

Patterns, timing, and environmental drivers of growth in two coexisting green-stemmed Mediterranean alpine shrubs species

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Summary

- The Mediterranean alpine is one of the most vulnerable ecosystems under future environmental change. Yet, patterns, timing and environmental controls of plant growth are poorly investigated. We aimed at an improved understanding of growth processes, as well as stem swelling and shrinking patterns, by examining two common coexisting green-stemmed shrub species.
- Using dendrometers to measure daily stem diameter changes, we separated these changes into water-related shrinking and swelling and irreversible growth. Implementing correlation analysis, linear mixed effects models, and partial least squares regression on time series of stem diameter changes, with corresponding soil temperature and moisture data as environmental predictors, we found species-specific growth patterns related to different drought-adaptive strategies.
- We show that the winter-cold-adapted species *Cytisus galianoi* uses a drought tolerance strategy combined with a high ecological plasticity, and is, thus, able to gain competitive advantages under future climate warming. In contrast, *Genista versicolor* is restricted to a narrower ecological niche using a winter-cold escape and drought avoidance strategy, which might be of disadvantage in a changing climate.
- Pregrowth environmental conditions were more relevant than conditions during growth, controlling the species' resource availability. Thus, studies focusing on current driver constellations of growth may fail to predict a species' ecological niche and its potential future performance.

Introduction

The Mediterranean alpine is considered one of the most vulnerable ecosystems under future global warming (Nogués-Bravo *et al.*, 2008; Benito *et al.*, 2011; Lamprecht *et al.*, 2021). However, little is known about the drivers of plant growth and productivity within this ecosystem (Tumajer *et al.*, 2021a; Blanco-Sánchez *et al.*, 2023) and the overarching question of when, how, and why woody plants grow (Jevšenak *et al.*, 2022) is still unanswered (Tumajer *et al.*, 2021a; Dobbert *et al.*, 2022a; Buchwal *et al.*, 2023). In general, climatic variability has a direct effect on xylem cell production in woody plants with cambial activity controlled by temperature and moisture (Vaganov *et al.*, 2006; Rossi *et al.*, 2016; Huang *et al.*, 2020). Yet, the temporal and spatial patterns in cambium dynamics, as well as seasonal growth dynamics and underlying physiological processes, remain poorly understood (Gamm *et al.*, 2018; Myers-Smith *et al.*, 2020). Here, identifying underlying mechanisms controlling water and carbon balance and, ultimately, long-term patterns in cambial phenology of Mediterranean woody plants (Steppe *et al.*, 2015) is crucial for predicting how species will perform

under current and future climate variability (Cotto *et al.*, 2017; Tumajer *et al.*, 2021a; Jevšenak *et al.*, 2022) and how their biogeographic ranges will evolve.

The ecophysiological processes controlling the responses of plant growth to abiotic drivers are well-studied (Unger *et al.*, 2009; Gordo & Sanz, 2010; Sharma *et al.*, 2020). However, assessing the temporal dynamics of secondary growth remains challenging since traditional methods (Pacheco *et al.*, 2018; Tumajer *et al.*, 2021b; Jevšenak *et al.*, 2022; Valeriano *et al.*, 2023) are incapable of capturing the timing of cambium activity and thus the seasonal dynamics and long-term trends in stem growth (Steppe *et al.*, 2015; Jevšenak *et al.*, 2022). Here, the use of dendrometers, which resolve annual radial growth at finer functional and temporal scales, may be key for bridging the gap between short-term environmental influences (such as frost and drought) on hydrological status and xylogenesis (Drew *et al.*, 2010). Fine-scale dendrometer data, combined with on-site measurements of environmental variables, generates insight into growth responses of shrubs at unprecedented temporal resolution and recently advanced our understanding of widespread phenomena such as greening and browning trends

across biomes (Dobbert *et al.*, 2021a, 2022a,b). Here, we applied this novel approach to study ecophysiological processes by inferring plant growth responses to abiotic drivers from patterns of stem diameter change as an indicator for relevant physiological processes.

In the Mediterranean climate with its warm, dry summers and cool, humid winters cambium activity in woody plants is maximized during spring and autumn, but reduced during unfavorable conditions in summer and winter (Gutiérrez *et al.*, 2011; Touchan *et al.*, 2012; Pacheco *et al.*, 2018). Such a bimodality in growth processes can be interpreted as an adaptation enabling shrub species to withstand the dual climatic stressors of winter cold and summer drought by maximizing growth during the favorable seasons (Mitrakos, 1980; Camarero *et al.*, 2010). In this context, spring growth initiation in the Mediterranean has been identified as controlled by temperatures (Deslauriers *et al.*, 2008; Vieira *et al.*, 2014; Zhang *et al.*, 2018) as well as increasing moisture availability from spring precipitation (Camarero *et al.*, 2010; Pellizzari *et al.*, 2017). Furthermore, resumption of radial growth after the dry summer period has been linked to autumn rains (de Luis *et al.*, 2007; Touchan *et al.*, 2012). Still, few studies address the influence of water availability on the onset of xylogenesis in cold semiarid climates (Ren *et al.*, 2018), while water scarcity due to summer droughts is considered the most limiting abiotic factor for plant growth and productivity in the Mediterranean (Battipaglia *et al.*, 2014; Szymczak *et al.*, 2020), with alpine areas additionally affected by water shortage during periods with frozen ground (Dobbert *et al.*, 2022a). To adapt, plants employ three common strategies: escape, tolerance, and avoidance (Chaves *et al.*, 2003). Escape involves successful reproduction before the onset of severe stress, while avoidance relies on delayed initiation of water scarcity in plant tissues, and tolerance is a result of coordinated physiological and biochemical alterations at the cellular and molecular level (Chaves *et al.*, 2003; Chen & Wang, 2009). These strategies are not mutually exclusive, and plants might use combined strategies (Guo *et al.*, 2017). However, little is known about the adaptive capacity necessary to use such strategies in alpine environments.

These prerequisites for plant growth in the Mediterranean have implications on carbon reserves (Galiano *et al.*, 2012; d'Andrea *et al.*, 2020), in particular for alpine plant species with short time frames for growth (Giménez-Benavides *et al.*, 2018). In order to use these brief growth opportunities effectively, carbon reserves and their remobilization during the active growth phase are crucial (Palacio *et al.*, 2007). In evergreen trees in the Mediterranean lowlands, studies have shown that winter assimilates are retained in the plant, with leaves and branches acting as carbon storage crucial for spring growth (Cerasoli *et al.*, 2004). Storage and remobilization of carbon, however, presupposes that alpine plant species, are able to photosynthesize at subzero temperatures (Pisek *et al.*, 1967; Semikhatova *et al.*, 1992; Lundell *et al.*, 2008; Körner, 2021) and even during severe droughts (Attia *et al.*, 2015). Thus, we assume that pregrowth conditions at least partially dictate growth during active growth phases and that photosynthetically active green stems play a crucial role for the species' carbon reserves (Bossard & Rejmanek, 1992).

Common functional traits (Fyllas *et al.*, 2020) such as green stems can be useful proxies for identifying life-history strategies (Reich *et al.*, 2003; Adler *et al.*, 2014), providing a basis for re-expressing fundamental ecological processes from first principles (McGill *et al.*, 2006). Common leaf, wood, and seed traits are thought to indicate how plants acquire resources, reproduce, and compete with other plants (Westoby *et al.*, 2002). This implies that the mechanisms determining growth are similar in species with common traits, which in turn implies congruencies in their biogeographic range.

Here, we aimed at a better understanding of alpine shrub growth in the Mediterranean by monitoring growth patterns in two coexisting green-stemmed species with similar traits but contrasting biogeographic patterns, coexisting on slope sites only (Löffler *et al.*, 2022). According to the general assumption that species with common traits exhibit similar growth strategies (Westoby *et al.*, 2002), we expected to find (a) congruencies in intra- and interannual growth patterns, (b) synchronicity of growth timing, and (c) similar environmental drivers of growth, despite differences in their biogeographical patterns. Thus, we expected that our two coexisting species evolved common strategies to cope with frost and drought and that underlying mechanisms are trait-based rather than species-specific. Based on anticipated common strategies, we further expected to identify synchronicity in patterns of water-related stem swelling and shrinking, irreversible growth, and the associated environmental drivers by mounting dendrometers on the shrubs' stems to monitor stem diameter changes in combination with high-resolution environmental data.

