On growth patterns and mechanisms in Mediterranean-alpine shrubs

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Abstract

In the context of open questions on the adaptability of alpine ecosystems to future global warming, this cumulative doctoral dissertation studies three Mediterranean alpine shrub species using a novel dendrometer-based approach. Under climate change, cold-adapted Mediterranean alpine might become exposed to severe summer droughts and milder winters. However, the complexity of driving forces of shrub growth, associated with above-ground biomass gain in these shrubs is not yet fully understood. Here, we used the shrub species *Cytisus galianoi* as a target species, which was abundant at all sites across the Sierra Nevada, Spain. *C. galianoi* co-occurred with *Astragalus granatensis* at exposed ridges and with *Genista versicolor* at snow-covered slopes. In contrast to previous dendroecological studies, that commonly use an anatomical ring-width-based approach, we aimed at understanding stem diameter changes, water-related stem expansion and contraction, and physiological growth mechanisms by using long-term high-resolution dendrometer measurements. From our overall findings, we deduced the species´ strategies to cope with winter cold and summer drought constraints. Using soil temperature and soil moisture data recorded directly at the growing sites, we identified the species-specific environmental controls of growth. With different statistical approaches, robust and significant driver constellations were found and allowed to argue for pronounced carry-over effects, which addresses the resource acquisition during favourable periods prior to the actual growth phase. Such effects were clearly visible for *C. galianoi*, which as a frost tolerant, green-stemmed species, was found to likely profit from cold and snow-free winters by mobilizing assimilates from winter photosynthesis for major spring growth. As a drought tolerant species, *C. galianoi* showed severe summer stem contractions, and had strong water-related stem diameter increase due to

rehydration in autumn, while growth rates were minor. Using this combined winter cold and summer drought adapted growth strategies, *C. galianoi* was shown to perform best at all alpine sites due to high growth plasticity. Compared to the two co-occurring shrub species, the combined cold and drought tolerance growth strategies in *C. galianoi* led to highly competitive advantages. We synthesized the different growth strategies and addressed a) the overall growth performance in *C. galianoi* over its distributional range across the Sierra Nevada, b) the advantages and disadvantages of the growth strategies in a green-stemmed vs. a seasonal dimorphic species, and c) the growth differences in comparison of two green-stemmed species at shared sites.

1 General introduction

This study is based on a long-term alpine ecosystem monitoring program from the Sierra Nevada in Spain (LTAER-ES). We investigated alpine shrub growth from 2012 until 2023 (and still ongoing), based on three alpine species, various sites along the elevational gradient, and micro-environmental measurements, in particular soil temperature and soil moisture. Our three focus species were *Astragalus granatensis*, *Cytisus galianoi*, and *Genista versicolor*. Here, we use a dataset from 2014 until 2020, which is mainly based on dendrometer measurements from the stems of the above shrub species. The data was published in a data paper (Löffler et al. 2022) and used for a comparison between alpine tundra and Mediterranean alpine shrub growth (Dobbert et al. 2022a).

In earlier studies related to our LTAER-NO program, we already looked closely into growth responses of deciduous and evergreen species from the Norwegian alpine tundra to long-term micro-environmental constraints (Köhler et al. 1994, Löffler 2002, Bär et al. 2008, Pape et al. 2009, Wundram et al. 2010, Pape and Löffler 2017, Weijers et al. 2018, Frindte et al. 2019, Löffler and Pape 2020, Löffler et al. 2021), and for the first time, we made use of high-precision dendrometers to monitor radial growth of dwarf shrubs at unprecedented temporal resolution, bridging the gap between classical dendroecology and the underlying growth physiology of a species (e.g. Dobbert et al. 2021a, 2021b, 2022b). Based on long-term experiences from arctic-alpine landscapes, we transposed our successful concepts from our projects in Norway to the Sierra Nevada, where we established a comparative scientific infrastructure. As such, we used novel datasets of on-site micro-environmental drivers in combination with innovative dendrometer measurements mounted on Mediterranean shrub species to gain new insights into the alpine ecosystems of the Sierra Nevada. Overall, our long-term alpine ecosystem research program from two contrasting biomes contributes to the ongoing scientific debate on future ecosystem responses to global change (Löffler et al. 2011).

