth in autumn *C. galianoi* was promoted by T_{RZ} of ~9°C (Figure 5). Unexpectedly, however, PLSR results showed hardly any clear SM_{RZ} thresholds for species performance in both growth phases (Figure 5), while correlation results revealed growth promotion by dry pre-growth summer to autumn conditions for the first growth phase and dry pre-growth winter but humid pre-growth summer conditions for the second growth phase (Figures S13 and S14).

4 | DISCUSSION

4.1 | Plasticity

Previous studies have shown growth adjustments to the conditions of their respective environment in trees (Kraus et al., 2016; Linares et al., 2012; Royce & Barbour, 2001) and in alpine shrubs (Dobbert et al., 2021a). However, the role of growth duration and growth rate for total growth have remained uncertain. Our results suggest environmental adjustment of growth duration along elevation and/or snow-cover gradients, with the number of annual growing days strongly influenced by spatial variations associated with site and topographical position (Figure 1). At the same time, measured variance in annual stem increment was linked to differences in initial stem diameter of the individual specimens (Figure 1), indicating high elasticity of stem cells, which may shrink upon water loss while maintaining high turgor (cf. Patakas & Nortsakis, 1999), resulting in elastic stems at variable stem diameters, and thus potentially for all ages. This specific trait is of physiological advantage under the dual climatic stress characterising the Mediterranean alpine (Tumajer, Shishov, et al., 2021). Growth during the second growth phase varied little with differences in initial stem diameter (Figure 1), indicating a high plasticity of autumn growth in consistence with the influence of site and autumn climate conditions on episodic xylogenesis (Camarero et al., 2010; Valeriano et al., 2023). Contrastingly, growth during the first growth phase varied with changing initial stem diameter of the specimens (Figure 1), suggesting that the species may profit from larger stems and stature, when water supply is sufficient. However, the role of plant size and potential growth rate in affecting productivity under stress are not well resolved, and size per se is unlikely to be the cause of the higher explained variance during spring. Differences in plant size may be associated with the difference in surface-volume ratio, which should lead to differential water availability and thus, to differences in resource allocation (Bloom et al., 1985; Zotz et al., 2001).

Furthermore, low explanatory power of inter-annual variance (Figure 1) suggests that high year-to-year variability of climatic constraints for growth in *C. galianoi* is matched by adjusted growth responses, that is in timing and magnitude of growth. Such temporal plasticity is associated with high climatic variability and, thus, common in the Mediterranean climate, where the pace of secondary growth must be adjusted to a broad array of climatic conditions

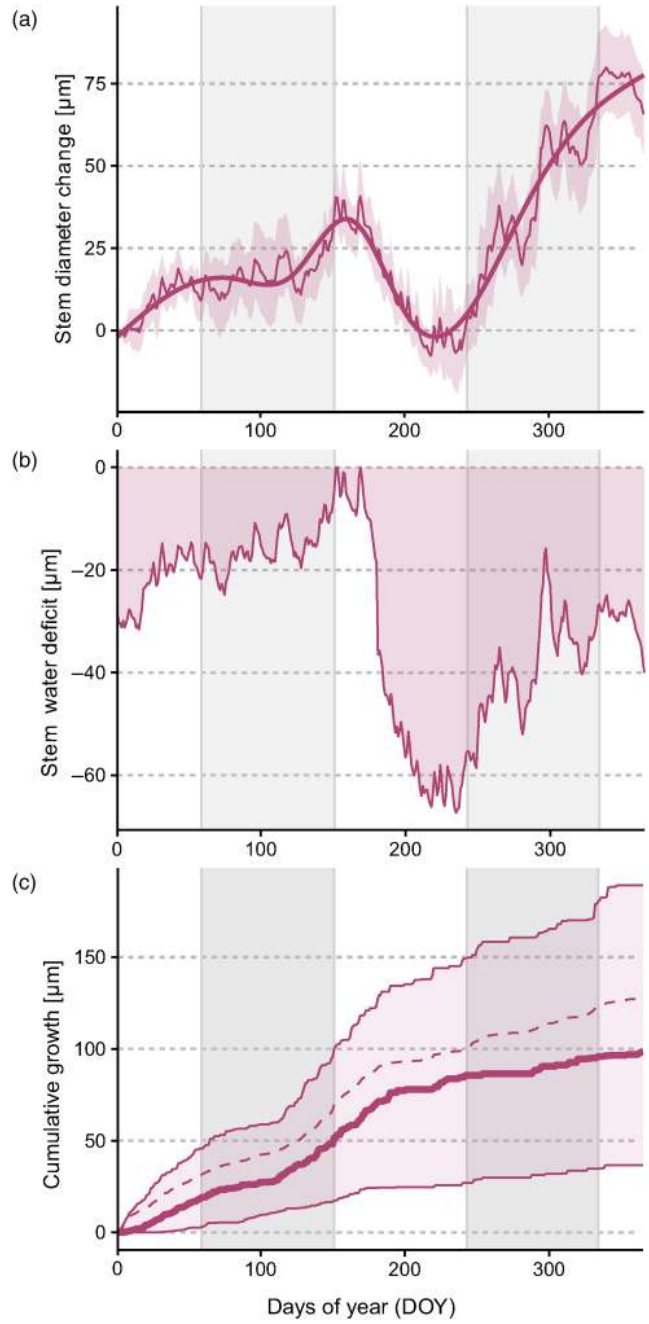


FIGURE 4 (a) Seasonal pattern of stem diameter change during the course of one year, averaged over the studied period 2015–2020 and represented by generalised additive models (GAMs). (b) Seasonal pattern of averaged stem water deficit over all positions (lower red curve) related to minimum, average, and maximum soil moisture (upper blue curve). Summer and winter drought periods were defined as $SM_{RZ} < 0.15\,m^3/m^3$ (vertical light blue bands). (c) Cumulative curve of stem diameter change (growth) in *Cytisus galianoi*, shown as median (solid line), average (dashed line), and the 25% and 75% quartiles (shaded) for the years 2015–2020 the course of one year. Altering white and grey background markers indicate the meteorological seasons (see Table S1).

(Camarero et al., 2010). Moreover, we found only minor effects of spatial variation on growth variance, contrasting recent studies of arctic-alpine shrub species, which showed stronger spatial coupling of growth patterns to their ecological niches (Dobbert et al., 2021a; Löffler & Pape, 2020). Instead, for *C. galianoi*, a consistent growth pattern emerged across a huge variation of different sites along multiple geographical gradients, suggesting annual bimodality with major spring growth and long-term carry-over effects to be a successful strategy in the Mediterranean alpine. Such strong adaptation to the spatial heterogeneity can be attributed as spatial plasticity to environmental variance, as has been elaborated in previous studies (Pacheco et al., 2018; Tumajer, Buras, et al., 2021; Valeriano et al., 2023).

In order to validate the consistent growth pattern emerging from the dendrometer measurements across a variation of different sites along multiple geographical gradients, we assessed the anatomical signatures of seven specimens at the respective sites (Figures S6 and S7). The large variation of each dendrometer-based growth pattern, both, between individual specimens and within individual shrubs, corresponded with each of our seven shrub specimens' anatomical signatures. This methodological validation is limited by the sampling size and, thus, needs further exploration in future studies examining the agreement of dendrometer derived phenology and the development status at the cellular level by detecting points in growth curves that correspond to the histological section, where the amount and development stage of the tissues at that particular time point can be observed (Cruz-García et al., 2019). However, the synchronicity between our dendrometer measurements and the respective annual anatomy-based time series is promising at least in terms of annual growth rates.