Materials and Methods

Shrub species

Here, we focused on two coexisting green-stemmed dwarf shrubs, namely *Cytisus galianoi* Talavera & Gibbs and *Genista versicolor* Boiss. (Fig. 1), abundant in the Sierra Nevada mountains (Spain) (Melendo *et al.*, 2003; Giménez *et al.*, 2004; Macek *et al.*, 2016) and overall, of similar habit with slight distinctions. Both shrubs produce a few small leaves only (up to 0.5 mm) during anthesis in May/June (Talavera & Gibbs, 1997). Their xylem anatomy and hydraulic architecture is similar, with both species showing semiring porous wood with clusters of vessels accompanied by small parenchyma cells (Supporting Information Fig. S1). However, the elasticity of the above ground biomass and the greenness of their photosynthetic stems vary (Bossard & Rejmanek, 1992), with *C. galianoi* having more elastic and greener stems than *G. versicolor*, whose branches are comparatively rigid and unbending and appear grayish. Both, differences in stem elasticity and stem greenness may cause different assimilation patterns and alter species response to drought, as differences in chlorophyll or chloroplast concentration control stem assimilation (Nilsen *et al.*, 1993), and an elastic cell wall tends to react more strongly to water loss (Bowman & Roberts, 1985; Patakas & Noitsakis, 1997; Patakas & Nortsakis, 1999). In addition, *C. galianoi* has an extensive, highly branched root system that

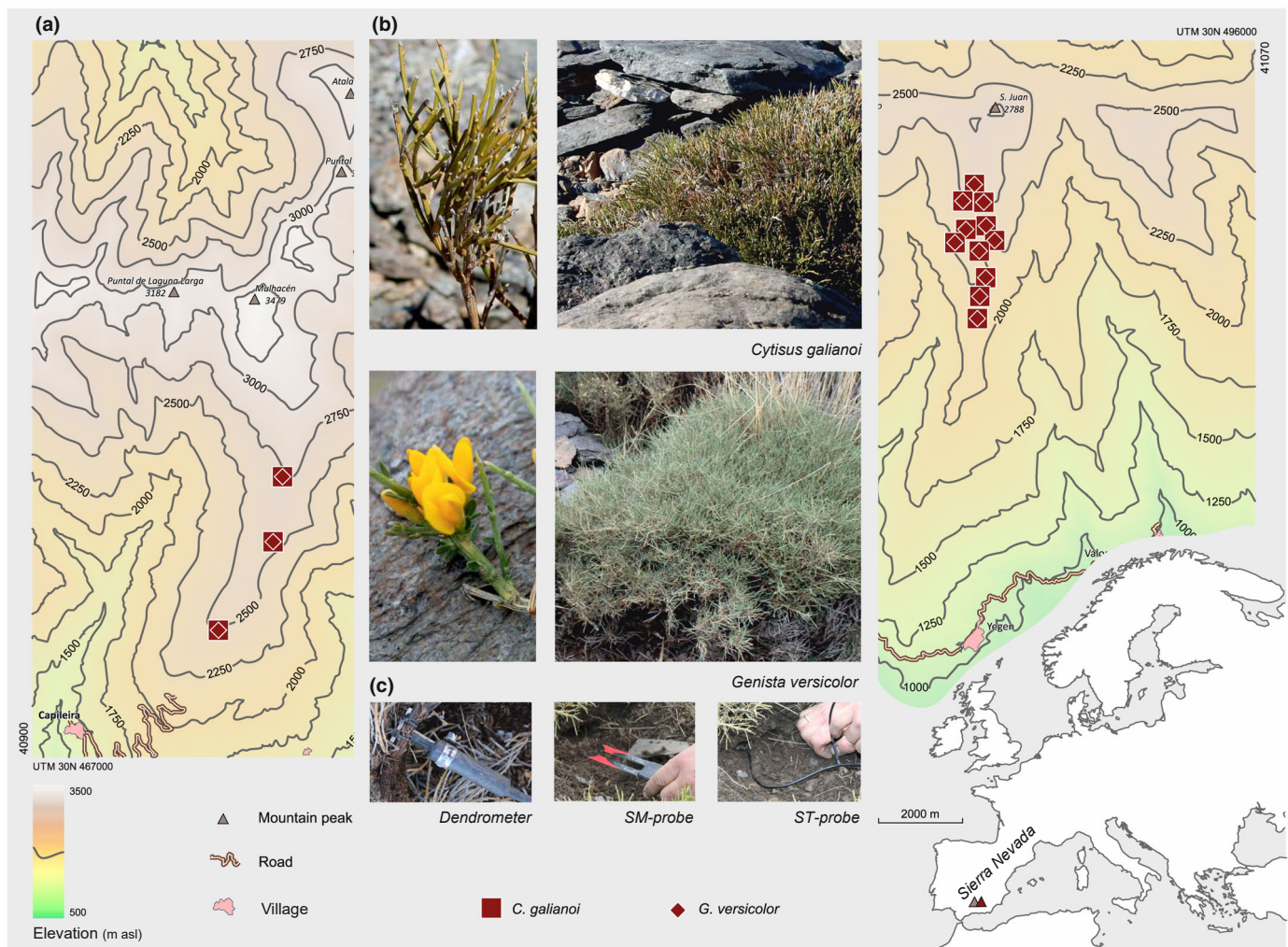


Fig. 1 Study regions in the Sierra Nevada (Spain) and location of the study sites (a). Photographs show our two focal species *Cytisus galianoi* Talavera & Gibbs and *Genista versicolor* Boiss. (b) as well as our monitoring setup with a mounted dendrometer, soil moisture probe, and soil temperatures probe (c).

extends *c.* 30 cm into the soil, with most fine roots distributed within 10 cm of soil depth and forming lateral ramets just below the soil surface (Fernández-Santos *et al.*, 2004), while *G. versicolor* forms a main taproot (up to 50 cm) combined with fine roots also distributed in the upper soil layers (Fig. S1).

Density and surface cover of the two focal species differ with elevation, aspect, slope, and curvature. *Cytisus galianoi* shows a relatively wide biogeographical and ecophysiological range, occurring at elevations up to 2700 m above sea level (asl) at a variety of sites ranging from exposed ridges with severe frosts during winter to early snowbeds. *Genista versicolor* diminishes with elevation (Lorite, 2001) and is restricted to the more protected early snowbeds and slopes (Löffler *et al.*, 2022). Both species presumably create their own microhabitat (Pistón *et al.*, 2016). In this study, nomenclature and taxonomy of the focal species follow Blanca *et al.* (2009).

Study sites and monitoring design

This study was conducted along two alpine transects above the local treeline in the Spanish Sierra Nevada, reaching from 2400

to 2700 m asl in the west, and from 2100 to 2600 m asl in the east, respectively (Fig. 1). Here, our focal species dominate the vegetation cover and coexist at the middle-alpine slopes (Löffler *et al.*, 2022). The overall climate is characterized by a stable high-pressure inversion layer in summer with autochthonous weather associated with continental easterly currents, resulting in hot and dry conditions (Roberts *et al.*, 2011; Jiménez-Moreno & Anderson, 2012). In autumn, winter, and spring, cyclonic activity of Atlantic low-pressure systems results in cool and humid conditions (Roberts *et al.*, 2011). Additionally, conditions are strongly influenced by the typical high mountain climate (Herrero & Polo, 2016; Gómez-Ortiz *et al.*, 2019), with plants exposed to cold winters, high solar radiation, strong winds, and snowfall, resulting in comparatively short growing seasons (Valle, 2003).

In this study, we focused on slope positions, which were stratified-randomly selected from the treeline upwards at *c.* 100-m intervals, following the framework of our long-term alpine ecosystem research project (LTAER-ES; Löffler *et al.*, 2022). At these positions, our species experience periodic snow cover caused by wind drift and lee-side effects in the complex alpine

topography, representing a fine-scaled mosaic of scattered shrub patches, grasses, open rock, and debris.

Dendrometer data, monitoring setup, and environmental data collection

To monitor radial stem diameter variations, we equipped the main stem of 29 randomly selected specimens of *C. galianoi* and *G. versicolor*, respectively, with high-precision point dendrometers (type DD-RO; Ecomatik, Dachau, Germany, temperature coefficient $< 0.2 \mu\text{m K}^{-1}$), which recorded data at 1-min intervals. The dendrometers were attached to the selected stems horizontally above the ground surface (*c.* 1 cm above ground) as close as possible to the root collar, integrating growth of all plant parts (Bär *et al.*, 2007; Ropars *et al.*, 2017; Fig. 1). To minimize 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 (Dobbert *et al.*, 2022b). To account for the variation within individual specimens and between multiple stems of the same specimen, we monitored a large number of specimens, representative of the conditions observed at each site. This also accounts for variations between the individual shrubs that are expected to exhibit pronounced temporal plasticity due to the high climatic variability common in the Mediterranean biome, where the rate of secondary growth must be adapted to a wide range of climatic conditions (Camarero *et al.*, 2010). We then obtained daily mean values from our raw dataset (Deslauriers *et al.*, 2007) and normalized the annual stem diameter curves by removing the initial stem diameter (ranging from 3970.98 to 8779.10 μm for *C. galianoi* and from 4453.43 to 13307.36 μm for *G. versicolor*) from the annual curves since dendrometers measure changes in stem diameter relative to the start of the measurement cycle. Finally, we checked the data for outliers (25th percentile/75th percentile $\pm 1.5 \times$ interquartile range as cutoff range). Since we did not find any outliers, all daily values per curve were retained. These processing steps resulted in time series comprising six full consecutive years (January 1, 2015 to December 31, 2020; Fig. S2).

