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Supplementary material for this article is available [online](#)

Abstract

Alpine plants are particularly sensitive to climate change, and in the Mediterranean, less frequent winter cold and prolonged summer drought are expected to shift the growth patterns of species, altering their range and strategies to cope with these dual climatic stressors. However, adaptive strategies for drought and frost and their impact on performance of species are poorly explored, with critical timescales relevant for growth insufficiently reflected and a focus on a limited set of environmental drivers. Here, we explored the growth processes of two physiologically distinct Mediterranean alpine shrub species: *Cytisus galianoi* (green-stemmed species) and *Astragalus granatensis* (dimorphic species). By measuring the daily stem diameter changes of 26 specimens over six consecutive years (2015–2020) using dendrometers, as well as the corresponding soil temperature and soil moisture conditions, we identified bimodal annual growth patterns (i.e. two phases of growth), water-related timing of growth, and drought- and frost-related environmental constraints. By implementing correlation analyses, linear mixed effects models, and partial least-squares regression, we found pregrowth temperature and moisture drivers to be highly relevant for growth in both species, suggesting a temporal decoupling of growth and resource acquisition. However, the underlying mechanisms were contrasting. While the spring growth of *C. galianoi* was promoted by pregrowth winter conditions, the autumn growth of *A. granatensis* was promoted by pregrowth summer conditions. Thus, resource acquisition is likely to be optimized when the traits of species allow physiological activity at high gain and low costs, i.e. when adaptive mechanisms reduce resource consumption to cope with frost and drought. This is during winter for frost-tolerant green-stemmed species and during summer for drought-avoidant dimorphic species, leading to species-specific time windows of growth. Understanding these species-specific growth mechanisms contributes to answering the overarching question of when and how woody plants grow and helps in understanding their adaptability to future climate variability, particularly in sensitive alpine environments, where plant species are evolutionally adapted to physical peculiarities and reach their low-temperature limit.

1. Introduction

Climate warming is expected to affect the productivity and performance of woody plants across biomes (Forbes *et al* 2010, Berner *et al* 2020, Myers-Smith *et al* 2020) and cause changes in vegetation structure with profound but complex implications for the global carbon cycle (Graven *et al* 2013, Myers-Smith *et al* 2020), potentially inducing an increase in the terrestrial carbon sink (Piao *et al* 2007). Therefore, assessing the seasonal growth dynamics of woody plants and environmental drivers of growth is of major importance in

understanding how species cope with current climate stressors and might respond to climate change (Jevšenak *et al* 2022). However, little is known about the temporal, spatial, and interspecific differences in growth dynamics and strategies (Tumajer *et al* 2021). Trends observed in the past decades are seasonally heterogeneous and spatially variable (IPCC 2021), making it difficult to obtain an understanding of overarching patterns and underlying physiological processes that might bring us closer to answering the question of when and how woody plants grow (Jevšenak *et al* 2022). Consequently, knowledge of seasonal growth patterns and underlying processes, as well as quantifying the effects of environmental drivers (Jevšenak *et al* 2022), is critical, especially for determining the limits of adaptability of species and predicting future performance of species (Magaña Ugarte *et al* 2019).

Cold-adapted alpine plant species are thought to be particularly sensitive to changing conditions, as they are evolutionally adapted to the physical peculiarities of the alpine environment, where temperatures are too low to support tree growth and plant species reach their low-temperature climate limit (Körner 2021). In the Mediterranean alpine region, where plant growth is constrained by both comparatively cold winters with little protective snow cover (Olano *et al* 2013) and severe drought during the summer months (Giménez-Benavides *et al* 2018), climate change might provoke opposing growth responses. Although predicted winter warming could enhance shrub growth by reducing thermal constraints and, consequently, lengthening the growing season (Castagneri *et al* 2018), warmer growing seasons coupled with increased aridification (Giorgi and Lionello 2008) might limit growth in these regions (Gazol and Camarero 2012). Both could lead to shifts in growth patterns of species, as growth may continue well into the winter months (Dobbert *et al* 2022a), while phases of reduced cambium activity during the summer drought might lengthen (Tumajer *et al* 2021). Moreover, changes may modify the distributional range of species (Bravo *et al* 2008, Dobbert *et al* 2022a) because shifts in biomass productivity, dispersal, and germination rates have been shown to result in an upward shift in distributions of species and vegetation belts (Grabherr 2003, Sanz-Elorza *et al* 2003, Körner 2004) and, as previous studies suggested, a shift toward vegetation types currently found in drier and warmer conditions in the Mediterranean mountains (Gritti *et al* 2006).

In the Mediterranean, mild and humid spring has been identified as the major growth period of woody species (e.g. Pellizzari *et al* 2017, Camarero *et al* 2021), followed by a second growth peak in the autumn, separated by reduced summer growth and short winter dormancy (e.g. Camarero *et al* 2010, Rammig *et al* 2010, Castagneri *et al* 2018, Tumajer *et al* 2021). The observed bimodality in cambial activity can be interpreted as a response to the separation of favorable conditions before and after summer drought (de Luis *et al* 2007, Camarero *et al* 2010). It has also been suggested to be present in Mediterranean alpine perennial forbs (Olano *et al* 2013) and was previously observed in the Mediterranean alpine shrubs studied here (Dobbert *et al* 2022a).

Winter conditions, such as low temperatures, frozen ground, and limited soil water availability, have been recognized as playing a major role in driving vegetation patterns (Choler 2018, Niittynen and Luoto 2018). Low temperatures increase the risk of frost-induced cavitation (Venn and Green 2018), with severe ground frosts limit access to soil moisture, and frost-triggered droughts might result in tissue damage caused by an internal water deficit (Mayr *et al* 2006, Körner 2016). These effects are potentially mediated by snow cover, mitigating extreme negative temperatures and frost by acting as an isolating barrier (Körner 2021), which is in turn highly variable within the complex topography of the alpine environment. Alpine woody plants adapt to frost by evolving frost survival mechanisms, such as tolerance to extracellular freezing and freeze dehydration, life cycles that allow species to escape frost, freeze avoidance mechanisms (Neuner 2014), and osmoregulation, whereby osmotic forces cause cellular dehydration, helping plants to avoid frost damage by preventing the formation of intracellular ice crystals (Ritonga and Chen 2020). The approach most commonly used by plants to cope with cold stress is cold acclimation, which allows plants to survive freezing by accumulating cryoprotective polypeptides and osmolytes (Ritonga and Chen 2020). Water availability is one of the most limiting factors for plant growth (Battipaglia *et al* 2014, Szymczak *et al* 2020), and in addition to summer drought, water shortage during periods with frozen ground is crucial (Dobbert *et al* 2022a). Plants employ different strategies to cope with drought (Chaves *et al* 2003, Guo *et al* 2017). The drought escape strategy involves successful reproduction before the onset of severe stress, whereas the drought avoidance strategy relies on delaying or even avoiding water scarcity in plant tissues, and the drought tolerance strategy is a result of retained physiological functionality despite significant dehydration of the plant tissues (see, Chaves *et al* 2003, Chen and Wang 2009). Little is known about the use of such strategies within the Mediterranean alpine region and their impact on the performance of species during phases of actual growth. Here, the critical timescale relevant for plant growth is usually insufficiently reflected when characterizing the environmental drivers of plant growth and the overall ecological niche of species (Löffler and Pape 2020). Analyses of spatiotemporal growth patterns and their environmental drivers may be the key to a better understanding of the response of species to climate change. Here, we aimed to understand such spatiotemporal growth patterns and their environmental drivers by comparing two