4.2 | Bimodality

Growth bimodality has been observed in a variety of shrub species (Tumajer, Buras, et al., 2021; Tumajer, Shishov, et al., 2021) and is considered an important factor in maintaining the ecological balance of dry Mediterranean ecosystems (Gazol & Camarero, 2012a; Sánchez-Salguero & Camarero, 2020; Valeriano et al., 2023). However, bimodality is usually linked to lowland plant growth (Magaña Ugarte et al., 2019; Szymczak et al., 2020). Yet, similar to growth patterns observed in Mediterranean trees (Mitrakos, 1980), we found periods of growth quiescence driven by winter cold and summer drought in *C. galianoi* (Figure 4a, Figure S4). Thus, our results confirm recent findings of bimodal growth patterns in alpine shrub species (Albrecht et al., 2023, 2024; Dobbert, Albrecht, et al., 2022; Olano et al., 2013). In contrast to lowland species, in which these bimodal patterns likely arise from favourable warm and humid conditions during spring and autumn, but reduced growth rates in summer, and short winter dormancy (Cherubini et al., 2003), we found additional winter stem contraction when frozen ground occurred in our alpine species (Figure 3), similar to arctic-alpine shrubs, where such processes have been interpreted as a mechanism to protect the plant from embolism under frost droughts (Dobbert et al., 2022b). At the same time, the observed overall low stem water deficit during winter (Figure 4b) suggests an

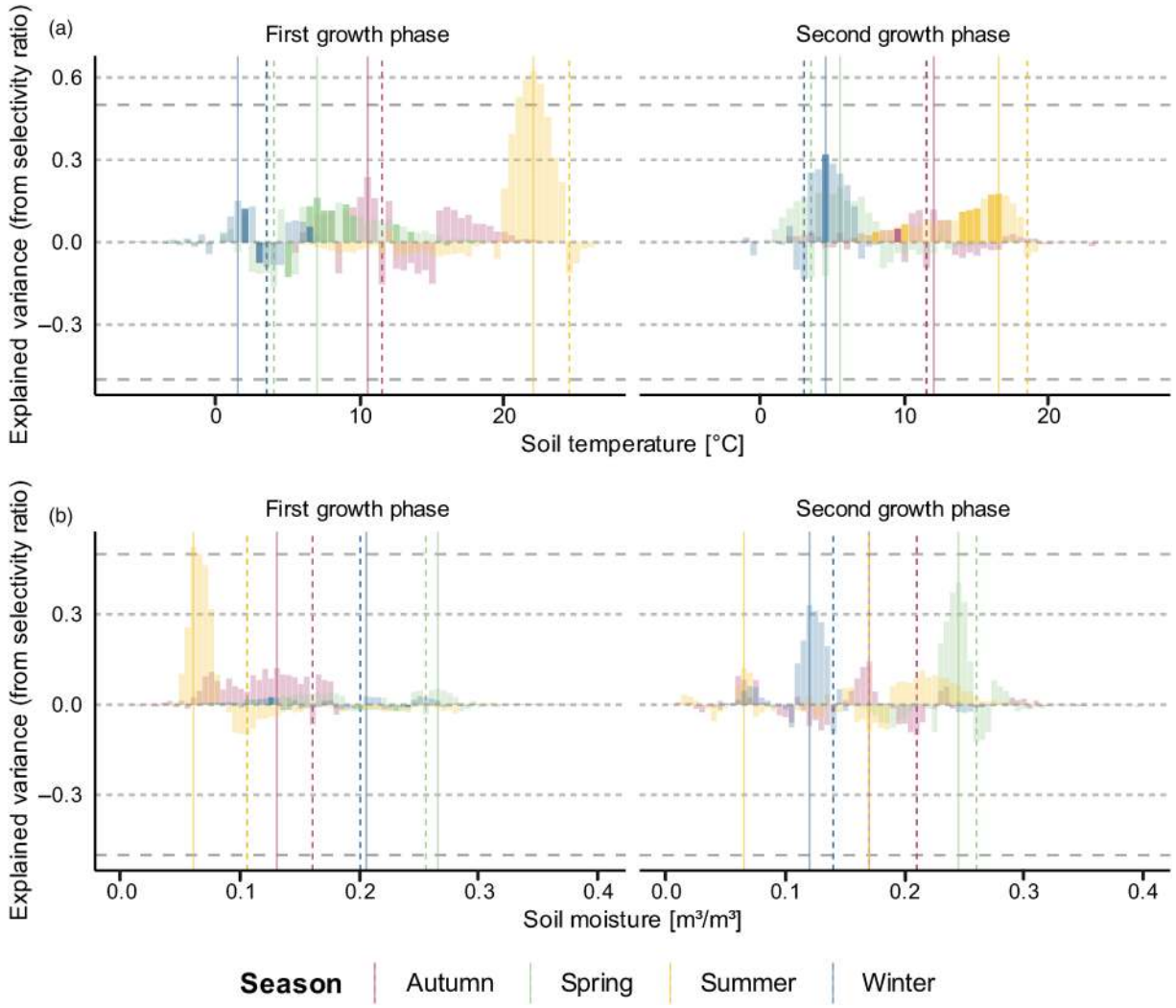


FIGURE 5 Partial least squares regression (PLSR) calculated for soil temperature (T_{RZ}, [a]) and soil moisture (SM_{RZ}, [b]) as drivers of growth in *C. galianoi*, pooled for all positions and for all seasons. Colours represent seasons, with solid-colour areas representing values designated as significant ($p < 0.05$) and shaded areas representing no significance. Solid lines underline the strongest positive and dashed lines the strongest negative correlations, regardless of significance. For the first growth phase, the analysis is based on pre-growth summer, autumn and winter and the current spring conditions, whereas for the second growth phase on previous winter, spring, summer, and the current autumn conditions.

overall high stem water potential of *C. galianoi*. This, together with the low diurnal changes in stem diameter indicating reduced transpiration induced water loss and rapid overnight replenishment (Figure S11), likely results in overall high cell turgor, allowing cell expansion and potential cambial activity during winter (Albrecht et al., 2024; Steppe et al., 2015). We therefore argue that our green-stemmed species can capitalise from additional opportunities for photosynthesis by maintaining physiological activity and possibly even growth at low temperatures (Figure 4c), like other wintergreen species (Lundell et al., 2008; Oribe & Kubo, 1997; Wyka & Oleksyn, 2014). However, as winter growth in *C. galianoi* occurred when growth conditions shifted to winter, that is when comparatively mild winter conditions that normally occur in early spring prevailed, our results do not challenge the current agreement on the thermal limits of secondary growth of perennial plants (Rossi et al., 2007), but rather the coupling of growth to specific seasons (usually spring, summer and autumn).

In contrast, during the summer, stem contraction in *C. galianoi* was pronounced and reflected by overall high stem water deficit (Figure 4a,b) indicating low stem water potential that causes water to flow from the living cells into the xylem conduits, thereby reducing cell turgor which ultimately inhibits growth (Sevanto et al., 2011; Steppe et al., 2015). Thus, summer drought stress, regarded as the main constraint for plant performance and survival in the Mediterranean, comprising the simultaneous effect of elevated temperatures, high irradiance and water scarcity (Larcher, 2000; Magaña Ugarte et al., 2019), also occurs in the alpine species *C. galianoi*. However, the observed diurnal pattern (Figure S11) suggests that transpiration-induced lowering of cell turgor during the day is followed by rapid replenishment

overnight, which is associated with increasing water potential and cell turgor (Steppe et al., 2015; Zweifel et al., 2021). This presumably allows physiological activity to be maintained throughout the summer, albeit at comparatively low levels (Albrecht et al., 2024) and with high risk of damage from prolonged drought stress (Attia et al., 2015), as maintained activity may lead to decelerated rehydration when transpiration exceeds root water uptake (Sevanto et al., 2011). Accordingly, summer stem contraction in our species proved a function of drought severity.