Micro-environmental conditions

To assess environmental drivers of radial stem diameter variations, we measured a set of variables at each site, namely soil temperatures ($^{\circ}\text{C}$, T_{RZ}) and volumetric soil water content ($\text{m}^3 \text{m}^{-3}$, SM_{RZ}). Thermistors (type S-TMB-002, $\pm 0.2^{\circ}\text{C}$ accuracy) and soil moisture probes (type S-SMD-M005, $\pm 3\%$ accuracy) were installed at 10 cm soil depth, that is within the root zone of each specimen (Löffler & Pape, 2020; Dobbert *et al.*, 2021a,b). Both were recorded at 1-min intervals and stored as hourly averages using ONSET's HOBO Loggers (type H21-002). This design assumes that in the generally shallow alpine soils, where deeper roots invade the source rock, lateral root growth at shallow depths is most important for accessing surface moisture and nutrients and thus a major influence on plant health (Muktadir *et al.*, 2020). Most of the lateral and fine roots of our focal species

are distributed at these shallow depths (Fig. S1), allowing us to capture a large part of the relevant soil conditions. The noninvasive design generates comparable data across large elevational and topographic gradients. Complementary, we recorded the following environmental variables at 2692 m asl, reflecting the climatic conditions in our study area: Relative air humidity (rH, %) and air temperature (AT, $^{\circ}\text{C}$) at 2 m above ground using Skye rht sensors (SKH 2065) with $\pm 2\%$ accuracy for rH and $\pm 0.2^{\circ}\text{C}$ for T, global radiation (GR_{SZ} , W m^{-2}) at 1 cm above ground in the shoot zone of one specimen using a silicon pyranometer (type S-LIB-M003) with $\pm 10 \text{ W m}^{-2}$ accuracy, air pressure (AP, hPa) at 2 m above ground using a barometric air pressure sensor (type Meier-NT-MNT10025) with ± 0.01 hPa accuracy, and precipitation (mm, P) at 100 cm above ground using a precipitation sensor (type LAMBRECHT-meteo-15 189) with $\pm 2\%$ accuracy. Sensors were mounted to an ADL-MX data logger that recorded data at hourly intervals. All environmental data were collected for the period January 1, 2015 to December 31, 2020, with additional data from 2014. There were no missing data.

Regional climate and micro-environmental conditions

Consistent with the bimodality of the Mediterranean climate (Mitrakos, 1980; Camarero *et al.*, 2012), our sites were characterized by mild and humid spring and autumn conditions, dry summer periods, and cold winters with periodic snow cover (Fig. S3; Table S1; Löffler *et al.*, 2022). A pronounced variability between years (Fig. S4), reflected the Mediterranean climate (Camarero *et al.*, 2010). Measured T_{RZ} at all monitored sites correspond to the AT regime in 2 m above ground (Fig. S5a) with T_{RZ} generally higher than AT and no indication for ground frost. Temperatures begin to rise in March/April (Fig. S6), with a time lag to the increase in GR_{SZ} (Fig. S5a). Precipitation peaks in spring and autumn with high interannual variability and in close accordance with SM_{RZ} (Fig. S5). P is also reflected in the rH pattern (Fig. S6; Mitrakos, 1980). Usually, SM_{RZ} is high-throughout winter and if low increases in March/April and peaks in May, ($> 0.20 \text{ m}^3 \text{m}^{-3}$; Figs S3, S5b). Overall, both, T_{RZ} and SM_{RZ} , were slightly higher for *C. galianoi* than for *G. versicolor*.

Analysis of growth patterns

From the measured dendrometer curves, we defined two growth phases during the first and second half of the year, which are intermitted by a phase of stem contraction during summer and a second contraction phase during winter. This 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 induce bimodal growth patterns in several Mediterranean lowland tree species (Camarero *et al.*, 2010) and potentially also in Mediterranean alpine species (Olano *et al.*, 2013).

Here, growth-induced irreversible stem expansion (growth) was calculated as the cumulative maximum, or current half-year stem diameter maximum minus the most recent maximum of the previous study period. Thus, growth is equivalent to an increase

in stem diameter when the measured diameter is greater than at any point in the past (Zweifel, 2016; Zweifel *et al.*, 2021). This approach is inspired by the ‘zero-growth approach’ proposed by Zweifel (2016), which we applied to semiannual rather than daily data as originally suggested by Zweifel (2016). Accordingly, growth can only take on positive values and does not necessarily occur during every growth phase. We refer to years in which there was no growth as dormant years. Whenever growth occurred, we calculated both the change in stem diameter and the temporal duration of the respective phase for all specimens and years. Since both growth phases represent irreversible stem growth, it can be assumed that both phases are also visible in the anatomical structure of the species and should therefore be directly comparable with classical measurement methods of radial stem growth, including ring width (Fig. S1). 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). All growth data were scaled and centered before further analysis, dividing the dataset by its standard deviation and subtracting the overall mean.

Correlation analysis and linear mixed effects models

To uncover climate–growth relations, we utilized Pearson’s correlation coefficients, calculated in the statistical software R (R Core Team, 2023) for semi-annual irreversible stem growth and daily mean values of T_{RZ} and SM_{RZ} . To account for potential lagged effects of previous-year conditions on current-year growth, we included environmental data from the respective previous year in our correlation (Bär *et al.*, 2008; Weijers *et al.*, 2018), including additional environmental measurements from before the start of our study period (2014). To account for variation between the individual sites, we additionally fitted linear mixed-effects models to our data, using the LME4 R package (Bates *et al.*, 2015). For these models, semi-annual irreversible stem growth entered as response variable, and monthly mean values for all environmental variables as fixed effect. The individual specimens were included as random effect. Specimens entered separately into the analysis, to avoid generalizations that might result from averaging the data. Averages were calculated for visualization purposes only.

Partial least squares regression

Finally, we applied partial least squares regression (PLSR; Wold, 1975; Abdi, 2010) to our dataset to identify crucial environmental thresholds promoting or impeding growth (Carrascal *et al.*, 2009; Frindte *et al.*, 2019; Löffler & Pape, 2020). Here, we used variable selection methods to define a subset of relevant conditions and to assess their relative importance. We aggregated our environmental data and rounded them to 0.5°C for T_{RZ} and 0.01 m³ 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; Dobbert *et al.*, 2021a) for each meteorological season, that is winter, spring, summer, and autumn (for definition see Trenberth, 1983), creating sets of predictor variables. The associated response values were the

semi-annual growth values calculated before (Fig. S7). For the final estimation of the single-response model, 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. From these models, we then derived the relevance of each independent variable using the selectivity ratio (SR; Mehmood *et al.*, 2012), defined as the ratio of explained to remaining (unexplained) variance for each variable in the target projection vector (Farrés *et al.*, 2015; Frindte *et al.*, 2019). In order to achieve better contrastable results, the explained variance (SR/abs (SR + 1)) was derived from the SR (Rajalahti *et al.*, 2009). By multiplying the SR of each variable by the sign of the corresponding regression coefficient, we determined which variables are positively or negatively associated with the dependent variable (Rajalahti *et al.*, 2009; Löffler & Pape, 2020; Dobbert *et al.*, 2021a,b). In this way, we clearly identified the environmental conditions that were significantly related to annual growth.

Results

Patterns of stem diameter change and growth

Overall, annual stem diameter change in our focal species was of bimodal character, yet we observed pronounced intra- and inter-annual variability, as well as species-specific patterns (Fig. 2). *Cytisus galianoi* showed a more pronounced bimodal pattern than *G. versicolor* (Figs 3a, S8), most apparent during the meteorological summer, when *C. galianoi* showed much stronger stem contraction than *G. versicolor* (Figs 2, 3a). Subsequently, stem water deficit was much higher in *C. galianoi* during summer. It then rapidly decreased in *G. versicolor* in early autumn, whereas in *C. galianoi*, first autumn rains caused only initial rehydration, with the main reduction in stem water deficit occurring in late autumn/winter (Fig. 3a,b). The diurnal pattern of stem diameter change also varied between species (Fig. 3d). While maximum stem swelling during the dry season occurred at c. 09:00 h in both species, in *C. galianoi*, the shrinking peak occurred with a time lag of c. 2 h at c. 17:00 h. During the wet seasons, *C. galianoi* showed a similar pattern, but with markedly less pronounced amplitude, while in *G. versicolor* the pattern turned into a concave curve, with the shrinking peak occurring at midday. Similarly, growth patterns were contrasting between our two species, with *G. versicolor* achieving highest growth rates in autumn, when growth coincided with the most pronounced stem diameter increase, while *C. galianoi* achieved its highest growth rates in spring (Figs 3c, S9, S10).