Here, I synthesize three manuscripts, prepared for publication in international journals. The overall aim was to understand growth mechanisms in a common and widespread green-stemmed Mediterranean alpine shrubs species, and to compare its growth patterns, the timing of growth, and its drivers of growth to those of two co-existing shrub species in the Sierra Nevada (Spain). Therefore, **Paper 1** focussed on the species *C. galianoi*, which has been studied along its entire distribution along alpine elevational and microtopographical gradients. In **Paper 2**, *C. galianoi* was studied in comparison to *A. granatensis* at the alpine ridges only, where both species experience harsh environmental conditions especially during snow-free winters. In **Paper 3**, *C. galianoi* was compared to *G. versicolor* at snow-covered slopes, where the latter species has its narrower niche within the alpine.

2 Relevance: alpine plant performance

In the light of a rapidly changing environment, knowledge on plant species performance has become essential to predict their adaptive capacity and their future spatial distribution (e.g., Cotto et al. 2017). Species in alpine environments are expected to strongly respond to changing conditions (e.g., Körner 2021). In particular, in the Mediterranean, where climatic drivers are intertwined with fire, grazing and conservation measures (e.g., López-Merino et al. 2009), it is essential to understand the feedback effects on plant performance. Dendroecological studies from arctic-alpine environments provide such information on functional traits and growth patterns of dwarf shrubs (e.g., Warren-Wilson 1964, Bär et al. 2007, Weijers et al. 2018). However, growth response and performance of dwarf shrubs in the Mediterranean alpine environment are still poorly investigated, but have received more attention in recent years (e.g., Copenheaver et al. 2010, Gazol and Camarero 2012, Olano et al. 2013). Knowledge is still lacking on wood-anatomical features that encode information about species adaptability to mechanical disturbance, fire impacts and future climate warming. Moreover, little is known about the temporal, spatial, and interspecific differences in cambium dynamics (Tumajer et al. 2021), and the species' adaptability to a warmer climate. Here, analyses of spatio-temporal growth patterns and environmental drivers of growth may be the key to a better understanding of changes in vegetation structure as well as productivity and performance of woody plants under ongoing climate change.

Plant species richness is high in the Mediterranean, and high phytodiversity is assumed to be associated with long-term isolation due to elevational ranges (e.g., Kropf et al. 2006, Steinbauer et al. 2013). Moreover, endemic species richness has been found to be strongly correlated with elevation (Molina-Venegas 2017, Eibes et al. 2017), and it has been suggested that topographical complexity may also be positively correlated with endemism in high mountain regions functioning as refugia (Crisp et al. 2001, Vetaas and Grytnes 2002). The Sierra Nevada in southern Spain is one of the most important biodiversity hotspots in the Mediterranean region (e.g., Blanca 1996, Médail and Quézel 1999, Barthlott et al. 2007, Cañadas et al. 2014), but spatial vegetation patterns are dominated by a small number of single species, such as *Cytisus galianoi*, which we observed colonizing a large variety of sites along the entire alpine environment, co-occurring with *Astragalus granatensis* or *Genista versicolor* depending on the topographical position. Such species play a dominant role concerning their potential distribution patterns in a changing environment (e.g., Pauli et al. 2012, Fernández Calzado and Molero Mesa 2013, Winkler et al 2016), but they have not yet been subject to studies of their physiological mechanisms under multiple ecological constraints. Here, timeseries-based approaches might offer valuable insights into plant performance under high climate variability. To our knowledge, studies focusing on Mediterranean alpine shrub growth are rare (but see Dobbert et al. 2022a, Löffler et al. 2022). Such information, however, might help to understand climatic driven modifications in alpine plant life and their biogeographical patterns in the context of climate warming.