In agreement with the literature, suggesting that growth bimodality is an adaptation enabling shrub species to withstand the dual climatic stress induced by the climatic regime (Camarero et al., 2010; Tumajer, Shishov, et al., 2021), we hypothesise that *C. galianoi* adapts to frost and drought by taking advantage from evergreen stems for photosynthetic activity under extreme temperatures, while reducing transpiration loss (Albrecht et al., 2023, 2024). This is evidenced by our findings on environmental growth control (Figure 5), showing that growth during both growth phases is closely linked to the environmental conditions prior to growth, with pre-growth winter conditions promoting growth during the first growth phase in spring (March, April and May) and pre-growth winter and summer conditions promoting growth during the second growth phase in autumn (September, October and November) (for timing of growth phases see Table S2, Figure S9). Consequently, by adapting to extreme winter and summer conditions *C. galianoi* may even benefit from the dual climatic stress, probably by remobilising previously attained resources during the phases of actual growth.

Similar to most Mediterranean woody plants (Alday et al., 2020; Camarero et al., 2021; Pellizzari et al., 2017), we found growth in *C. galianoi* to be highest during spring (Figure 4c, Figure S12), related to annual ring formation during this first growth phase (Camarero et al., 2010; Valeriano et al., 2023). Here, we found complex environmental growth controls with high short-term variability of significant drivers during the phase of actual growth: (a) Early-spring growth activity (February/March; Figure 4c, Figures S13 and S14) regardless of high freeze–thaw activity suggests that, as aforementioned, our species can be physiologically active at low temperatures, likely down to 0°C (cf. Oribe & Kubo, 1997). (b) High temperatures in the middle of the first growth phase (April; Figures S13 and S14) allow for maximum photosynthetic activity supported by the first unfolded leafs under cloudless high-pressure weather conditions when solar radiation is heading towards solstice (cf. Peri et al., 2011; Starr, 2001; Starr & Oberbauer, 2003). (c) Mild and humid conditions during late spring (May/June; Figures S13 and S14) likely promote a high water potential when plants have leaves (cf. Gucci et al., 1997; Jones, 1998), which is in agreement with previous studies from the Mediterranean, showing a predominant and coherent growth response to May–June precipitation (Campelo et al., 2021; Gutiérrez et al., 2011; Touchan et al., 2014).

Furthermore, we found a pronounced water-related stem diameter increment in autumn, yet only minor growth rates during this time (Figure 4c, Figure S12). Such contrasting patterns in stem diameter change and actual growth have not been disentangled before (Valeriano et al., 2023), with the question whether autumn radial increment represents actual growth or stem swelling due to rehydration of stem tissues after summer drought being left (Mäkinen et al., 2008; Zweifel, 2016). Here, our results show that both, swelling and growth, simultaneously occur, but in *C. galianoi*, post-summer rehydration is stronger than growth (Figure 4a,c), likely due to its elastic cells allowing the species to tolerate severe dehydration (Albrecht et al., 2024), while maintaining high water potential (cf. Patakas & Nortsakis, 1999). During the second growth phase, humid and cool conditions promoted growth (Figure 5, Figures S13 and S14), which are likely associated with a lower risk of transpiration loss and allow for constant high turgor pressure in the plants.

Overall, spring and autumn precipitation have been identified as main drivers for growth in the Mediterranean (de Luis et al., 2007; Pellizzari et al., 2017), making soil water available and thus reactivating the cambium (Alday et al., 2020; Campelo et al., 2018; Tumajer, Shishov, et al., 2021). Therefore, it is generally assumed that bimodal growth is triggered by climatic drivers (Camarero et al., 2010; Pacheco et al., 2018; Valeriano et al., 2023), with the role of plant internal processes remaining unclear (de Micco et al., 2016). Our results confirm the environmental control of bimodal growth in *C. galianoi* but critically highlight the importance of pre-growth conditions, especially for spring growth.

4.3 | Carry-over effects

Our results on bimodal growth patterns suggest that pre-growth conditions determine growth during the active growth phases. After quiescence, alpine plant species are facing short windows of growth opportunities under favourable conditions. Earlier studies have shown that previous year's meteorological conditions are reflected in the morphological and physiological characteristics of current-year's leaves, and acclimation to changes in light intensity even occurs over multiple growing seasons (e.g. Ishii & Ohsugi, 2011; Koike et al., 1997; Sumida et al., 2018). Earlywood of annual rings has been shown to also contain photo-assimilates from the previous summer and autumn as well as from the current season (Helle & Schleser, 2004; Kagawa et al., 2006; Krepkowski et al., 2013). Presupposing that all alpine plants are able to photosynthesise at sub-zero temperatures (Körner, 2021; Pisek et al., 1967) and some even during severe droughts (Attia et al., 2015), it can be assumed that evergreen/green-stemmed Mediterranean alpine shrub species exhibit such carry-over effects by seasonally preceding photosynthetic activity. Resources accumulated during pre-growth assimilation likely help the plant to perform even under unfavourable conditions during the active growth phase, facilitated by the ability to store and mobilise carbohydrates (Palacio et al., 2007) and decouple growth from carbon uptake (Iwasa & Kubo, 1997; Meloche & Diggle, 2003; Wyka, 1999). Even for minor autumn growth, pre-growth conditions were of major importance.

Growth was likely promoted by long-term storage of assimilates from both, cloudless high-pressure winters during the previous year (Wyka & Oleksyn, 2014), and mild pre-growth summers (cf. Attia et al., 2015). Overall, our study suggests, that for alpine species, the concept of bimodality needs to be rethought, and common assumptions on the actuality of driver—growth relations have to be viewed with caution.

5 | CONCLUSIONS

The combined strategies of bimodality and adaptation to the environment by relocating the assimilation phase to periods with harmless (i.e. low) transpiration losses together with its high growth plasticity not only gives *C. galianoi* an advantage compared to coexisting species at individual sites (Albrecht et al., 2023, 2024) but also allows the species to colonise a wide biogeographical range in the Mediterranean alpine and to withstand a wide range of temporal fluctuations of the weather and climate regime. Here, we show the species´ adaptation to the spatial heterogeneity across its range using a comprehensive dataset comprising continuous time-series of stem diameter change across a huge variety of different sites along multiple geographical gradients. We managed to derive consistent growth patterns across the species' range, identifying annual bimodality with major growth in spring and long-term carry-over effects as a successful strategy in the Mediterranean alpine. Furthermore, previous findings highlighting the importance of pre-growth conditions (Albrecht et al., 2023, 2024) may be explained by preceding photosynthetic activity under favourable conditions during the seasons usually considered dormant (winter/summer). This may help the plant to perform even under unfavourable conditions in winter and during the active growth phase, challenging the general assumption of coupling growth to specific seasons. Overall, our results confirm that *C. galianoi* is probably well adapted to future climate variability by taking advantage from warmer winters, and tolerating even longer summer droughts. Should our found carry-over effects for alpine growth control also be relevant in other biomes and, as such, occur between life-history stages, developmental stages, and physiological states associated with a discrete time-scale (as suggested by O'Connor et al., 2014), ecological and biogeographical aspects of future climate change responses may have to be reconsidered.