Timing of growth

The timing of growth is shown in Fig. 4 and Table S2. For both species, the onset and cessation of the first growth phase was usually in February/March and May/June, respectively, occurring slightly earlier for *G. versicolor* compared with *C. galianoi*.

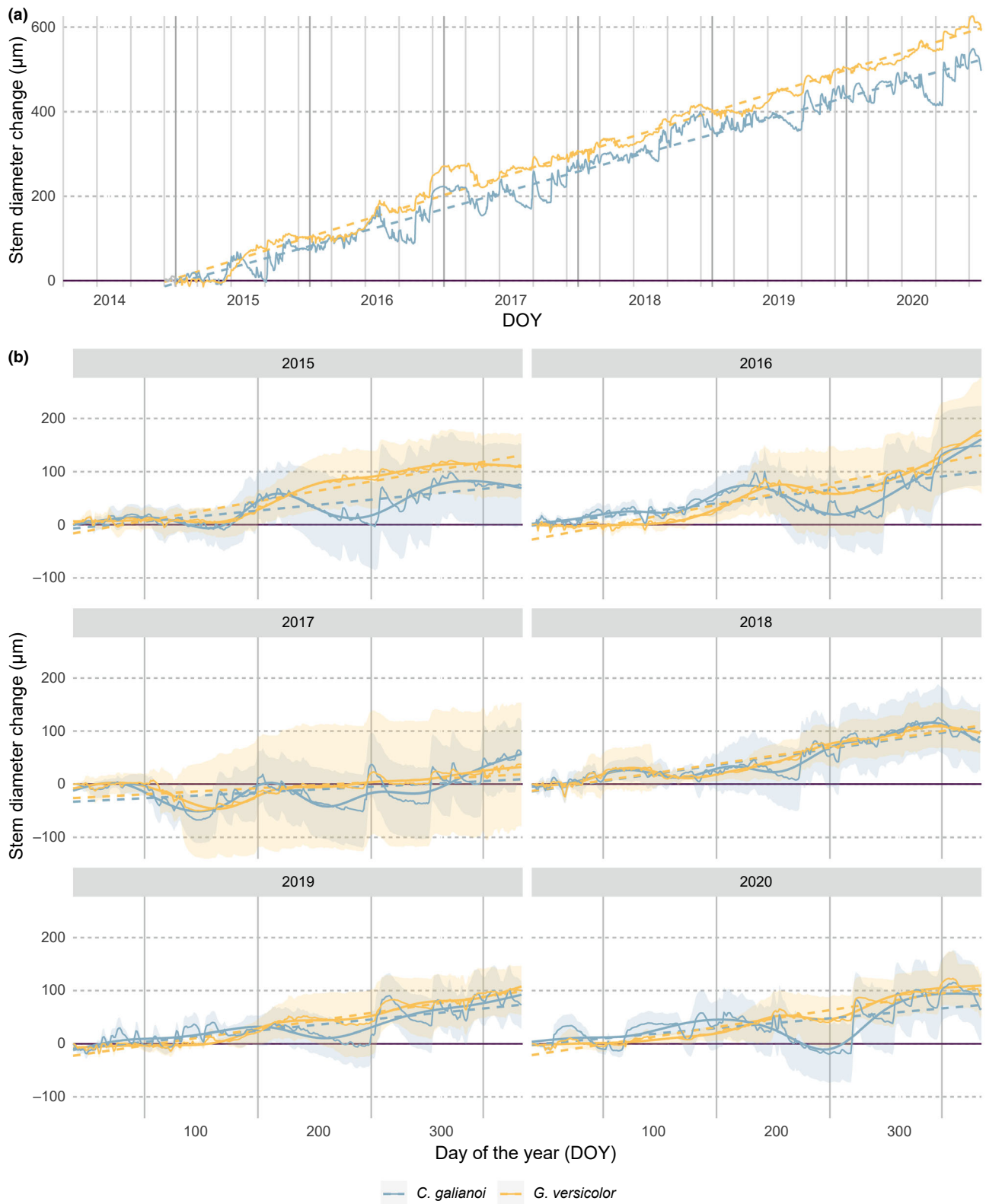


Fig. 2 Stem diameter change of *Cytisus galianoi* Talavera & Gibbs and *Genista versicolor* Boiss. relative to the start of the measuring period (a) and averaged annual stem diameter change relative to the previous year's maximum represented by generalized additive splines (bold) and linear trends (dashed) (b). Transparency shows the standard deviation (\pm SD) and vertical gray lines indicate the meteorological seasons.

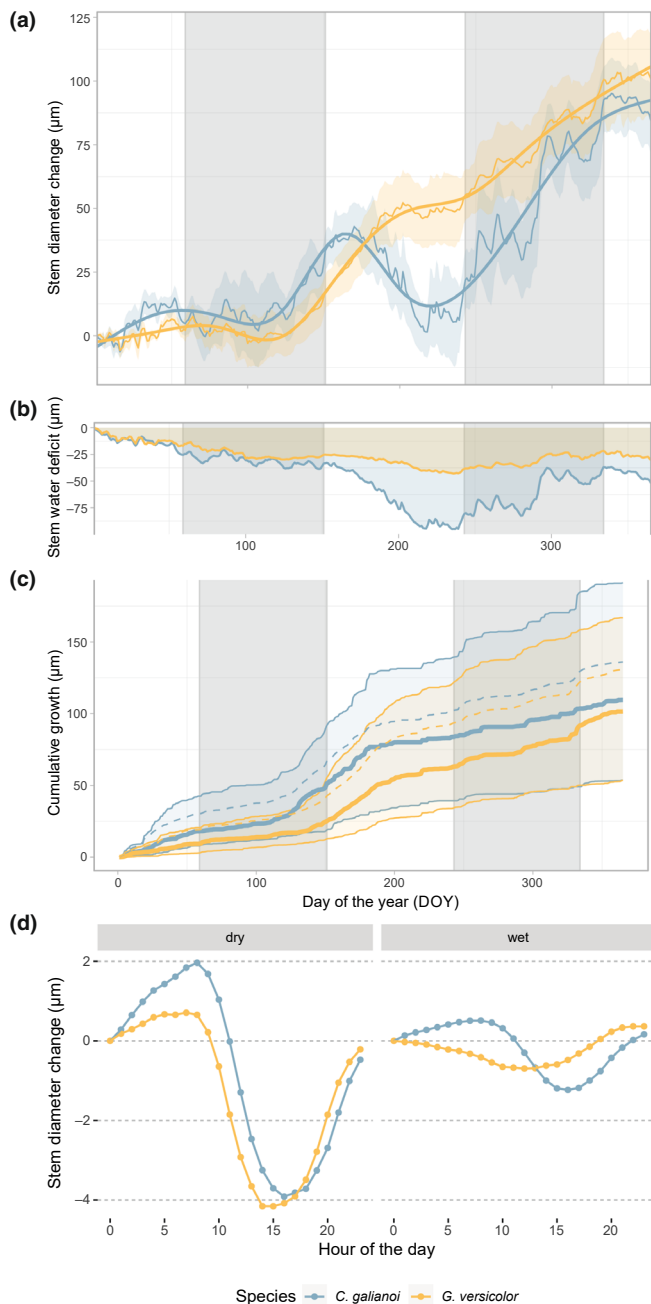


Fig. 3 Seasonal pattern of stem diameter change (\pm SD) (a) and stem water deficit (b) averaged over the studied period 2015–2020, with the seasonal pattern of stem diameter change represented by generalized additive models (GAMs). (c) Cumulative curve of stem diameter change (growth) in *Cytisus galianoi* Talavera & Gibbs and *Genista versicolor* Boiss., shown as median (solid line), average (dashed line), and the 25% and 75% quartiles (shaded) for the years 2015–2020. (d) Diurnal variation in stem diameter change. Hourly values were averaged for all observed specimens for the dry period in summer (soil moisture $< 0.1 \text{ m}^3 \text{ m}^{-3}$), and the rest of the year (soil moisture $> 0.1 \text{ m}^3 \text{ m}^{-3}$).

Growth resumption after summer drought, that is the onset of the second growth phase, usually took place in August/September for *C. galianoi*, several weeks after *G. versicolor* (July/August). Growth cessation, however, was similar in both species (November/December). The interannual variability of the duration of the

two growth phases was high, and growth rates in both species were decoupled from this duration (Fig. S10; Table S2).

Environmental drivers of growth

Overall, we found complex, species-specific environmental controls of stem diameter change, strongly differing between the growth phases, with growth significantly linked to the environmental conditions before the onset of growth in both species (pregrowth conditions; Figs 5, S11).