Mediterranean alpine species with distinctly different traits. While *Cytisus galianoi* is a green-stemmed species with a photosynthetically active stem (Bossard and Rejmanek 1992), suggesting year-round cambial activity, as observed in other Mediterranean evergreen plants (Liphschitz and Lev-Yadun 1986, Gimeno *et al* 2012), *Astragalus granatensis* exhibits seasonal dimorphism that likely allows photosynthetic and thus cambial activity during the deciduous season in summer and late autumn (see Liphschitz and Lev-Yadun 1986). However, due to the dual climatic stress of winter cold and summer drought in the Mediterranean alpine region (Giménez-Benavides *et al* 2018), we expected to find general similarities in the growth patterns of species, driven by this seasonality, despite the fundamental differences in their traits. At the same time, differences in their susceptibility to drought and frost are likely, with *C. galianoi* being potentially more susceptible to both because of its inability to shed its leaves like *A. granatensis* if conditions become too extreme. More specifically, by separating growth from water-related stem diameter changes, we expected to find (a) two phases of growth during the typically mild and humid spring and autumn months, i.e. bimodal growth patterns, as described for Mediterranean lowland plants (e.g. Camarero *et al* 2010, Castagneri *et al* 2018, Tumajer *et al* 2021); (b) water-related stem diameter changes reflecting the seasonal moisture conditions of the Mediterranean climate regime (Mitrakos 1980); and (c) drought- and frost-related environmental limitations of growth in both species, but depending on their traits, differences in their susceptibility to drought and frost.

2. Materials and methods

2.1. Studied species

In this study, we focused on the shrub species *C. galianoi* Talavera and Gibbs and *A. granatensis* Lam. (figure 1; taxonomy and nomenclature after Blanca *et al* 2009). Both are long-living cushion-forming chamaephytes (Melendo *et al* 2003) that belong to the Fabaceae family. They are abundant across the Sierra Nevada (Spain), but they differ in distribution and are of distinctly different habitus. While *C. galianoi* has green stems with only a few small leaves formed during anthesis (May/June) (Talavera and Gibbs 1997), *A. granatensis* has pubescent, paripinnate, spiny leaves (Blanca *et al* 2009), being formed twice a year in May/June and November/December (seasonal dimorphism). Both green stems and seasonal dimorphism have been described for many Mediterranean plant species (Liphschitz and Lev-Yadun 1986) and are regarded as adaptive strategies to Mediterranean living conditions (Aronne and de Micco 2001). This also probably applies to the gel-like sap within the intracellular space of the xylem of *A. granatensis*, which exudes when twigs, stems, and roots are incised (Gorji *et al* 2014, Kaya *et al* 2016). The amount of gum exuding is highest at the beginning of winter, suggesting its important role in frost protection through osmoregulation (Boughalleb *et al* 2016). In addition, the xylem anatomy and hydraulic architecture of this species (figure S1) provide indications of its ability to cope with drought and frost (Sperry and Tyree 1988, Sperry 1993) and to repair drought-induced embolism (Brodersen and McElrone 2013). For example, the gum contained in the extracellular cavities of the medullary rays of *A. granatensis* is thought to serve numerous storage functions, allowing the species to partially decouple from environmental conditions by utilizing stored water, nutrients, and osmolytes for growth (Boughalleb *et al* 2016), whereas the parenchyma cells surrounding the vascular clumps of *C. galianoi* allow the species to repair air emboli, which can occur after severe dehydration (Salleo *et al* 2009, Arbellay *et al* 2012).

2.2. Study sites and specimens

Our study focused on alpine sites along an extended transect (2200–2800 m above sea level (a.s.l.)) on the southern slope of the Sierra Nevada (figure 1). These sites are characterized by the overarching climate signal of the Mediterranean region, with hot and dry conditions during summer and cool and humid conditions throughout the rest of the year (Roberts *et al* 2011; figure S2). Reaching its highest peak at 3479 m a.s.l., the Sierra Nevada is characterized by an alpine climate and a winter snowcap, including comparatively short growing seasons, cold winters, high solar radiation, and strong winds (Herrero and Polo 2016). In combination with the complex topography, these conditions affect the spatial distribution of our focal species. *C. galianoi* dominates the vegetation of the middle alpine belt (2200–2700 m a.s.l.) and above, where vegetation is increasingly transitioning into a high alpine belt. *C. galianoi* disappears from the latest snow beds, whereas *A. granatensis* dominates the hilltops at about 2800 m a.s.l. (Löffler *et al* 2022).

We selected sites on exposed ridges following our long-term alpine ecosystem research project (e.g. Löffler *et al* 2022). Here, high air temperatures (maximum of 25.3 °C) with high solar radiation (maximum of 1153.8 W m⁻²) prevail during summer, whereas strong winds (maximum of 70.0 m s⁻¹) lead to snowdrifts during winter, leaving the ridges with discontinuous snow cover and occasionally frozen ground (minimum of -7.8 °C). As such, our sites represent the most extreme conditions in the area, where shrub specimens of comparable sizes were randomly selected, leading to a monitoring design of 16 *C. galianoi*