AUTHOR CONTRIBUTIONS

Jörg Löffler had the idea, designed the research platform and together with Eike Corina Albrecht conducted the fieldwork and ran the long-term LTAER-ES project. Svenja Dobbert conducted the statistical analysis and helped with data management and figures. Eike Corina Albrecht led the writing of the manuscript and analysed the data, with contributions from Svenja Dobbert, Roland Pape and Jörg Löffler.

ACKNOWLEDGEMENTS

We thank Blanca Ramos Losada and José Enrique Granados Torres (Management Team, Sierra Nevada National Park and Natural Park; project number 38_21) for long-term collaboration and research permissions; Cecilio Tarifa, Mercedes Cano and Manuel Peregrina (Staff, Sierra Nevada National and Natural Park) for field support; the Spanish authorities of Granada Province, particularly Francisco Mingorance Castillo and the staff of the town hall in Mecina Bombarón for overall support; Javier Herrero Lantarón (University of Córdoba) for access to climate data from the alpine meteorological station "Refugio Poqueira"; Yolanda Jiménez Olivencia, Andrés Caballero and Laura Porcel Rodríguez (University of Granada) for long-term collaboration; Joaquín Molero Mesa (University of Granada) for species identification; Maria Dolores Moreno Ferrer and Manuel de Toro Moreno for hospitality in Mecina Bombarón; and Gloria López Guerrero in Capileira, Francisco Marin de la Torre (Servicio de Interpretacion Altas Cumbres, Capileira) and Alejandro Mingorance Rodríguez (Mecina Bombarón) for off-road services. Parts of this study were supported by the Deutsche Forschungsgemeinschaft (DFG) (grants LO 830/16-1, LO 830/32-1). We conducted fieldwork under the project number licence 38_21 granted by the Sierra Nevada National Park and Natural Park. Open Access funding enabled and organized by Projekt DEAL.

CONFLICT OF INTEREST STATEMENT

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

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14321.

DATA AVAILABILITY STATEMENT

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://doi.org/10.3112/erdkunde.2022.dp.01 (Löffler et al., 2022).

ORCID

Jörg Löffler https://orcid.org/0000-0002-9320-6168

REFERENCES

Albrecht, E. C., Dobbert, S., Pape, R., & Löffler, J. (2023). Patterns, timing, and environmental drivers of secondary growth in two physiologically distinct Mediterranean alpine shrub species. *Environmental Research: Ecology*, *2*(4), 045002. https://doi.org/10.1088/2752-664X/acffcc

Albrecht, E. C., Dobbert, S., Pape, R., & Löffler, J. (2024). Patterns, timing, and environmental drivers of growth in two coexisting green-stemmed Mediterranean alpine shrubs species. *New Phytologist*, *241*, 114–130. https://doi.org/10.1111/nph.19285

Alday, J. G., Camarero, J. J., Revilla, J., & Resco de Dios, V. (2020). Similar diurnal, seasonal and annual rhythms in radial root expansion

across two coexisting Mediterranean oak species. *Tree Physiology*, *40*(7), 956–968. https://doi.org/10.1093/treephys/tpaa041

Anderson, R. S., Jiménez-Moreno, G., Carrión, J. S., & Pérez-Martínez, C. (2011). Postglacial history of alpine vegetation, fire, and climate from Laguna de Río Seco, Sierra Navada, southern Spain. *Quaternary Science Reviews*, *30*(13–14), 1615–1629. https://doi.org/10.1016/j.quascirev.2011.03.005

Arbellay, E., Fonti, P., & Stoffel, M. (2012). Duration and extension of anatomical changes in wood structure after cambial injury. *Journal of Experimental Botany*, *63*(8), 3271–3277. https://doi.org/10.1093/jxb/ers050

Attia, Z., Domec, J. C., Oren, R., Way, D. A., & Moshelion, M. (2015). Growth and physiological responses of isohydric and anisohydric poplars to drought. *Journal of Experimental Botany*, *66*(14), 4373–4381. https://doi.org/10.1093/jxb/erv195

Bär, A., Bräuning, A., & Löffler, J. (2007). Ring-width chronologies of the alpine dwarf shrub *Empetrum hermaphroditum* from the Norwegian mountains. *IAWA Journal*, *28*(3), 325–338. https://doi.org/10.1163/22941932-90001644

Bär, A., Pape, R., Bräuning, A., & Löffler, J. (2008). Growth-ring variations of dwarf shrubs reflect regional climate signals in alpine environments rather than topoclimatic differences. *Journal of Biogeography*, *35*(4), 625–636. https://doi.org/10.1111/j.1365-2699.2007.01804.x

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, *67*, 1–48. https://doi.org/10.48550/arXiv.1406.5823

Battipaglia, G., de Micco, V., Brand, W. A., Saurer, M., Aronne, G., Linke, P., & Cherubini, P. (2014). Drought impact on water use efficiency and intra-annual density fluctuations in *Erica arborea* on Elba (Italy). *Plant, Cell and Environment*, *37*(2), 382–391. https://doi.org/10.1111/pce.12160

Benito, B., Lorite, J., & Peñas, J. (2011). Simulating potential effects of climatic warming on altitudinal patterns of key species in Mediterranean-alpine ecosystems. *Climatic Change*, *108*(3), 471–483. https://doi.org/10.1007/s10584-010-0015-3

Blanca, G., Cabezudo, B., Cueto, M., Fernández López, C., & Morales Torres, C. (2009a). *Flora Vascular de Andalucía Oriental* (Vol. *2*). Consejería de Medio Ambiente. Junta de Andalucía.

Blanca, G., Cabezudo, B., Cueto, M., Fernández López, C., & Morales Torres, C. (2009b). *Flora Vascular de Andalucía Oriental* (Vol. *1*). Consejería de Medio Ambiente. Junta de Andalucía.

Bloom, A. J., Chapin, F. S., III, & Mooney, H. A. (1985). Resource limitation in plants - an economic analogy. *Annual Review of Ecology and Systematics*, *16*(1), 363–392.

Bossard, C. C., & Rejmanek, M. (1992). Why have green stems? *Functional Ecology*, *6*, 197–205. https://www.jstor.org/stable/2389755

Bravo, D. N., Araújo, M. B., Lasanta, T., & Moreno, J. I. L. (2008). Climate change in Mediterranean mountains during the 21st century. *Ambio*, *37*(4), 280–285. https://doi.org/10.1579/0044-7447(2008)37[280:CCIMMD]2.0.CO;2

Brodersen, C. R., & McElrone, A. J. (2013). Maintenance of xylem network transport capacity: A review of embolism repair in vascular plants. *Frontiers in Plant Science*, *4*, 108. https://doi.org/10.3389/fpls.2013.00108

Camarero, J. J., Olano, J. M., Alfaro, S. J. A., Fernández-Marín, B., Becerril, J. M., & García-Plazaola, J. I. (2012). Photoprotection mechanisms in *Quercus ilex* under contrasting climatic conditions. *Flora-Morphology, Distribution, Functional Ecology of Plants*, *207*(8), 557–564. https://doi.org/10.1016/j.flora.2012.06.003

Camarero, J. J., Olano, J. M., & Parras, A. (2010). Plastic bimodal xylogenesis in conifers from continental Mediterranean climates. *New Phytologist*, *185*(2), 471–480. https://doi.org/10.1111/j.1469-8137.2009.03073.x

Camarero, J. J., Valeriano, C., Gazol, A., Colangelo, M., & Sánchez-Salguero, R. (2021). Climate differently impacts the growth of coexisting trees and shrubs under semi-arid Mediterranean conditions. *Forests*, *12*(3), 381. https://doi.org/10.3390/f12030381