During the first growth phase, *C. galianoi* was promoted by high T_{RZ} during the previous year (March–November), while there was no strong preyear T_{RZ} control in *G. versicolor* (Figs 5, S11) and previous year's SM_{RZ} conditions were not relevant for the first growth phase in both species. Yet, winter conditions before growth onset showed contrasting relations to spring growth in both species, affecting *C. galianoi* slightly negatively (Fig. 5), with growth promoted by relatively low T_{RZ} but impeded by T_{RZ} reaching 3.5°C during the pregrowth winter (Fig. 6). At the same time, growth in *G. versicolor* was positively linked to winter T_{RZ} (Figs 5, S11), with T_{RZ} of 5°C promoting and T_{RZ} of 1.0°C hindering growth during pregrowth winter and spring (Fig. 6). Growth in both species was promoted by SM_{RZ} values indicating unfrozen ground ($0.19\text{--}0.24 \text{ m}^3 \text{ m}^{-3}$; Fig. 6). However, our results also indicate a positive effect of comparatively dry winter conditions in both species (Figs 5, S11). Thus, we found high spring growth rates in *C. galianoi* following a cold, snow-free winter (2015), but low spring growth rates following a mild, snow-rich winter (2017; Fig. S8; Table S1). In contrast, we found high spring growth rates in *G. versicolor* following a warm snow-free winter (2016), moderate growth rates after a snow-rich winter (2017), and low spring growth rates following a cold winter (2015; Fig. S8; Table S1).

During the second growth phase, growth was similarly linked to pregrowth conditions, and both species performed best after a warm, dry winter, with winter conditions being particularly significant in *G. versicolor* (Figs 5, S11), promoting growth at T_{RZ} of 5.0°C but impeding growth at a T_{RZ} below 1.0°C (Fig. 5). Both species benefitted from low SM_{RZ} during early spring and *C. galianoi* performed best under high SM_{RZ} before the beginning of the dry period, whereas moisture supply during the dry period was detrimental (July), while *G. versicolor* was promoted by an earlier onset of the drought period (June) (Figs 5, S11). Again, the PLSR analysis showed no thermal nor hydric growth control from pregrowth spring conditions (Fig. 6), indicating a high temporal complexity of these relations. However, autumn growth in *C. galianoi* was promoted when summer conditions were mild ($10.0\text{--}16.5^\circ\text{C}$) and dry ($c. 0.05 \text{ m}^3 \text{ m}^{-3}$), with T_{RZ} of 20.0°C having a negative influence on species performance. After the summer drought, only *C. galianoi* showed a positive moisture control, while autumn growth in *G. versicolor* was positively linked to high T_{RZ} in late August (Figs 5, S11). Furthermore, both species were promoted by high September T_{RZ} followed by cool and humid conditions during October/November (Figs 5, S11). The PLSR confirmed these results (Fig. 6). Thus, low growth rates observed in autumn during the years 2017 and

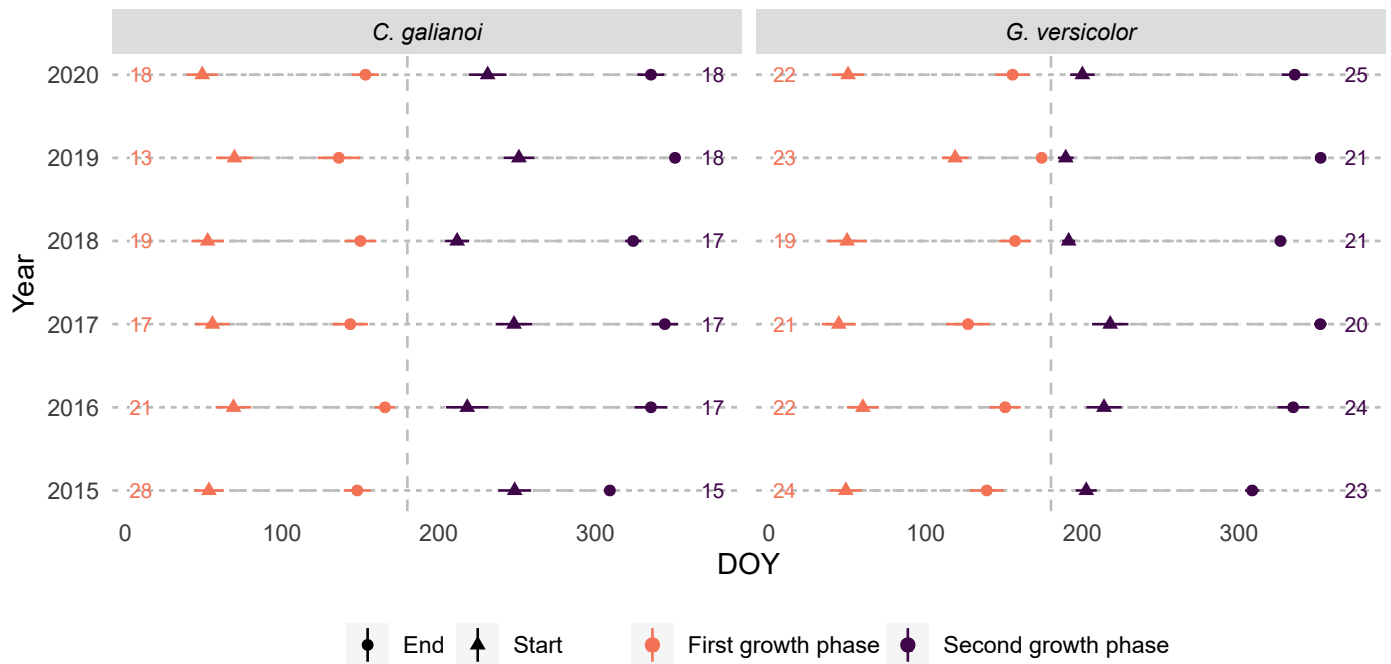


Fig. 4 Timing of growth (mean onset and cessation) for *Cytisus galianoi* Talavera & Gibbs and *Genista versicolor* Boiss. derived from stem diameter curves averaged across all studied sites for the years 2015–2020. Numbers indicate the sample depth of the growing specimens. Short solid lines indicate the standard deviation of growth onset and cessation (\pm SD).

2019 can be attributed to repeated drought spells in late autumn. By contrast, highest growth rates were achieved when the first autumn rains were followed by a warm, moderately humid autumn (Fig. S3; Table S2).

Overall, our main findings highlight the importance of pre-growth conditions for growth compared to the environmental conditions during the actual growth phases. Growth during the major growth phases in *C. galianoi* (spring) and in *G. versicolor* (autumn) was superiorly driven by pre-growth winter conditions.

Discussion

Growth patterns

We observed bimodal patterns of annual stem diameter change in two coexisting alpine shrub species, leading to pronounced but contrasting bimodal patterns in annual growth. While the observed stem diameter changes showed strong similarities between the two species, they did not necessarily correspond to their growth patterns but rather reflected differences in rehydration patterns. In general, it is assumed that major growth processes in Mediterranean woody plants occur during spring, with a minor second growth phase in autumn (Pasho *et al.*, 2012; Pellizzari *et al.*, 2017; Alday *et al.*, 2020; Camarero *et al.*, 2021). This assumption does not hold true for our species. The observed growth patterns rather imply that the seasonality of xylogenesis is highly species-specific. Distinguishing between growth defined as irreversible stem expansion caused by dividing and enlarging cells in the cambium, and reversible shrinking and swelling of the stem caused by imbalances between transpiration and root water uptake (Zweifel *et al.*, 2005; Zweifel, 2016) helped to deduce the

species' water use strategies and understand their contrasting growth patterns. Summer stem contractions and dehydration, that is strong increase of stem water deficit, in *C. galianoi* suggest drought tolerance at the cost of reduced performance during autumn (Bacelar *et al.*, 2012), when rehydration is prioritized to increase the water potential before growth resumption, but with the advantage of benefiting from carbon fixation in winter and to maximize growth at high water potential in spring (Bossard & Rejmanek, 1992). This is supported by contrasting patterns in diurnal stem diameter during the wet and dry seasons, with a high amplitude during the wet season, suggesting an overall higher water potential when major growth processes occur. Overnight replenishment allows cell turgor, cell expansion, and thus stem growth to resume as the rising water potential of the stem allows water to flow from the xylem conduits into the living cells of the stem (Steppe *et al.*, 2015). In contrast, during the dry season, when the soil is no longer fully hydrated, water stores in the phloem and xylem are not fully replenished overnight (Steppe *et al.*, 2015), which inhibits growth because water potential in the xylem decreases when transpiration exceeds root water uptake (Sevanto *et al.*, 2011), causing water to flow from the living cells into the xylem conduits, with cell turgor following the same downward trend as water potential in the stem, resulting in stem shrinkage rather than cell expansion and growth (Steppe *et al.*, 2015). Despite the similarities in the diurnal pattern of stem diameter change during the dry season, the marginal increase in stem water deficit and the less pronounced summer stem contraction suggest high water potential throughout summer in *G. versicolor*. This, in turn, suggests drought avoidance without compromising performance while maintaining physiological functionality for carbon fixation at high tissue water