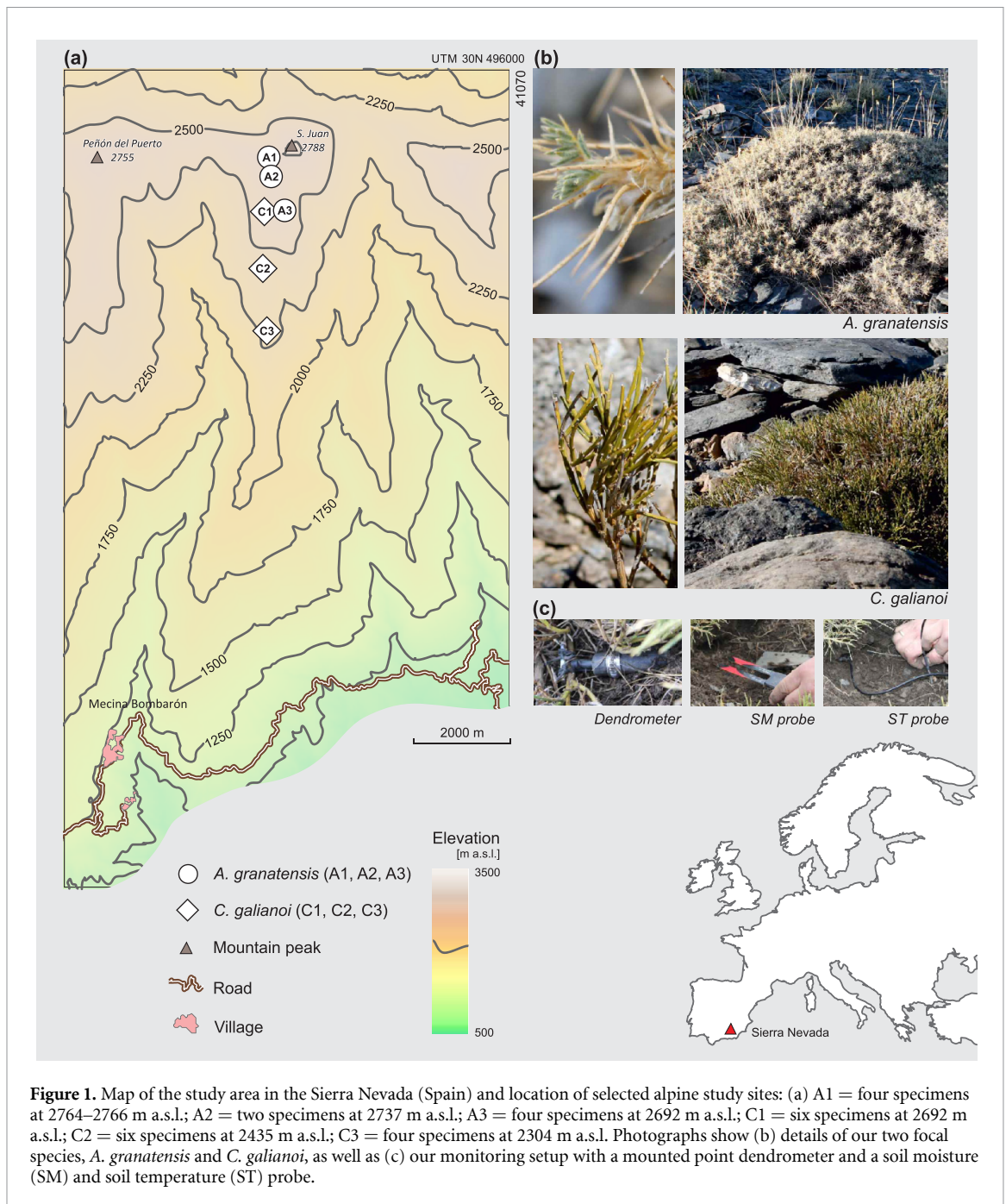


Figure 1. Map of the study area in the Sierra Nevada (Spain) and location of selected alpine study sites: (a) A1 = four specimens at 2764–2766 m a.s.l.; A2 = two specimens at 2737 m a.s.l.; A3 = four specimens at 2692 m a.s.l.; C1 = six specimens at 2692 m a.s.l.; C2 = six specimens at 2435 m a.s.l.; C3 = four specimens at 2304 m a.s.l. Photographs show (b) details of our two focal species, *A. granatensis* and *C. galianoi*, as well as (c) our monitoring setup with a mounted point dendrometer and a soil moisture (SM) and soil temperature (ST) probe.

(2300–2700 m a.s.l.) and 10 *A. granatensis* (2700–2800 m a.s.l.) specimens with two to six replications per elevation (figure 1), which we monitored for six full consecutive years (1 January 2015 to 31 December 2020).

2.3. Dendrometer data, monitoring setup, and environmental data

To monitor the radial stem diameter variations, we equipped the main stems of selected specimens with high-precision point dendrometers (type DRO; Ecomatik, Dachau, Germany), using sensors with a temperature coefficient of $<0.2 \mu\text{m K}^{-1}$ to record data at 1 min intervals. Dendrometers were attached to the selected stems with a UV-resistant rubber band in a stationary system provided by a T-shaped aluminum bar placed horizontally above the ground surface (~ 1 cm above ground) (figure 1). To minimize the influence of hygroscopic swelling and shrinking of the bark (Zweifel and Häslér 2001), we removed the outermost layers of the dead periderm at the contact point of the dendrometer pistons (see Dobbert *et al* 2022b). The dendrometers were placed close to the presumed root collar of the main stem, which is believed to represent the growth of the entire plant (Bär *et al* 2007, Ropars *et al* 2017). However, the extent to which changes in the radial stem diameter vary within individual specimens and between multiple stems of the same specimen, as well as along single stems and elevational gradients, has not yet been fully resolved (Dobbert *et al* 2021a).

Given this enormous variation, we ensured that the 26 selected specimens were representatives of each site. However, despite the arguably small sample size, we found significant correlations and clear matches in the growth patterns, allowing us to infer general trends. We obtained daily mean values from our raw data by averaging the hourly dendrometer data following the ‘daily mean approach’ (Deslauriers *et al* 2007). Additionally, we normalized the annual stem diameter curves by removing the initial stem diameter, which ranged from 7344.4 to 12 948.8 μm for *A. granatensis*, and from 3633.5 to 10 240.5 μm for *C. galianoi*, from the curves. This is necessary because dendrometers measure changes in stem diameter relative to the start of the measurement period (not including the initial stem diameter) and not the absolute stem diameter of the specimen. Finally, we checked for outliers, defining the interquartile range (IQR) and the 25th (Q1) and 75th (Q3) percentiles ($Q1/Q3 \pm 1.5 \times \text{IQR}$) as cutoff ranges. Because we did not find any outliers, all daily measurements per curve were retained.

2.4. Environmental conditions

To assess the potential drivers of the monitored radial stem diameter variations, we measured the microenvironmental variables at each site and for each specimen separately. As we aimed to record the in situ environmental data reflecting the precise root zone conditions of each specimen, we installed the sensors at 10 cm soil depth within the root zone of each specimen directly below the main stem selected for the dendrometer measurements while being careful not to damage the roots (see Löffler and Pape 2020, Dobbert *et al* 2021a, 2021b). Root zone temperatures (T_{RZ}) were recorded as hourly averages using ONSET’s HOBO Loggers (type H21-002) and thermistors (type S-TMB-002) with ± 0.2 °C accuracy. Additionally, we measured the volumetric soil water content (SM_{RZ} , $\text{m}^3 \text{m}^{-3}$) at the same depth, as hourly means using soil moisture probes (type S-SMD-M005) with $\pm 3\%$ accuracy. Complementarily, we recorded the global radiation (W m^{-2}) (GR_{SZ}) in the stem area of one specimen at one ridge site at 2692 m a.s.l. using a silicon pyranometer (type S-LIB-M003) with $\pm 10 \text{ W m}^{-2}$ accuracy at 1 cm above the ground surface. All microenvironmental data were collected from 1 January 2015 to 31 December 2020, and additional data from 2014 were used to calculate the previous year’s environmental conditions for 2015. There were no missing data.