Campelo, F., Gutiérrez, E., Ribas, M., Sánchez-Salguero, R., Nabais, C., & Camarero, J. J. (2018). The facultative bimodal growth pattern in *Quercus ilex*—A simple model to predict sub-seasonal and interannual growth. *Dendrochronologia*, *49*, 77–88. https://doi.org/10.1016/j.dendro.2018.03.001

Campelo, F., Ribas, M., & Gutiérrez, E. (2021). Plastic bimodal growth in a Mediterranean mixed-forest of *Quercus ilex* and *Pinus halepensis*. *Dendrochronologia*, *67*, 125836. https://doi.org/10.1016/j.dendro.2021.125836

Carrascal, L. M., Galván, I., & Gordo, O. (2009). Partial least squares regression as an alternative to current regression methods used in ecology. *Oikos*, *118*(5), 681–690. https://doi.org/10.1111/j.1600-0706.2008.16881.x

Castagneri, D., Battipaglia, G., von Arx, G., Pacheco, A., & Carrer, M. (2018). Tree-ring anatomy and carbon isotope ratio show both direct and legacy effects of climate on bimodal xylem formation in *Pinus pinea*. *Tree Physiology*, *38*(8), 1098–1109. https://doi.org/10.1093/treephys/tpy036

Chapin, F. S., III, Bloom, A. J., Field, C. B., & Wa, R. H. (1987). Plant response to multiple environmental factors. *BioScience*, *37*(1), 49–57. https://doi.org/10.2307/1310177

Cherubini, P., Gartner, B. L., Tognetti, R., Bräker, O. U., Schoch, W., & Innes, J. L. (2003). Identification, measurement and interpretation of tree rings in woody species from Mediterranean climates. *Biological Reviews*, *78*(1), 119–148. https://doi.org/10.1017/S1464793102006000

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

de Jong, S. (1993). SIMPLS: An alternative approach to partial least squares regression. *Chemometrics and Intelligent Laboratory Systems*, *18*(3), 251–263. https://doi.org/10.1016/0169-7439(93)85002-X

de Luis, M., Gričar, J., Čufar, K., & Raventós, J. (2007). Seasonal dynamics of wood formation in *Pinus halepensis* from dry and semi-arid ecosystems in Spain. *IAWA Journal*, *28*(4), 389–404. https://doi.org/10.1163/22941932-90001651

de Micco, V., Balzano, A., Čufar, K., Aronne, G., Gričar, J., Merela, M., & Battipaglia, G. (2016). Timing of false ring formation in *Pinus halepensis* and *Arbutus unedo* in southern Italy: Outlook from an analysis of xylogenesis and tree-ring chronologies. *Frontiers in Plant Science*, *7*, 1–14. https://doi.org/10.3389/fpls.2016.00705

Deslauriers, A., Rossi, S., & Anfodillo, T. (2007). Dendrometer and intra-annual tree growth: What kind of information can be inferred? *Dendrochronologia*, *25*(2), 113–124. https://doi.org/10.1016/j.dendro.2007.05.003

Dobbert, S., Albrecht, E. C., Pape, R., & Löffler, J. (2022). Alpine shrub growth follows bimodal seasonal patterns across biomes–unexpected environmental controls. *Communications Biology*, *5*(1), 1–12. https://doi.org/10.1038/s42003-022-03741-x

Dobbert, S., Pape, R., & Löffler, J. (2021a). How does spatial heterogeneity affect inter-and intraspecific growth patterns in tundra shrubs? *Journal of Ecology*, *109*(12), 4115–4131. https://doi.org/10.1111/1365-2745.13784

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

Dobbert, S., Pape, R., & Löffler, J. (2022b). On growth patterns and mechanisms in arctic-alpine shrubs. *Erdkunde*, *76*, 199–226. https://doi.org/10.3112/erdkunde.2022.03.04

Dobbert, S., Pape, R., & Löffler, J. (2022c). The application of dendrometers to alpine dwarf shrubs–a case study to investigate stem growth

responses to environmental conditions. *Biogeosciences*, *19*(7), 1933–1958. https://doi.org/10.5194/bg-19-1933-2022

Farrés, M., Platikanov, S., Tsakovski, S., & Tauler, R. (2015). Comparison of the variable importance in projection (VIP) and of the selectivity ratio (SR) methods for variable selection and interpretation. *Journal of Chemometrics*, *29*(10), 528–536. https://doi.org/10.1002/cem.2736

Fernández-Santos, B., Martínez, C., García, J. A., & Puerto, A. (2004). Postfire regeneration in *Cytisus oromediterraneus*: Sources of variation and morphology of the below-ground parts. *Acta Oecologica*, *26*(2), 149–156. https://doi.org/10.1016/j.actao.2004.03.011

Firn, J., Nguyen, H., Schütz, M., & Risch, A. C. (2019). Leaf trait variability between and within subalpine grassland species differs depending on site conditions and herbivory. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1907), 20190429. https://doi.org/10.1098/rspb.2019.0429

Frindte, K., Pape, R., Werner, K., Löffler, J., & Knief, C. (2019). Temperature and soil moisture control microbial community composition in an arctic-alpine ecosystem along elevational and micro-topographic gradients. *The ISME Journal*, *13*(8), 2031–2043. https://doi.org/10.1038/s41396-019-0409-9

Gärtner, H., & Schweingruber, F. H. (2013). *Microscopic preparation techniques for plant stem analysis*. Remagen-Overwinter: Dr. Kessel.

Gazol, A., & Camarero, J. J. (2012a). Mediterranean dwarf shrubs and coexisting trees present different radial-growth synchronies and responses to climate. *Plant Ecology*, *213*, 1687–1698. https://doi.org/10.1007/s11258-012-0124-3

Gazol, A., & Camarero, J. J. (2012b). The performance of Mediterranean subshrubs depends more on microsite than on regional climate conditions. *Journal of Vegetation Science*, *23*(6), 1062–1070. https://doi.org/10.1111/j.1654-1103.2012.01429.x

Ghalambor, C. K., McKay, J. K., Carroll, S. P., & Reznick, D. N. (2007). Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology*, *21*(3), 394–407. https://doi.org/10.1111/j.1365-2435.2007.01283.x

Giménez, E., Melendo, M., Valle, F., Gómez-Mercado, F., & Cano, E. (2004). Endemic flora biodiversity in the south of the Iberian Peninsula: Altitudinal distribution, life forms and dispersal modes. *Biodiversity and Conservation*, *13*, 2641–2660. https://doi.org/10.1007/s10531-004-2140-7

Giménez-Benavides, L., Escudero, A., García-Camacho, R., García-Fernández, A., Iriondo, J., Lara-Romero, C., & Morante-López, J. (2018). How does climate change affect regeneration of Mediterranean high-mountain plants? An integration and synthesis of current knowledge. *Plant Biology*, *20*, 50–62. https://doi.org/10.1111/plb.12643

Giorgi, F., & Lionello, P. (2008). Climate change projections for the Mediterranean region. *Global and Planetary Change*, *63*(2–3), 90–104. https://doi.org/10.1016/j.gloplacha.2007.09.005

Gjærevoll, O. (1956). The plant communities of the Scandinavian alpine snow-beds. *Det Kunglige Norske Videnskabers Selskaps Skrifter*, *1*, 1–405.