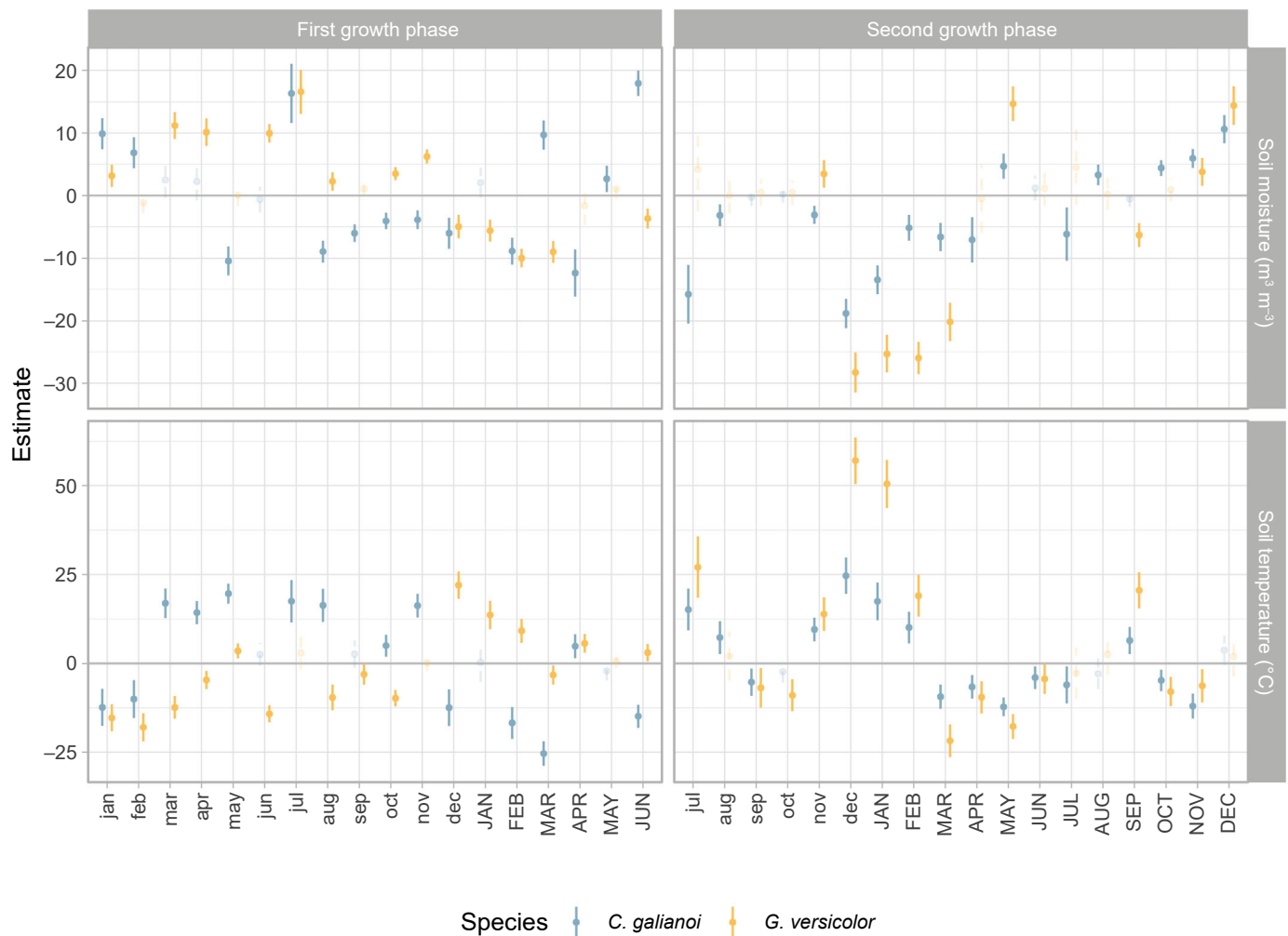


Fig. 5 Linear mixed effects analysis for growth during the first and second growth phase as derived from the dendrometer curves (dependent variable) and monthly environmental data (means) as fixed effects. The individual specimens of the species *Cytisus galianoi* Talavera & Gibbs and *Genista versicolor* Boiss. entered as random effects. Short solid lines indicate the 95% confidence interval, transparency indicating nonsignificance. Abbreviations of months from the previous year are in lowercase letters and those of the current year are given in capitals.

potential throughout summer (Chaves *et al.*, 2003; Bacelar *et al.*, 2012), allowing the species to maximize growth with autumn rains when marginal diurnal changes in stem diameter indicate high water potential, likely significantly increasing the time period for growth (major autumn growth).

Timing of growth

Our results confirm that the duration of rehydration processes depends on the duration and intensity of drought connected to the risk of embolism (Cochard & Delzon, 2013) and on the species' ability to withstand negative water potentials before cavitation occurs (Ennajeh *et al.*, 2008), that is air is aspirated into the vessels, disrupting the cohesion of the water column (Sperry & Tyree, 1988; Lens *et al.*, 2013). Thus, the discrepancy in the timing of growth resumption between our two species is probably linked to differences in the species' strategy to cope with drought. Their photosynthetically active stems might be key in achieving positive net photosynthetic rates in contrasting ways (Bossard &

Rejmanek, 1992; Nilsen *et al.*, 1993). The intensely green stems of *C. galianoi* indicate a higher chlorophyll content and the species might achieve higher photosynthetic rates at the expense of a higher stem water deficit (stem contraction). *Cytisus galianoi* tolerates higher fluctuations in plant water potential, possibly related to stomata limitation during water stress (Nilsen *et al.*, 1993), with weak stem stomata control indicating pronounced anisohydric behavior (Jones, 1998; Tardieu & Simonneau, 1998; Leuschner *et al.*, 2022). Despite water limitation causing a decrease in carbon gain due to stomatal limitation (Nilsen *et al.*, 1993), there is evidence that anisohydric plants can keep high assimilation rates while leaf water potential declines, allowing for higher productivity (Attia *et al.*, 2015). The species is, thus, able to still achieve high photosynthetic rates even under increasing water stress (Attia *et al.*, 2015). However, because positive stem assimilation depends on stem water potential (Nilsen *et al.*, 1993), photosynthetic rates are likely to be lower during the dry season when stem water-deficit increases. Unlike species that maintain carbon gain and water potential throughout