2.5. Analysis of seasonal growth patterns

To discern the seasonal growth patterns of the species from our dendrometer curves, we calculated growth semiannually, defining two growth phases: one during the first half of the year and one during the second. These phases of radial stem increment are intermitted by two phases of stem contraction: one during summer and one during winter. This subdivision of intra-annual growth is essential, as it accounts for the bimodal rhythm of the Mediterranean climate, known to induce bimodal growth patterns in several Mediterranean lowland shrubs and trees (Camarero *et al* 2010) and, potentially, in Mediterranean alpine species (Olano *et al* 2013). Therefore, we defined growth-induced irreversible stem expansion (hereafter growth) as the cumulative stem diameter maximum of the current half-year minus the most recent maximum of the previous study period. Although applied to semiannual rather than daily data, as originally suggested by Zweifel (2016), this definition of growth parallels that of the ‘zero-growth approach’, where growth has been 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 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, including the onset and cessation of each individual growth phase.

2.6. Correlation analysis and linear mixed effects analysis

To uncover the relationship between on-site environmental conditions and growth patterns of the species described earlier, we conducted a correlation analysis and utilized linear mixed effects models. Using the statistical software R (R Core Team 2020), we calculated Pearson’s correlation coefficients between the semiannual irreversible stem growth obtained from dendrometer measurements (figure S6) and daily mean values for our environmental variables T_{RZ} and SM_{RZ} . To account for possible lagged effects of previous-year conditions on current-year growth, we included daily averages for the entire previous year (i.e. 365 additional values) in our correlation analyses for the first growth phase and the period from June to December of the previous year for the second growth phase, similar to common approaches used in analyses of growth chronologies derived from the ring width series (e.g. Bär *et al* 2008, Weijers *et al* 2018). For this purpose, we included additional microenvironmental measurements from 2014 in our calculations, i.e. measurements from before the start of our study period. Subsequently, we fitted linear mixed effects models to our data using the lme4 R package (Bates *et al* 2015). For these models, we chose semiannual irreversible stem growth as the response variable and daily values for all environmental variables as fixed

effects. Individual specimens and sites were included as random effects to account for the differences at individual sites. Separate models were fitted for each month, from January of the previous year to December of the current year. To compare our focal species, we performed all correlation analyses separately for each *A. granatensis* and *C. galianoi* specimen to avoid generalizations that might result from averaging the data measured at each site. The averages were calculated for visualization purposes only.

2.7. Partial least-squares regression analysis

We applied partial least-squares regression (PLSR) (Wold 1975) to our dataset to complement the correlation analysis. Here, we used variable selection methods to identify relevant environmental conditions and their relative importance in promoting or impeding growth. As it is especially suited for data where the number of predictors exceeds the number of observations or the predictors are highly correlated (Geladi and Kowalski 1986), PLSR has been implemented in several recent ecological studies (Frindte *et al* 2019, Löffler and Pape 2020, Dobbert *et al* 2021a). Here, we aggregated our environmental data and rounded them to 0.5 °C for T_{RZ} and 0.01 m³ m⁻³ for the SM_{RZ} values (Löffler and Pape 2020). We then counted and summed the frequency of each value occurring within the rounded time series for each meteorological season (i.e. winter (December, January, and February), spring (March, April, and May), summer (June, July, and August), and autumn (September, October, and November), hereafter used to define the timing of periods), yielding sets of scaled predictor variables. The previously calculated growth values (figure S3) were entered into the analysis as associated response variables. We used the SIMPLS algorithm (de Jong 1993) implemented in the R package *mdatools* (Kucheryavskiy 2020) to estimate the single-response model. 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 using tenfold cross-validation. Subsequently, we used the selectivity ratio (SR) to assess the relevance of each independent variable in the models created. SR is defined as the ratio of explained to remaining (unexplained) variances for each variable in the target projection vector (Farrés *et al* 2015, Frindte *et al* 2019). To achieve better contrastable results, the explained variance (SR/abs (SR + 1)) was derived from SR (Rajalahti *et al* 2009). Finally, we multiplied the SR of each variable by the sign of the corresponding regression coefficient to identify which variables were positively or negatively associated with the dependent variable (Rajalahti *et al* 2009, Löffler and Pape 2020). In this way, we identified the environmental conditions that are significantly related to annual growth.

3. Results

3.1. Patterns of stem diameter change and growth

Overall, we observed bimodal patterns of seasonal stem diameter change in our focal species with pronounced stem contraction during summer and less pronounced stem contraction during winter (figure 2(a)). Species-specific, intra-annual, and interannual variability in these patterns was high, with the most pronounced summer stem contractions in both species occurring in 2018 and 2019 (figures S4 and S5). Over the years, *C. galianoi* showed a stronger bimodality than *A. granatensis*, with the latter showing a more right-skewed pattern of stem diameter change (figure 2(a)). In *C. galianoi*, summer stem contraction usually started in May/June (~day of the year, DOY 150) and continued until mid-August (~DOY 225), whereas in *A. granatensis*, stem contraction usually peaked at the end of June (~DOY 175), and its stem diameter increased slightly throughout the summer drought (figure 2(a)). Growth patterns were similarly contrasting between the two species, with *C. galianoi* achieving the highest relative growth rates during spring when stem diameter was overall high and slightly increased until May/June (~DOY 150), although the stem diameter increase was strongest during autumn (figures 2(a), (b) and S6, and table S1), suggesting that rehydration was prioritized after summer drought. In contrast, *A. granatensis* achieved the highest relative growth rates during autumn, when growth coincided with the most pronounced increase in stem diameter (figures 2(a), (b), and S6, and table S1).

3.2. Timing of growth

The onset of the first growth phase usually occurred in February/March (~DOY 42–55) for *C. galianoi*, whereas in *A. granatensis*, it occurred in late March/April (~DOY 65–98), with high interannual variability (figure 3; table S1). For both species, the onset was exceptionally delayed in individual years (2019 for *C. galianoi* and 2015 for *A. granatensis*), whereas it was exceptionally early in 2016 for *A. granatensis*. The cessation of the first growth phase mostly occurred by the end of May (~DOY 150) in *C. galianoi*, whereas it was highly variable in *A. granatensis* (middle of April to end of May; ~DOY 105–146). The onset of the second growth phase was highly variable in *C. galianoi*, usually occurring in September/October (~DOY 260–281), with a delay in 2016 and 2019 and an advance in 2018. For *A. granatensis*, growth resumption took place between the middle and end of August (~DOY 219–243; figure 3; table S1). Growth cessation usually