Gómez-Ortiz, A., Oliva, M., Salvador-Franch, F., Palacios, D., Tanarro, L. M., de Sanjosé-Blasco, J. J., & Salvà-Catarineu, M. (2019). Monitoring permafrost and periglacial processes in Sierra Nevada (Spain) from 2001 to 2016. *Permafrost and Periglacial Processes*, *30*(4), 278–291. https://doi.org/10.1002/ppp.2002

Gucci, R., Lombardini, L., & Tattini, M. (1997). Analysis of leaf water relations in leaves of two olive (*Olea europaea*) cultivars differing in tolerance to salinity. *Tree Physiology*, *17*(1), 13–21. https://doi.org/10.1093/treephys/17.1.13

Gutiérrez, E., Campelo, F., Camarero, J. J., Ribas, M., Muntán, E., Nabais, C., & Freitas, H. (2011). Climate controls act at different scales on the seasonal pattern of *Quercus ilex* L. stem radial increments in NE Spain. *Trees*, *25*, 637–646. https://doi.org/10.1007/s00468-011-0540-3

Gutiérrez-Girón, A., & Gavilán, R. G. (2013). Plant functional strategies and environmental constraints in Mediterranean high mountain grasslands in central Spain. *Plant Ecology and Diversity*, *6*(3–4), 435–446. https://doi.org/10.1080/17550874.2013.783641

Helle, G., & Schleser, G. H. (2004). Beyond CO_2-fixation by rubisco—An interpretation of $^{13}C/^{12}C$ variations in tree rings from novel intra-seasonal studies on broad-leaf trees. *Plant, Cell and Environment*, *27*(3), 367–380. https://doi.org/10.1111/j.0016-8025.2003.01159.x

Henn, J. J., Buzzard, V., Enquist, B. J., Halbritter, A. H., Klanderud, K., Maitner, B. S., Michaletz, S. T., Pötsch, C., Seltzer, L., Telford, R. J., Yang, Y., Zhang, L., & Vandvik, V. (2018). Intraspecific trait variation and phenotypic plasticity mediate alpine plant species response to climate change. *Frontiers in Plant Science*, *9*, 1548. https://doi.org/10.3389/fpls.2018.01548

Herrero, J., & Polo, M. J. (2016). Evaposublimation from the snow in the Mediterranean mountains of Sierra Nevada (Spain). *The Cryosphere*, *10*(6), 2981–2998. https://doi.org/10.5194/tc-10-2981-2016

Ishii, H., & Ohsugi, Y. (2011). Light acclimation potential and carry-over effects vary among three evergreen tree species with contrasting patterns of leaf emergence and maturation. *Tree Physiology*, *31*(8), 819–830. https://doi.org/10.1093/treephys/tpr079

Iwasa, Y., & Kubo, T. (1997). Optimal size of storage for recovery after unpredictable disturbances. *Evolutionary Ecology*, *11*, 41–65. https://doi.org/10.1023/A:1018483429029

Jones, H. G. (1998). Stomatal control of photosynthesis and transpiration. *Journal of Experimental Botany*, *49*, 387–398. https://www.jstor.org/stable/23695972

Kagawa, A., Sugimoto, A., & Maximov, T. C. (2006). $^{13}CO_2$ pulse-labelling of photoassimilates reveals carbon allocation within and between tree rings. *Plant, Cell and Environment*, *29*(8), 1571–1584. https://doi.org/10.1111/j.1365-3040.2006.01533.x

Koike, T., Miyashita, N., & Toda, H. (1997). Effects of shading on leaf structural characteristics in successional deciduous broad-leaved tree seedlings and their silvicultural meaning. *Forest Research and Environment-Tokyo University of Agriculture and Technology (Japan)*, *35*, 9–25.

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

Körner, C. (2021). *Alpine plant life: Functional plant ecology of high mountain ecosystems*. Springer Nature.

Kraus, C., Zang, C., & Menzel, A. (2016). Elevational response in leaf and xylem phenology reveals different prolongation of growing period of common beech and Norway spruce under warming conditions in the Bavarian Alps. *European Journal of Forest Research*, *135*, 1011–1023. https://doi.org/10.1007/s10342-016-0990-7

Krepkowski, J., Gebrekirstos, A., Shibistova, O., & Bräuning, A. (2013). Stable carbon isotope labeling reveals different carry-over effects between functional types of tropical trees in an Ethiopian mountain forest. *New Phytologist*, *199*(2), 431–440. https://doi.org/10.1111/nph.12266

Kucheryavskiy, S. (2020). Mdatools – R package for chemometrics. *Chemometrics and Intelligent Laboratory Systems*, *198*, 103937. https://doi.org/10.1016/j.chemolab.2020.103937

Larcher, W. (2000). Temperature stress and survival ability of Mediterranean sclerophyllous plants. *Plant Biosystems*, *134*(3), 279–295. https://doi.org/10.1080/11263500012331350455

Li, Z., Liu, G., Fu, B., Zhang, Q., Ma, K., & Pederson, N. (2013). The growth-ring variations of alpine shrub *Rhododendron przewalskii* reflect regional climate signals in the alpine environment of Miyaluo town in Western Sichuan Province, China. *Acta Ecologica Sinica*, *33*(1), 23–31. https://doi.org/10.1016/j.chnaes.2012.12.004

Linares, J. C., Covelo, F., Carreira, J. A., & Merino, J. Á. (2012). Phenological and water-use patterns underlying maximum growing

season length at the highest elevations: Implications under climate change. *Tree Physiology*, *32*(2), 161–170. https://doi.org/10.1093/treephys/tps003

Lionello, P., & Scarascia, L. (2018). The relation between climate change in the Mediterranean region and global warming. *Regional Environmental Change*, *18*, 1481–1493. https://doi.org/10.1007/s10113-018-1290-1

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

Löffler, J., & Pape, R. (2020). Thermal niche predictors of alpine plant species. *Ecology*, *101*(1), e02891. https://doi.org/10.1002/ecy.2891

Lundell, R., Saarinen, T., Åström, H., & Hänninen, H. (2008). The boreal dwarf shrub *Vaccinium vitis-idaea* retains its capacity for photosynthesis through the winter. *Botany*, *86*, 491–500. https://doi.org/10.1139/B08-022

Macek, P., Prieto, I., Macková, J., Pistón, N., & Pugnaire, F. I. (2016). Functional plant types drive plant interactions in a Mediterranean mountain range. *Frontiers in Plant Science*, *7*, 662. https://doi.org/10.3389/fpls.2016.00662

Magaña Ugarte, R., Escudero, A., & Gavilán, R. G. (2019). Metabolic and physiological responses of Mediterranean high-mountain and alpine plants to combined abiotic stresses. *Physiologia Plantarum*, *165*(2), 403–412. https://doi.org/10.1111/ppl.12898

Mäkinen, H., Seo, J. W., Nöjd, P., Schmitt, U., & Jalkanen, R. (2008). Seasonal dynamics of wood formation: A comparison between pinning, microcoring and dendrometer measurements. *European Journal of Forest Research*, *127*, 235–245. https://doi.org/10.1007/s10342-007-0199-x

McLean, E. H., Prober, S. M., Stock, W. D., Steane, D. A., Potts, B. M., Vaillancourt, R. E., & Byrne, M. (2014). Plasticity of functional traits varies clinically along a rainfall gradient in *Eucalyptus tricarpa*. *Plant, Cell and Environment*, *37*(6), 1440–1451. https://doi.org/10.1111/pce.12251

Meloche, C. G., & Diggle, P. K. (2003). The pattern of carbon allocation supporting growth of preformed shoot primordia in *Acomastylis rossii* (Rosaceae). *American Journal of Botany*, *90*(9), 1313–1320. https://doi.org/10.3732/ajb.90.9.1313

Mitrakos, K. (1980). A theory for Mediterranean plant life. *Acta Oecologica. Série Oecologia Plantarum Montreuil*, *1*(3), 245–252.