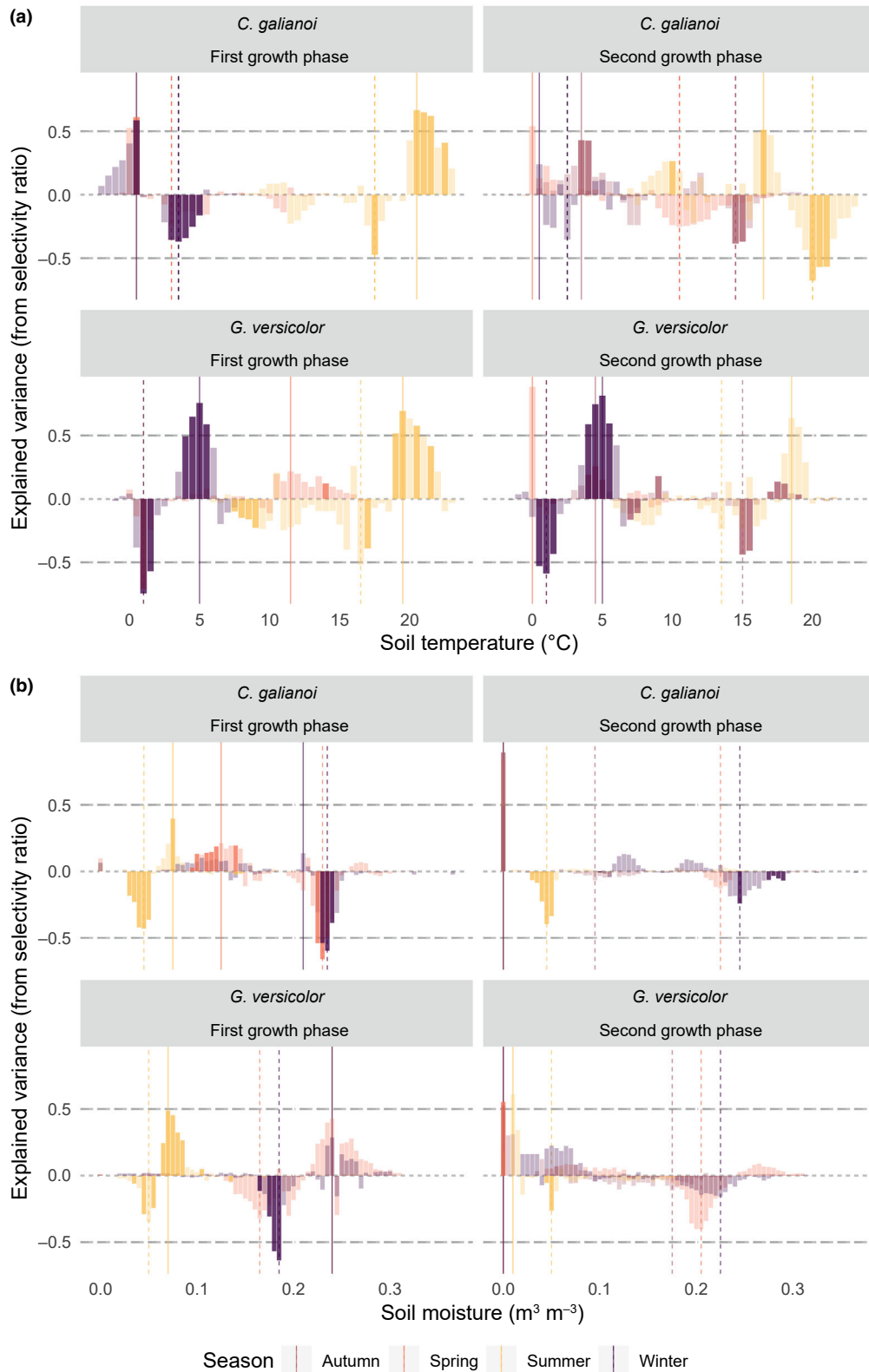


Fig. 6 Variance explained derived from selectivity ratio multiplied with the sign of its corresponding regression coefficient for root zone temperature (T_{RZ} , a) and root zone soil moisture (SM_{RZ} , b) (independent variables) and total annual growth (dependent variable) of *Cytisus galianoi* Talavera & Gibbs and *Genista versicolor* Boiss., derived from PLSR analysis. Shaded areas represent values rendered significance ($P < 0.05$) and colors represent seasons. Vertical solid lines indicate maxima, vertical dashed lines minima. For the first growth phase, the analysis is based on pregrowth summer, autumn and winter, and the current spring conditions, whereas for the second growth phase on pregrowth winter, spring and summer, and the current autumn conditions.

the year (Nilsen *et al.*, 1993), carbon gain in *C. galianoi* likely decreases during the dry season. However, this decrease might be partially mitigated by assimilation in the morning hours when high water potential promotes photosynthetic activity. Thus, carbon uptake likely continues throughout summer, albeit at lower levels, allowing the species to benefit from high radiation input on the one hand, but making it more susceptible to damage from prolonged drought stress on the other hand (Attia *et al.*, 2015), which ultimately may reduce photosynthetic rates, and may lead to decelerated rehydration and, consequently, to delayed growth resumption. By contrast, *G. versicolor*, whose photosynthetically active stems are more grayish-green, retains high water potential throughout summer, which likely related to reduced hydraulic and stomatal conductance to maintain a consistent water potential. This rather isohydric behavior comes at the cost of lower net photosynthesis, as it reduces the species' ability to fix carbon for growth when the soil dries out (Attia *et al.*, 2015). Ultimately, the species experiences faster rehydration and, consequently, earlier growth resumption. Overall, we conclude that even slight variations in morphological traits in our alpine shrub species result in distinct variations of the species' hydraulic behavior and thus in the timing of growth resumption.

At the same time, the timing of growth in our species proved independent of the length of the growing season, confirming that plant performance under variable season lengths largely depends on the specific environmental drivers during and before the growth period (Hollesen *et al.*, 2015; Weijers *et al.*, 2018; Dobbert *et al.*, 2021a). The strong influence of pregrowth conditions on species performance has been linked to the critical timescale relevant to plant growth (Löffler & Pape, 2020) and is often still a missing dimension (Choler, 2018; Niittynen & Luoto, 2018). As such, we argue that the impact of intensity and duration of the environmental driver constellations on plant performance is relative to the species' traits and ecophysiological strategies.

Environmental drivers of growth

Observed growth responses to the alpine environment are in line with earlier studies of Mediterranean tree growth, showing the importance of late autumn to winter conditions before spring growth (Bogino & Bravo, 2008; Camarero *et al.*, 2013). Both of our species were promoted by dry winter conditions, while winter T_{RZ} had contrasting effects, with *C. galianoi* showing a negative and *G. versicolor* a positive growth response. These contrasts in controlling winter conditions suggest that *C. galianoi* can cope with relatively low (but > 0) T_{RZ} , possibly due its potential to tolerate dehydration by active stem contraction, similar to mechanisms shown in arctic-alpine shrubs (Dobbert *et al.*, 2021b, 2022b). Using its intensely green stems, *C. galianoi* may capitalize from additional photosynthetic opportunities (Bossard & Rejmanek, 1992; Wyka & Oleksyn, 2014), which allow carbon fixation throughout winter, if snow cover does not hinder photosynthetic activity. Moreover, our findings confirm physiologically activity of winter-green species at low temperatures (Oribe & Kubo, 1997), which was shown to increase at temperatures just $< 0^{\circ}\text{C}$ (Lundell *et al.*, 2008), and in some high latitude vascular

plants even at temperatures $< -4.0^{\circ}\text{C}$ (Semikhatova *et al.*, 1992). *Cytisus galianoi* may benefit from increased synthesis of carbohydrates during the period of reduced respiration (Gimeno *et al.*, 2012; Camarero *et al.*, 2013), when low T_{RZ} promote the storage of carbohydrates in root parenchyma (Sperling *et al.*, 2017). Thus, the major role of spring growth is most likely explained by continued carbon gain throughout the winter, with N-fixation likely playing an additional role (Wheeler *et al.*, 1979; Larsen *et al.*, 2012). By contrast, our findings regarding *G. versicolor* indicate that it is sensitive to winter frosts and may therefore better perform under snow cover at lower alpine elevations, where south-facing slopes experience periodic snow cover with moderate snow depth (up to 2 m) that persists over weeks, re-establishes after warmer winter periods, and may last into spring after a long, cold, and snow-rich winter (Löffler *et al.*, 2022). As such, our results explain the biogeographical patterns of the species (Löffler *et al.*, 2022).

Cytisus galianoi's preference of humid and cool spring conditions suggests that the species can capitalize from early defrost water and meltwater even during short windows of photosynthetic opportunities (Starr & Oberbauer, 2003), and is able to increase photosynthetic capacity even when snow is present to raise nonstructural and storage carbohydrate content in the stems before snowmelt (Starr & Oberbauer, 2003; Lundell *et al.*, 2008). By contrast, *G. versicolor*'s preference of warm and dry spring conditions suggests that solid precipitation, that is snow in the alpine, may hinder photosynthesis, possibly due to limited stomata conductance (Starr, 2001; Starr & Oberbauer, 2003) and the less green stems, preventing the species to exploit the light passing the physical structure of snow (Liston *et al.*, 1999) and thus to increase the level of carbohydrates before snowmelt. Both species showed a positive correlation to April T_{RZ} , corresponding to findings in other Mediterranean alpine species, related to early cambium reactivation (Olano *et al.*, 2013). However, since we found growth onset in our species significantly earlier than April, April T_{RZ} conversely affect the species' performance later during the first growth phase. This is consistent with studies in arctic-alpine evergreen shrubs, which were promoted by mid-growing season temperatures (Bär *et al.*, 2008; Franklin, 2012). At the end of the first growth phase, *C. galianoi* preferred cold, humid conditions, while *G. versicolor* preferred continued drought and high T_{RZ} , suggesting that *C. galianoi* benefits from early summer rains, which provide sustained water supply well into the summer, essential for the species' tolerance to desiccate. By contrast, *G. versicolor* adjusts its hydraulic mode to drought avoidance, and early summer rains might disrupt the species' water-use efficiency.

During the second growth phase, we found winter, spring, and early summer conditions still highly relevant, with only *C. galianoi* additionally impeded by water supply in July. Such occasional summer rains may enforce the species' stomata activity and disrupt water-use efficiency. Overall, both of our species are well-adapted to summer drought (Dobbert *et al.*, 2022a), albeit using different strategies. These differences are related to morphological variations in the species' stems and roots with *C. galianoi*'s drought tolerance potentially based on elastic stems, which may

shrink upon water loss while maintaining high turgor (Patakas & Nortsakis, 1999), probably through osmotic adjustment that allows maintenance of turgor in living cells (Kozłowski & Palardy, 2002). This rather prodigal water use strategy (Bacelar *et al.*, 2009) requires a highly branched root system (Fernández-Santos *et al.*, 2004), allowing to absorb water from a large volume of soil (Arndt, 2000) with the adjustment of its allocation pattern to the roots (Jackson *et al.*, 2000). However, despite its extensive root system, *C. galianoi* is unable to draw water from the deep soil, leading to moisture stress when the topsoil dries (Muktadir *et al.*, 2020), resulting in stem shrinking. By contrast, *G. versicolor*'s drought avoidance strategy is likely based on rigid stems, which may increase water uptake from dry soil (Schulte, 1993). Therefore, a conservative water use strategy (Bacelar *et al.*, 2009) presupposes access to sufficient water during drought, which the species likely has due to its long taproot that permits a sustainable water supply (Passioura, 1983; Bacelar *et al.*, 2012), avoiding seasonal fluctuations in water availability (de Micco & Aronne, 2012).