3 Geographical setting

Study area

For our study, we chose a typical Mediterranean mountain area in which multiple variables, such as climate, human impacted grazing, nature conservation, forestry, and wildfires are coupled in complex ways (Anderson et al. 2011, Gómez-Ortiz et al. 2013). We selected a pronounced elevation gradient, located at the southern slope of the Sierra Nevada mountain range (SE Spain), within the protected area of the National Park and the encircling Natural Park (Gómez-Ortiz et al. 2013). The natural treeline is built by autochthonous Scots pines (Linares et al. 2014, Piper et al. 2016), which is partially intermitted by widespread holm oak forest, reaching up to 2000 m a.s.l. (Linares et al. 2014). These natural forests are dominated by the evergreen species *Quercus ilex* ssp. *rotundifolia* which is partly replaced by afforested pines, mainly *Pinus sylvestris* and *Pinus pinaster*, originating from the mid-20th century (Mesa Garrido 2019, Anderson et al. 2011). Therefore, the reconstruction of original treeline and the natural distribution limit of *Q. ilex* is difficult as the entire area has been settled and exploited since Neolithic times (Anderson et al. 2011, Carrión et al. 2007) and profound anthropogenic transformation has taken place since Medieval times (Gómez-Ortiz et al. 2013, Sayadi et al. 2009). Our elevation gradient covered mainly the alpine environment above the treeline at about 2000 m a.s.l. (Troll 1973). Figure 1 shows a topographical map of the mountain area in which our study sites represent the overall spatial gradients of the area.