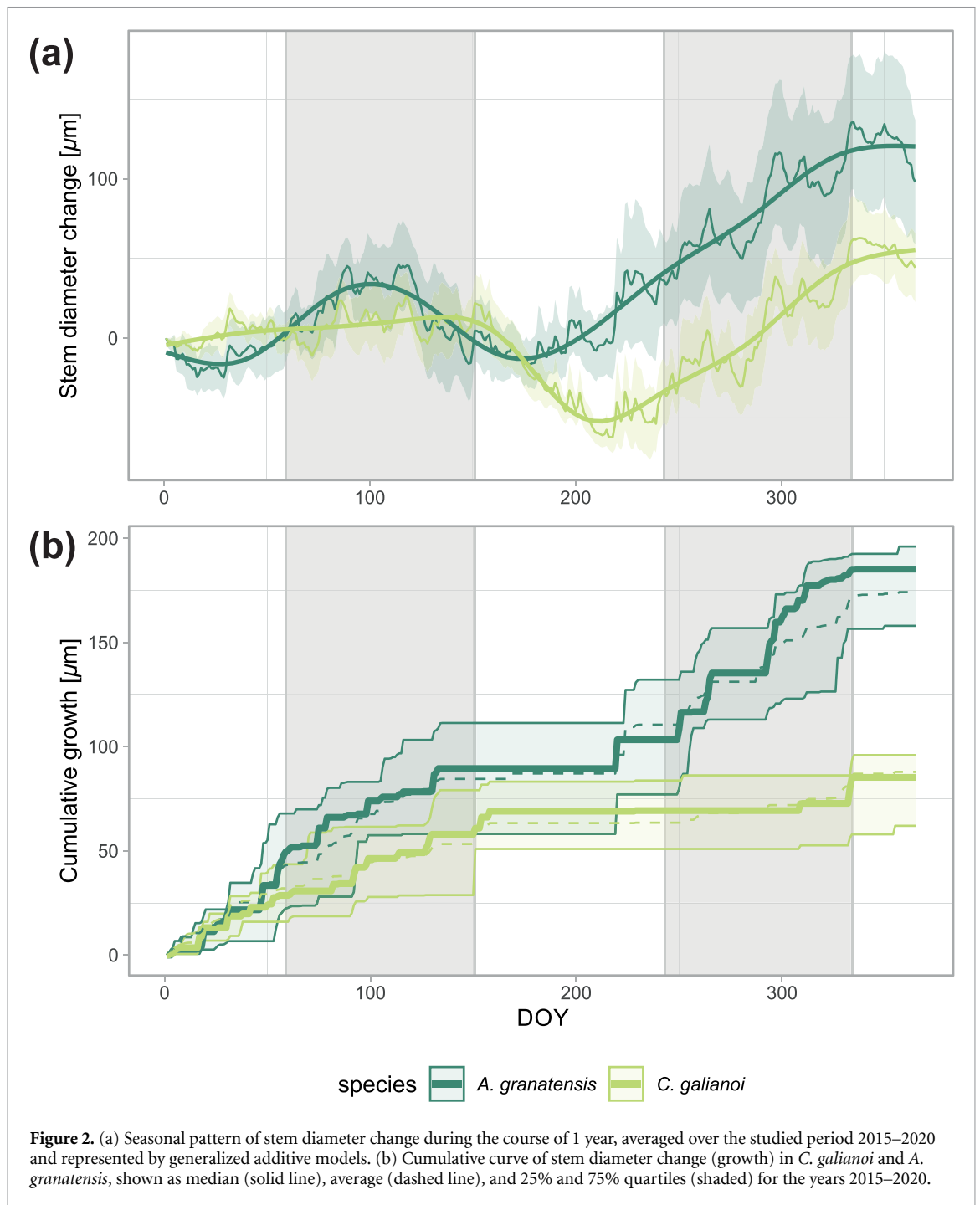
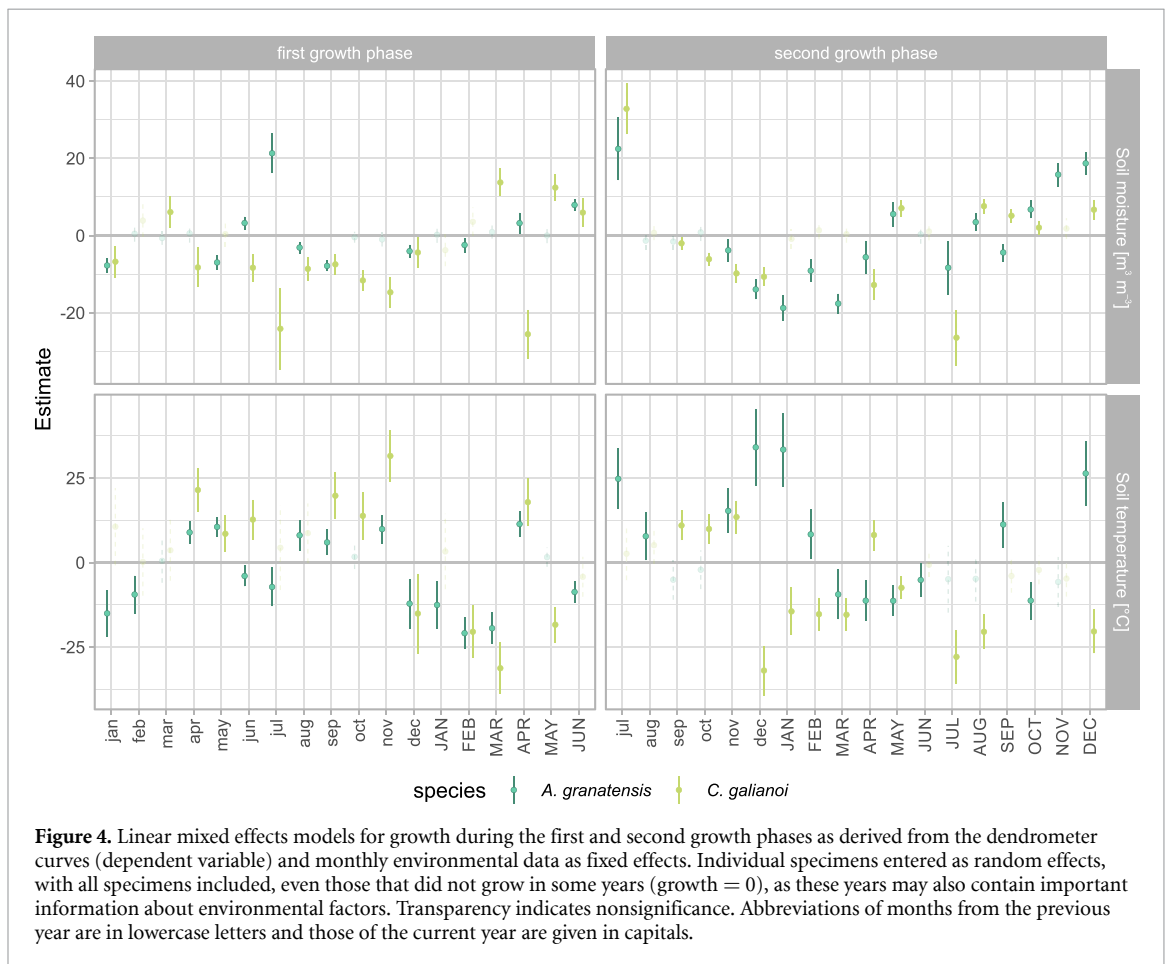
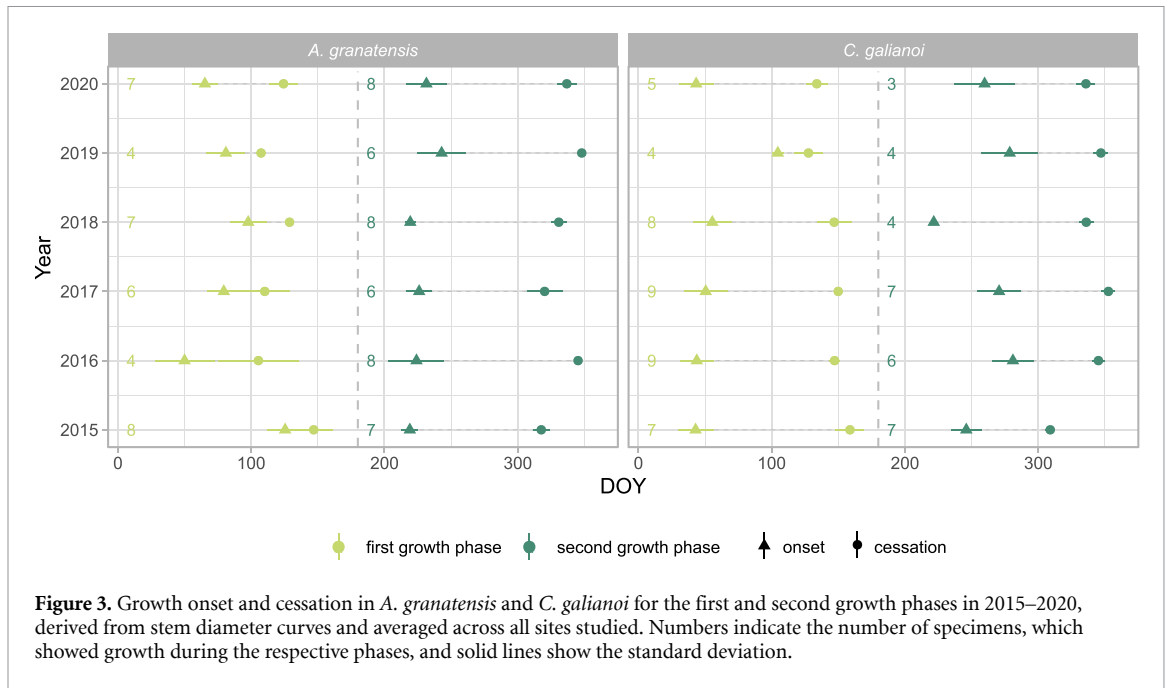