At the end of summer drought, only *C. galianoi* showed a positive SM_{RZ} signal, while *G. versicolor* was promoted by high T_{RZ} . The abrupt increase in stem diameter is therefore probably based on the extensive root system, which enables the species to benefit from pregrowing season water supply (Bossard & Rejmanek, 1992) by absorbing surface water with its lateral fine roots at shallow depths. This promotes rapid replenishment of water resources, leading to an increase in stem water potential and cell turgor required for growth (Lockhart, 1965; Cabon *et al.*, 2020; Zweifel *et al.*, 2021). To achieve and maintain cell turgor in autumn, stomata adjustment may play an additional role, as patterns of stem diameter change observed suggest a shift from anisohydric stomata behavior during summer, to partial isohydry during autumn, which has been shown to be effective after prolonged droughts when predictable seasonal rainfall occurs (Guo *et al.*, 2020). By contrast, we assume that *G. versicolor* uses its taproot to absorb water from the deeper ground and maintains a high water potential throughout the summer. However, the taproot is unlikely to obtain water for growth (Muktadir *et al.*, 2020) and more likely to act as a long-term water reservoir. Thus, autumn rains are more likely to be absorbed by lateral fine roots at shallow depths, which, due to the overall high water potential, rapidly leads to adequate cell turgor and thus growth resumption at still high temperatures. Here, maintaining a high water potential could involve an isohydric mode until sufficient autumn precipitation has occurred (Reynolds *et al.*, 1999; Ogle & Reynolds, 2004), at the cost of productivity (Attia *et al.*, 2015). Growth preference of sustained heat lasted until September, while cool and moist conditions became promotive in October and November and autumn droughts were growth limiting in both our focal species. During autumn, growth conditions in the Mediterranean alpine are overall favorable, and species-specific ecophysiological adaptation might not be necessary, which is in agreement with previous studies showing strong precipitation drivers of growth across different species (de Luis *et al.*, 2007; Valeriano *et al.*, 2023).

Collectively, our findings highlight contrasting patterns of carbon gain resulting from different strategies for coping with frost and drought, and at the same time underscore the critical importance of resource accumulation before growth in both species, albeit with seasonal variation. Pronounced frost and drought tolerance allows *C. galianoi* to benefit from additional carbon gain during winter and summer, with assimilation before growth leading to carry-over effects that allow it to perform even under adverse conditions during the active growth phase, which is facilitated by the ability to store and mobilize carbohydrates (Palacio *et al.*, 2007) in order to decouple growth from carbon uptake (Iwasa & Kubo, 1997; Wyka, 1999; Meloche & Diggle, 2003). Although *G. versicolor* also benefits from such carry-over-effects, the extent is likely much lower with an avoidance strategy slowing its activity during these periods. Therefore, the major amount of carbon reserves in this species is likely attained during the active growth phases, with surplus assimilates being stored whenever available and remobilized whenever needed.

These unexpected contrasting patterns leave no doubt that mechanisms underlying growth are species-specific and determined by covariation in traits (Fyllas *et al.*, 2020), that is in stem greenness and root morphology. Along with differences in the species' distribution (Löffler *et al.*, 2022), this suggests overall high growth plasticity (Pacheco *et al.*, 2018; Tumajer *et al.*, 2021b; Valeriano *et al.*, 2023). As such, we agree that common trait-by-trait scaling relationships should be treated with caution (Fyllas *et al.*, 2020) as these relationships may not be robust at local scales (Messier *et al.*, 2017).

Overall, the contrasting relation to winter temperatures probably determine the species' distributional range, with *G. versicolor* being limited to the slopes where there is no risk of soil freezing, while *C. galianoi* is able to occupy a widespread ecological niche all over the Mediterranean alpine (Dobbert *et al.*, 2022a; Löffler *et al.*, 2022). Since both species were able to benefit from additional photosynthetic opportunities during snow-free winters, warmer winters will most likely enhance species performance as they shorten periods of snow cover and consequently lengthen the period of resource acquisition (Dobbert *et al.*, 2022a). In addition, reduced temperature constraints likely allow xylem differentiation to continue during winter (de Luis *et al.*, 2007; Vieira *et al.*, 2014). Likewise, an expected decrease in precipitation and extension of summer drought (Giorgi & Lionello, 2008) may affect the species less than expected, as both were well-adapted to severe summer drought, with their cambial rhythm closely linked to seasonal water dynamics (Dobbert *et al.*, 2022a). However, differences in the species' drought resistance strategies may make *C. galianoi* a better competitor under increased droughts, using drought tolerance as the 'ultimate drought strategy' (Connor, 2005), with the disadvantage of risking a drop of the plant water potential under continued carbon fixation (Arndt, 2000). The ability to postpone or avoid tissue water deficits allows for short-term survival, but may threaten the species' long-term survival, if it fails to prevent dehydration of tissues, which are relatively sensitive to desiccation (Ludlow, 1980).

Conclusions

Here, we compare radial stem diameter changes of two coexisting green-stemmed Mediterranean alpine shrub species. By using fine-scale dendrometer data, combined with on-site measurements of environmental variables directly within the root zone of the respective specimens, we succeeded in detecting complex processes across elevational and topographic gradients, including clear differences in growth patterns, timing of growth, and the environmental drivers controlling growth processes, linked to contrasting winter freezing and summer-drought adaptation strategies. Nevertheless, there are some physiological processes, which are not reflected in the patterns of stem diameter change but might be indirectly coupled to it, such as photosynthesis, respiration and biomass partitioning, as well as leaf and growth phenology. We propose an integrative approach that, by combining methods from different scientific fields (anatomy, ecophysiology, dendrochronology, ecology; Steppe *et al.*, 2015), would help to fill our knowledge gaps and bring us even closer to answering the question of when, how, and why plants grow.

Here, we show that *C. galianoi* uses winter-cold tolerance and summer-drought tolerance, whereas *G. versicolor* uses winter-cold escape and summer-drought avoidance strategies. As such, *G. versicolor* has a far narrower ecological niche than *C. galianoi*, yet might profit from warmer winters. However, the species might suffer from severe summer droughts and might be threatened by extreme winter cold, when a protective snow cover is missing/shortened. Both species were driven by pregrowth conditions, albeit with differences depending on the season, and, pregrowth environmental conditions were more relevant than conditions during actual growth, controlling species' resource availability and performance. This suggests that studies focusing on the current driver constellations of growth may fail to predict the species' ecological niche and thus their potential future performance. As a winter-cold-adapted species, *C. galianoi* has the higher ecological plasticity, and thus might be the winner under future climate warming.

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Competing interests

None declared.

Author contributions

JL had the idea, designed the research platform and together with ECA conducted the fieldwork and ran the long-term LTAER-ES project. SD wrote the statistical codes and helped with data management and figures. ECA led the writing of the manuscript, analyzed the data, with contributions from SD, RP and JL.

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Data availability

All underlying data pertinent to the results presented in this publication are publicly available in a data publication in ERD-KUNDE – Archive for Scientific Geography (<https://doi.org/10.3112/erdkunde.2022.dp.01>).

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

- Fig. S1** Illustration of the focal species and their traits.
- Fig. S2** Example time series for two specimens at 2100 m above sea level (asl).
- Fig. S3** Illustration of micro-environmental data.
- Fig. S4** Ridgeline plot of root zone temperature and root zone soil moisture.
- Fig. S5** Illustration of the overall climate regime.
- Fig. S6** Boxplots of air pressure, air temperature (2 m above ground), global radiation, precipitation and relative humidity recorded at 2692 m asl.

Fig. S7 Histogram for growth in *Cytisus galianoi* and *Genista versicolor*.

Fig. S8 Stem diameter change for all *Cytisus galianoi* and *Genista versicolor* specimens.

Fig. S9 Boxplots illustrating growth during both growth phases and in both species.

Fig. S10 Boxplots illustrating growth rates in *Cytisus galianoi* and *Genista versicolor*.

Fig. S11 Pearson's correlation coefficients calculated between stem diameter change and on-site measured daily root zone soil moisture and root zone temperature for the two growth phases.

Table S1 Micro-environmental conditions from 2015 to 2020 averaged over all studied sites (\pm SE), for the focal species.

Table S2 Onset, cessation, duration (day of year), and growth (μm) averaged over all studied sites (\pm SE), aggregated by previously defined growth phases, for the focal species.

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