Morales, A. I. G. C., Mendoza, J. M. O., Gozalbo, M. E., & Martínez, J. J. C. (2012). Arboreal and prostrate conifers coexisting in Mediterranean high mountains differ in their climatic responses. *Dendrochronologia*, *30*(4), 279–286. https://doi.org/10.1016/j.dendro.2012.02.004

O'Connor, C. M., Norris, D. R., Crossin, G. T., & Cooke, S. J. (2014). Biological carryover effects: Linking common concepts and mechanisms in ecology and evolution. *Ecosphere*, *5*(3), 28. https://doi.org/10.1890/ES13-00388.1

Olano, J. M., Almería, I., Eugenio, M., & von Arx, G. (2013). Under pressure: How a Mediterranean high-mountain forb coordinates growth and hydraulic xylem anatomy in response to temperature and water constraints. *Functional Ecology*, *27*(6), 1295–1303. https://doi.org/10.1111/1365-2435.12144

Oribe, Y., & Kubo, T. (1997). Effect of heat on cambial reactivation during winter dormancy in evergreen and deciduous conifers. *Tree Physiology*, *17*(2), 81–87. https://doi.org/10.1093/treephys/17.2.81

Pacheco, A., Camarero, J. J., Ribas, M., Gazol, A., Gutierrez, E., & Carrer, M. (2018). Disentangling the climate-driven bimodal growth pattern in coastal and continental Mediterranean pine stands. *Science of the Total Environment*, *615*, 1518–1526. https://doi.org/10.1016/j.scitotenv.2017.09.133

Palacio, S., Maestro, M., & Montserrat-Martí, G. (2007). Seasonal dynamics of non-structural carbohydrates in two species of Mediterranean sub-shrubs with different leaf phenology. *Environmental and Experimental Botany*, *59*(1), 34–42. https://doi.org/10.1016/j.envexpbot.2005.10.003

Patakas, A., & Nortsakis, B. (1999). Mechanisms involved in diurnal changes of osmotic potential in grapevines under drought conditions. *Journal of Plant Physiology*, *154*(5–6), 767–774. https://doi.org/10.1016/S0176-1617(99)80256-9

Pellizzari, E., Camarero, J. J., Gazol, A., Granda, E., Shetti, R., Wilmking, M., Moiseev, P., Pividori, M., & Carrer, M. (2017). Diverging shrub and tree growth from the Polar to the Mediterranean biomes across the European continent. *Global Change Biology*, *23*(8), 3169–3180. https://doi.org/10.1111/gcb.13577

Pellizzari, E., Pividori, M., & Carrer, M. (2014). Winter precipitation effect in a mid-latitude temperature-limited environment: The case of common juniper at high elevation in the Alps. *Environmental Research Letters*, *9*(10), 104021. https://doi.org/10.1088/1748-9326/9/10/104021

Peri, P. L., Arena, M., Pastur, G. M., & Lencinas, M. V. (2011). Photosynthetic response to different light intensities, water status and leaf age of two *Berberis* species (Berberidaceae) of Patagonian steppe, Argentina. *Journal of Arid Environments*, *75*(11), 1218–1222. https://doi.org/10.1016/j.jaridenv.2011.06.003

Pescador, D. S., de Bello, F., Valladares, F., & Escudero, A. (2015). Plant trait variation along an altitudinal gradient in mediterranean high mountain grasslands: Controlling the species turnover effect. *PLoS One*, *10*(3), e0118876. https://doi.org/10.1371/journal.pone.0118876

Pisek, A., Larcher, W., & Unterholzner, R. (1967). Kardinale Temperaturbereiche der Photosynthese und Grenztemperaturen des Lebens der Blätter verschiedener Spermatophyten. I. Temperaturminimum der Nettoassimilation, Gefrier-und Frostschadensbereiche der Blätter. *Flora*, *157*(2), 239–264. https://doi.org/10.1016/S0367-1801(17)30068-6

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing.

Rajalahti, T., Arneberg, R., Kroksveen, A. C., Berle, M., Myhr, K.-M., & Kvalheim, O. M. (2009). Discriminating variable test and selectivity ratio plot: Quantitative tools for interpretation and variable (biomarker) selection in complex spectral or chromatographic profiles. *Analytical Chemistry*, *81*(7), 2581–2590. https://doi.org/10.1021/ac802514y

Rixen, C., Schwoerer, C., & Wipf, S. (2010). Winter climate change at different temporal scales in *Vaccinium myrtillus*, an Arctic and alpine dwarf shrub. *Polar Research*, *29*(1), 85–94. https://doi.org/10.1111/j.1751-8369.2010.00155.x

Roberts, N., Brayshaw, D., Kuzucuolu, C., Perez, R., & Sadori, L. (2011). The mid-Holocene climatic transition in the Mediterranean: Causes and consequences. *Holocene*, *21*(1), 3–13. https://doi.org/10.1177/0959683610388058

Ropars, P., Angers-Blondin, S., Gagnon, M., Myers-Smith, I. H., Lévesque, E., & Boudreau, S. (2017). Different parts, different stories: Climate sensitivity of growth is stronger in root collars vs. stems in tundra shrubs. *Global Change Biology*, *23*(8), 3281–3291. https://doi.org/10.1111/gcb.13631

Rossi, S., Deslauriers, A., Anfodillo, T., & Carraro, V. (2007). Evidence of threshold temperatures for xylogenesis in conifers at high altitudes. *Oecologia*, *152*, 1–12. https://doi.org/10.1007/s00442-006-0625-7

Royce, E. B., & Barbour, M. G. (2001). Mediterranean climate effects. II. Conifer growth phenology across a Sierra Nevada ecotone. *American Journal of Botany*, *88*(5), 919–932. https://doi.org/10.2307/2657045

Sánchez-Salguero, R., & Camarero, J. J. (2020). Greater sensitivity to hotter droughts underlies juniper dieback and mortality in Mediterranean shrublands. *Science of the Total Environment*, *721*, 137599. https://doi.org/10.1016/j.scitotenv.2020.137599

Sevanto, S., Hölttä, T., & Holbrook, N. M. (2011). Effects of the hydraulic coupling between xylem and phloem on diurnal phloem diameter

variation. *Plant, Cell and Environment*, *34*, 690–703. https://doi.org/10.1111/j.1365-3040.2011.02275.x

Sperry, J. (1993). *Water Transport in plants under climatic stress: Winter xylem embolism and spring recovery in* Betula cordifolia, Fagus grandifolia, Abies balsamea *and* Picea rubens. Cambridge University Press.

Sperry, J. S., & Tyree, M. T. (1988). Mechanism of water stress-induced xylem embolism. *Plant Physiology*, *88*(3), 581–587. https://doi.org/10.1104/pp.88.3.581

Starr, G. (2001). *A multi-scale assessment of physiological processes in arctic tundra plants under natural and simulated climate change scenarios* (Doctoral dissertation). Florida International University.