Figure 2. (a) Seasonal pattern of stem diameter change during the course of 1 year, averaged over the studied period 2015–2020 and represented by generalized additive models. (b) Cumulative curve of stem diameter change (growth) in *C. galianoi* and *A. granatensis*, shown as median (solid line), average (dashed line), and 25% and 75% quartiles (shaded) for the years 2015–2020.

occurred in November/December (\sim DOY 309–348) for both species. Overall, the interannual variability in the duration of the two growth phases was high, but the growth rates in both species were independent of the duration of the growth phases, i.e. species achieved high growth rates even if the growth phase was comparatively short (figure S6; table S1). In addition, it is worth noting that although more common in *C. galianoi*, both species exhibit phases of dormancy and years of dormancy, suggesting overall high growth plasticity.

3.3. Environmental drivers of growth

During the first growth phase, both focal species were promoted by the previous year's summer T_{RZ} (April–November for *C. galianoi* and July/August for *A. granatensis*) (figures 4, 5(a), and S7). High April T_{RZ} was also beneficial in both species, particularly in *C. galianoi* (figures 4 and S7), whereas low spring T_{RZ} at 0.0 °C and 2.0 °C–3.0 °C impeded growth for *C. galianoi* and *A. granatensis*, respectively (figure 5(a)). Furthermore, we found positive correlations with spring SM_{RZ} in *C. galianoi*, whereas growth in *A. granatensis* was positively correlated with June SM_{RZ} only (figures 4 and S7). The subzero pre-winter T_{RZ}



(−2.5 °C) negatively affected *C. galianoi*, whereas the unfrozen ground (indicated by an SM_{RZ} of $0.26 \text{ m}^3 \text{ m}^{-3}$) promoted growth. In contrast, growth in *A. granatensis* was positively linked to such thermal conditions (T_{RZ} of −5.0 °C to −1.0 °C) (figure 5(b)) and impeded by SM_{RZ} $0.22 \text{ m}^3 \text{ m}^{-3}$ in winter, but in spring promoted by SM_{RZ} $0.25\text{--}0.26 \text{ m}^3 \text{ m}^{-3}$.

Growth during the second growth phase was mostly decoupled from the conditions during the previous year for *C. galianoi* (figures 4, 5(a), (b), and S7). However, in the majority of our *A. granatensis* specimens,

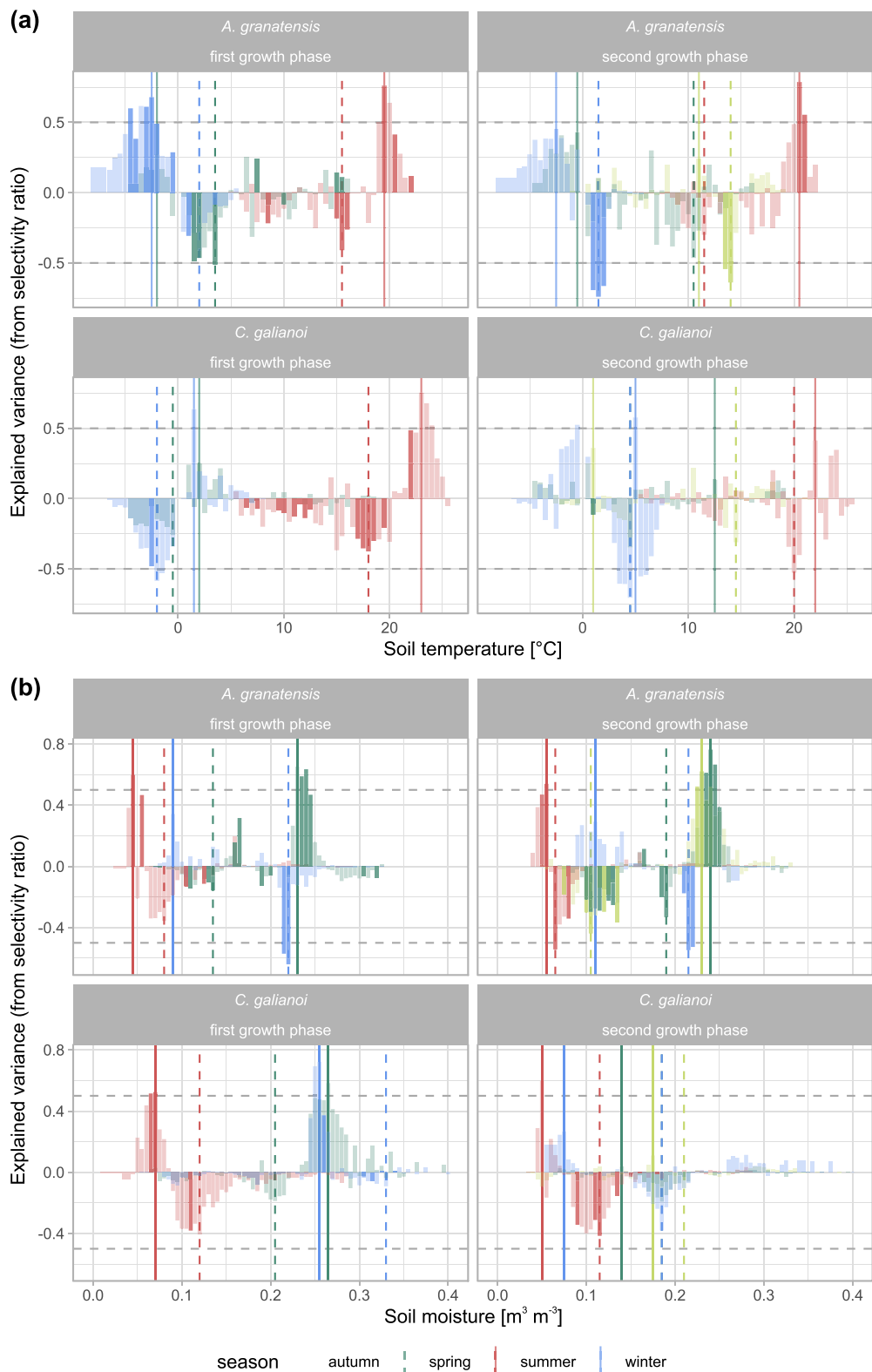


Figure 5. PLSR calculated for soil temperature (T_{RZ} , a) and soil moisture (SM_{RZ} , b) for *A. granatensis* and *C. galianoi* in all seasons. Colors represent seasons, with solid-colored areas representing significant values and shaded areas representing no significance. The solid lines underline the strongest positive correlations, and the dashed lines show 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 pre-growth winter, spring and summer, and the current autumn conditions.

pregrowth T_{RZ} control indicated that winter cold and summer heat (T_{RZ} 21.0 °C) were significant drivers, with winter T_{RZ} of 2.0 °C impeding growth (figures 4, 5(a), and S7). At the same time, the species favored humid springs (figure 4); however, our models and correlation analysis indicated no pre-growth SM_{RZ}

control (figures 4 and S7). After growth resumed in the second growth phase, there was no robust T_{RZ} control in both species, which was rather controlled by SM_{RZ} , with *C. galianoi* being driven by SM_{RZ} during August/September and *A. granatensis* being driven by SM_{RZ} during October/November (SM_{RZ} of $0.22\text{--}0.23\text{ m}^3\text{ m}^{-3}$) (figures 5(b) and S7) and impeded at $14.0\text{ }^\circ\text{C}$ autumn T_{RZ} .

4. Discussion

4.1. Growth patterns

Overall, we observed bimodal patterns of stem diameter changes in both alpine shrub species despite their physiological differences. This is consistent with the bimodal seasonal cycle observed in other shrub species in semi-arid environments, where this seasonal cycle has been attributed to seasonal interactions with temperature and precipitation (Warter *et al* 2023). However, these stem diameter changes did not always correspond to seasonal growth patterns but rather reflected differences in summer-heat- and winter-cold-induced droughts and corresponding dehydration and rehydration patterns (Albrecht *et al* 2023). Distinguishing between irreversible growth and reversible water-induced shrinking and swelling of the stem (Zweifel 2016) allowed us to deduce the water use strategies of the species from the overall stem diameter changes and to understand their contrasting growth patterns.

Summer drought and winter frost led to water-related stem contraction in the two species, which interrupted the growth process (Zweifel *et al* 2016). The observed patterns suggest drought tolerance in *C. galianoi* at the cost of a reduced performance during autumn (Bacelar *et al* 2012) when rehydration is prioritized to increase the water potential prior to growth resumption. The ability of the species to uptake low daily dew precipitation (see Mooney *et al* 1980) is compensated by relatively high transpiration loss, which is likely regulated by the anisohydry of its obviously photosynthetically active green stems (see Bossard and Rejmanek 1992), resulting in long-term shrinkage at high water potential. In winter, we observed only minor stem contractions for *C. galianoi*, which suggests high frost tolerance of its tissue (Lindfors *et al* 2019), likely allowing the species to benefit from short-term windows of photosynthetic opportunities (Wyka and Oleksyn 2014) and to potentially maintain cambial activity throughout the year, similar to other evergreen species (Gimeno *et al* 2012). Carbon fixation in winter allows the species to maximize growth at high water potential in spring (see, Bossard and Rejmanek 1992). In contrast, the observed pattern of stem contraction in *A. granatensis* suggests drought avoidance without compromising performance while maintaining physiological functionality for carbon fixation at high tissue water potential throughout summer (see Chaves *et al* 2003, Bacelar *et al* 2012), allowing the species to maximize growth during autumn rains. The ability to ideally capture, uptake, and store low daily dew precipitation in its tissue (Guarino *et al* 2005) via stem succulence (Giffits and Males 2017) is probably controlled by the presumably isohydric summer leaves, resulting in a long-term steady increase in its water potential. In *A. granatensis*, winter stem contraction suggests that the species is able to induce water efflux by osmoregulation (see, Boughalleb *et al* 2016) to protect cells from frost damage.

The observed seasonality of growth patterns suggests an overall high growth plasticity in both species, allowing them to tolerate the harsh alpine environment by maintaining a stable positive hydraulic safety margin and avoiding cavitation during both the long dry season and the short but cold winter season, albeit with different water use strategies (see Feng *et al* 2023).

4.2. Timing of growth

The timing of growth onset in spring and growth resumption in autumn differed strongly between the two species. In *C. galianoi*, green stems (Bossard and Rejmanek 1992), low stature (Körner 2016), and frost tolerance (Neuner 2014) allow for early onset of spring growth. In contrast, the late and variable onset of spring growth despite early stem diameter increase in *A. granatensis* suggests that water uptake after winter dehydration is osmotic and thus retarded during the leafless period. The timing of spring growth cessation in *C. galianoi* was most likely drought triggered, whereas growth cessation in *A. granatensis* was largely independent of environmental drivers, suggesting endogenous control of growth cessation, possibly related to the completion of vessel formation.