Starr, G., & Oberbauer, S. F. (2003). Photosynthesis of arctic evergreens under snow: Implications for tundra ecosystem carbon balance. *Ecology*, *84*(6), 1415–1420. https://doi.org/10.1890/02-3154

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

Sumida, A., Watanabe, T., & Miyaura, T. (2018). Interannual variability of leaf area index of an evergreen conifer stand was affected by carry-over effects from recent climate conditions. *Scientific Reports*, *8*(1), 1–11. https://doi.org/10.1038/s41598-018-31672-3

Szymczak, S., Häusser, M., Garel, E., Santoni, S., Huneau, F., Knerr, I., Katja Trachte, K., Bendix, J., & Bräuning, A. (2020). How do Mediterranean pine trees respond to drought and precipitation events along an elevation gradient? *Forests*, *11*(7), 758. https://doi.org/10.3390/f11070758

Touchan, R., Anchukaitis, K. J., Shishov, V. V., Sivrikaya, F., Attieh, J., Ketmen, M., Stephan, J., Mitsopoulos, I., Christou, A., & Meko, D. M. (2014). Spatial patterns of eastern Mediterranean climate influence on tree growth. *Holocene*, *24*(4), 381–392. https://doi.org/10.1177/0959683613518594

Trenberth, K. E. (1983). What are the seasons? *Bulletin of the American Meteorological Society*, *64*, 1276–1282. https://doi.org/10.1175/1520-0477(1983)064<1276:WATS>2.0.CO;2

Tumajer, J., Buras, A., Camarero, J. J., Carrer, M., Shetti, R., Wilmking, M., Altman, J., Sangüesa-Barreda, G., & Lehejček, J. (2021). Growing faster, longer or both? Modelling plastic response of *Juniperus communis* growth phenology to climate change. *Global Ecology and Biogeography*, *30*(11), 2229–2244. https://doi.org/10.1111/geb.13377

Tumajer, J., Shishov, V. V., Ilyin, V. A., & Camarero, J. J. (2021). Intra-annual growth dynamics of Mediterranean pines and junipers determines their climatic adaptability. *Agricultural and Forest Meteorology*, *311*, 108685. https://doi.org/10.1016/j.agrformet.2021.108685

Valeriano, C., Gutiérrez, E., Colangelo, M., Gazol, A., Sánchez-Salguero, R., Tumajer, J., Shishov, V., Bonet, J. A., de Aragón, J. M., Ibáñez, R., Valerio, M., & Camarero, J. J. (2023). Seasonal precipitation and continentality drive bimodal growth in Mediterranean forests. *Dendrochronologia*, *78*, 126057. https://doi.org/10.1016/j.dendro.2023.126057

von Büren, R. S., & Hiltbrunner, E. (2022). Low winter temperatures and divergent freezing resistance set the cold range limit of widespread alpine graminoids. *Journal of Biogeography*, *49*(8), 1562–1575. https://doi.org/10.1111/jbi.14455

Weijers, S., Beckers, N., & Löffler, J. (2018). Recent spring warming limits near-treeline deciduous and evergreen alpine dwarf shrub growth. *Ecosphere*, *9*(6), e02328. https://doi.org/10.1002/ecs2.2328

Wold, H. (1975). Soft modelling by latent variables: The non-linear iterative partial least squares (NIPALS) approach. *Journal of Applied Probability*, *12*(S1), 117–142. https://doi.org/10.1017/S0021900200047604

Wold, S. (1978). Cross-validatory estimation of the number of components in factor and principal components models. *Technometrics*, *20*(4), 397–405. https://doi.org/10.1080/00401706.1978.10489693

Wyka, T. (1999). Carbohydrate storage and use in an alpine population of the perennial herb *Oxytropis sericea*. *Oecologia*, *120*, 198–208. https://doi.org/10.1007/s004420050849

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

Yang, Y., Wang, G., Klanderud, K., & Yang, L. (2011). Responses in leaf functional traits and resource allocation of a dominant alpine sedge (*Kobresia pygmaea*) to climate warming in the Qinghai-Tibetan plateau permafrost region. *Plant and Soil*, *349*, 377–387. https://doi.org/10.1007/s11104-011-0891-y

Zotz, G., Hietz, P., & Schmidt, G. (2001). Small plants, large plants: The importance of plant size for the physiological ecology of vascular epiphytes. *Journal of Experimental Botany*, *52*(363), 2051–2056. https://doi.org/10.1093/jexbot/52.363.2051

Zweifel, R. (2016). Radial stem variations - a source of tree physiological information not fully exploited yet. *Plant, Cell and Environment*, *39*(2), 231–232. https://doi.org/10.1111/pce.12613

Zweifel, R., & Häsler, R. (2001). Dynamics of water storage in mature subalpine *Picea abies*: Temporal and spatial patterns of change in stem radius. *Tree Physiology*, *21*(9), 561–569. https://doi.org/10.1093/treephys/21.9.561

Zweifel, R., Sterck, F., Braun, S., Buchmann, N., Eugster, W., Gessler, A., Häni, M., Peters, R. L., Walthert, L., Wilhelm, M., Ziemińska, K., & Etzold, S. (2021). Why trees grow at night. *New Phytologist*, *231*(6), 2174–2185. https://doi.org/10.1111/nph.17552

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Timing of the meteorological seasons.

Table S2. Average duration and timing of the first and second growth phase derived from dendrometer measurements.

Figure S1. (a) Photos of the seasonal aspect of our focal species *Cytisus galianoi*.

Figure S2. (a) Illustration of the anatomical features in a base segment of *Cytisus galianoi*.

Figure S3. Illustration of the methodical procedure of annual ring width measurements along five radii (R 1, 2, 3, 4, 5) in (a) a cross section of a 7-year-old shoot segment and (b) a cross-section of a 10-year-old root segment.

Figure S4. Illustration of environmental data. Root zone temperature (ST_{RZ}), root zone soil moisture (SM_{RZ}) regimes (daily means, derived from hourly measurements) averaged over ridge and slope sites, with shaded areas indicating standard deviation (±SE), vertical light grey lines indicating the meteorological seasons and vertical dark grey lines and grey shaded areas indicating the years.

Figure S5. A representative annual dendrometer curve for one *Cytisus galianoi* specimen during one year, illustrating the calculation of the two growing phases during the first and second half of the year (arrows).

Figure S6. Comparison between annual growth curves calculated from dendrometer measurements at the base of ten *Cytisus galianoi* specimens and annual growth ring width curves measured at the shoot, base and root of seven *C. galianoi* specimens at the same sites at local slope and ridge positions within the study area.

Figure S7. Spearman's correlation coefficients for annual growth calculated from dendrometer measurements and annual growth-ring widths of seven *Cytisus galianoi* specimens from the same sites at local slope and ridge positions.

Figure S8. Stem diameter change for all *Cytisus galianoi* specimens at ridges and slopes, as derived from dendrometer measurements, with the overall means shown in red.

Figure S9. Average growth onset and cessation in *Cytisus galianoi* for the first and second growth phases in 2015–2020, derived from stem diameter curves and pooled for all positions.

Figure S10. Time-series of mean (solid line, with standard deviation shown as shaded area) stem diameter changes from all *Cytisus galianoi* specimens as derived from dendrometer measurements pooled for all positions, and phases of irreversible stem increment (growth), as shown in Figure S9 and represented by bars.

Figure S11. Diurnal variation in stem diameter change.

Figure S12. Boxplot showing the distribution of total annual growth pooled for all positions and separately for ridges and slopes, as well as growth during the first and the second growth phases in *Cytisus galianoi*.

Figure S13. Pearson's correlation coefficients calculated between first (a) and second (b) growth phase as derived from the dendrometer curves and daily soil moisture (SM_{RZ}) and soil temperature (T_{RZ}) data for each month, measured at the individual sites.

Figure S14. Linear mixed-effects analysis for growth during the first and second growth phase as derived from the dendrometer curves (dependent variable) and monthly environmental data (means) as fixed effects. Individual specimens entered as random effects.

How to cite this article: Albrecht, E. C., Dobbert, S., Pape, R., & Löffler, J. (2024). Complex environmental control of growth in a dominant Mediterranean-alpine shrub species. *Journal of Ecology*, *112*, 1516–1532. https://doi.org/10.1111/1365-2745.14321