The discrepancy in the timing of growth resumption during autumn between both species is likely linked to differences in the drought resistance strategies of the species. In drought-tolerant *C. galianoi*, photosynthetically active stems may be the key trait for achieving positive net photosynthetic rates (Bossard and Rejmanek 1992). The species, which we hypothesized to exhibit pronounced anisohydry, tolerates variations in plant water potential, probably caused by weak stem stomata regulation (Tardieu and Simonneau 1998). Like other anisohydric species, *C. galianoi* likely exhibits high stomatal conductance and high photosynthetic capacity and performance (Meinzer *et al* 2017). Thus, even with increased water stress, it may still achieve high photosynthetic rates but is probably more susceptible to damage from prolonged

droughts due to continued carbon uptake (Attia *et al* 2015) because complete stomatal closure tends to occur later under drought, reducing the safety margin before hydraulic failure (Limousin *et al* 2022). This may ultimately reduce photosynthetic rates, lead to decelerated rehydration, and delay growth resumption. In drought-avoiding *A. granatensis*, summer leaves are probably hypostomatic and xerophytic, effectively protecting the plant during summer drought (Puglielli 2019). These presumed leaf traits might allow the regulation of transpiration-induced water loss and thus minimize fluctuations in tissue water potential (Franks *et al* 2007), as is typical for plants with stomatal-driven isohydric drought avoidance behavior (Attia *et al* 2015, Eyland *et al* 2022), which we believe to be present in *A. granatensis*. A high osmotic potential allows for rapid water uptake, which explains the resumption of immediate growth. The synchronous timing of autumn growth cessation in both species was most likely triggered by the onset of winter cold (Carbon *et al* 2020), probably resulting in limited stomatal conductance (Starr 2001) in *C. galianoi* and winter leaf shedding in *A. granatensis*.

The observed ability to remain dormant during both single growth phases and for entire years when there is a risk of damage due to unfavorable conditions but to resume growth whenever favorable conditions prevail contributes to overall high growth plasticity in both species, which is more pronounced in *C. galianoi*. This suggests that *C. galianoi*, in particular, is able to withstand the harsh and highly variable living conditions in the Mediterranean alpine region, which explains its overall wide biogeographic range.

4.3. Environmental drivers of growth

We found that for both species, pregrowth environmental drivers are most relevant for growth, with contrasting mechanisms. Moreover, both the correlation and PLSR results indicate a strong temporal decoupling of growth from its photosynthetic constraints. Therefore, we hypothesized that the spring growth of *C. galianoi*, promoted by overall high previous-year T_{RZ} and favorable pregrowth winter conditions, is closely coupled to the ability of the species to remobilize assimilates from the previous year's photosynthesis and to benefit from early defrost water, both of which promote the formation of earlywood cells and vessels (Gimeno *et al* 2012, Camarero *et al* 2013). Consequently, *C. galianoi* growth was impeded by subzero T_{RZ} during the previous winter, suggesting that the species profits from unfrozen ground during the winter when its green stems allow for additional photosynthetic opportunities (Wyka and Oleksyn 2014). As such, *C. galianoi* can cope with relatively low (but above zero) T_{RZ} and benefits from increased synthesis of carbohydrates during the period of reduced respiration (Gimeno *et al* 2012, Camarero *et al* 2013) when low T_{RZ} promotes the storage of carbohydrates in the root parenchyma (see Sperling *et al* 2017). Thus, the major importance of spring growth is most likely due to continued carbon gain throughout winter, with N fixation playing an additional role (Larsen *et al* 2012). Furthermore, our results suggest that the species benefits from early summer rains, which provide sustained water supply well into summer, being essential for the tolerance of the species to desiccation. *C. galianoi* is therefore well adapted to the environmental constraints at the exposed snow-free ridges.

As a deciduous ring-porous species, *A. granatensis* relies on new conductive tissue in spring to replace the previous year's nonfunctioning xylem (Essiamah and Eschrich 1986), and as such shows only minor growth rates from vessel formation during spring (Marcati *et al* 2006). Here, our findings regarding growth promotion by subzero pre-winter T_{RZ} in *A. granatensis* suggest growth onset depends on winter chilling, a phenomenon described in the context of bud break (Pop *et al* 2000), and spring growth, for being heterotrophic, as known from leaf formation in deciduous trees (Crang *et al* 2018). The preference for humidity at the end of the first growth phase in *A. granatensis* suggests a high water demand during leaf unfolding. In both species, high T_{RZ} during spring growth promotes vessel formation, whereas low T_{RZ} may reduce stomatal conductance in *C. galianoi* and hinder vascularization in *A. granatensis*. This is consistent with various studies from cold regions (Starr 2001, Bär *et al* 2008, Olano *et al* 2013, Dobbert *et al* 2022b) and helps to understand the superior role of early growth in alpine plant species (Callaway *et al* 2002).

For the second growth phase, pregrowth control by summer drought was low in *C. galianoi*, as the species tolerates drought, although most likely with the disadvantage of reduced photosynthetic capacity hampering autumn growth. In contrast, winter cold and summer heat were significant drivers in *A. granatensis*, which avoids droughts, most likely with the benefit of maximized photosynthetic capacity supporting autumn growth. In this context, anisohydric species have been shown to achieve high photosynthetic rates under water stress, but continued carbon uptake and sustained activity make them vulnerable to drought-induced damage, whereas isohydric species have been shown to exhibit high water use efficiency under increased water stress (Attia *et al* 2015). At the end of the summer drought, only *C. galianoi* showed a positive SM_{RZ} signal, whereas *A. granatensis* was promoted by SM_{RZ} during October/November. In *C. galianoi*, a switch from anisohydry to partial isohydry at the onset of the humid period is likely because the latter has been shown to be effective after prolonged droughts when seasonal but predictable rainfall occurs (Guo *et al* 2020). Such a rapid switch is supported by the extensive root system of the species, enabling it to benefit from

pre-growing season water supply (see, Bossard and Rejmanek 1992). In contrast, we assumed that *A. granatensis*, being leafless after summer, is influenced by environmental constraints only when heterotrophic growth gradually ceases, and the second leaf cohort is unfolded with new photosynthetic opportunities.

5. Conclusion

Overall, the environmental influences on plant performance are closely linked to the traits and physiological strategies of species. In contrast to the literature (Camarero *et al* 2010, Rammig *et al* 2010, Olano *et al* 2013), the decoupling of growth from environmental drivers during phases of actual growth pinpoints the dependency of growth on resources attained prior to growth. In *C. galianoi*, presumably high photosynthetic rates during winter allow for high spring growth, whereas in *A. granatensis*, presumably high photosynthetic rates during the short-term summer solstice allow for high autumn growth. As such, resource acquisition is rather optimized during phases when the traits and growth strategies of the species allow for physiological activity at high gain and low costs, resulting in species-specific windows of maximum growth (and heterotrophic growth in *A. granatensis*). This is of major importance for understanding the adaptive capacity in alpine environments under future climate variability (Olano *et al* 2013, Kramp *et al* 2022, Dobbert *et al* 2022a) and contributes to the question of when and how woody plants grow (Jevšenak *et al* 2022), the knowledge of which is crucial for assessing vegetation evolution across biomes.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: <https://doi.org/10.3112/erdkunde.2022.dp.01>.

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