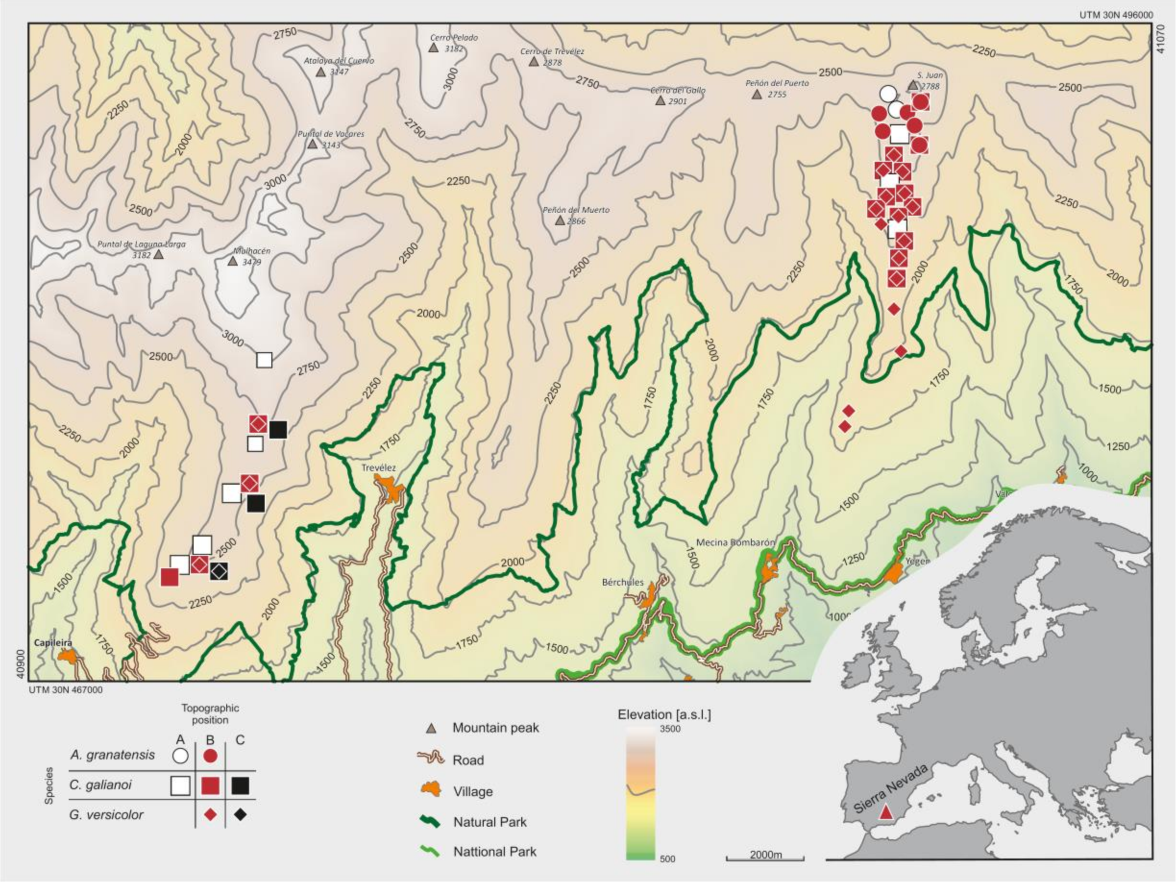

Fig. 1 Cut of topographical map of the Sierra Nevada, showing the investigated mountain region and location of the sampling sites at ridges (A), slopes (B) and within snowbeds (C) along the elevation gradient (modified after Löffler et al. 2022).

Human impact

Population data from 1787 to 2018 (INE 2019a, UGR-IDR 2019, INE 2019b) outlines the human impact on our study area, showing significant changes of population patterns within the municipality Alpujarra de la Sierra since 1910 (Fig. 2A). The comparison of the total population number from Alpujarra de la Sierra with those of entire Andalusia showed an antagonistic development. While the population number of Andalusia has constantly increased since 1842, the number of Alpujarra de la Sierra decreased from its highest historical population density in the mid-19th century until 1910 (Calatrava and Sayadi 2019), when it has started to strongly increase again until 1950 (Cámara 2009). After a short period with a large population number, population has decreased rapidly, resulting in the recent number of 978 inhabitants. The constant population increase of entire Andalusia has been attributed to economic growth in Spain (Prados de la Escosura and Rosés 2010), return migration since the 1980s and the immigration to Andalusia of nationals from European countries (retirees) and developing countries (Moroccans), searching for job opportunities (Rodríguez et al. 2002). Instead, the strong and rapid population decrease of Alpujarra de la Sierra from 1950 onwards, has been interpreted as the result of the universal rural-urban migration that especially affected the mountain villages of the Sierra Nevada (Calatrava and Sayadi 2019, Sayadi et al. 2009). As to the population decrease, land use activity has changed and formerly intensively used land was either abandoned or extensified (Douglas et al. 1994). Land abandonment and extensification of farming and management might have been also reinforced by the installation of the Sierra Nevada Natural Park in 1989, regulating land management with a focus on adapted traditional agricultural practices (Gómez-Ortiz et al. 2013). But, despite governmental regulations on faming and land management, which have also been reinforced by the establishment of the National Park Sierra Nevada in 1999 (IUCN 1998), land abandonment slightly decelerated, most likely as a consequence of current European Rural-Development policies (Sayadi et al. 2009) and because of “naturbanization” in conjunction with conservation (Prados 2005).

Animal numbers for Granada province from 1906 to 2000 (Zambrana Pineda 2006) and 2001 to 2015 (Junta de Andalucía 2019a) show that during this period, animal numbers have undergone various fluctuations (Fig. 2B), which have been driven by the overall socio-economic development of the region. Congruent to the high population density during the mid-19th century, livestock (mainly goats and sheep) associated with agriculture has become abundant and persisted, with slight changes, until the rural exodus in the mid-20th century. The sharp reduction of the population, and thus workforce, have caused the decrease of semi-nomadic summer grazing in areas of higher elevation and livestock herded by salaried herders has disappeared (Calatrava and Sayadi 2019). This fundamental change of grazing mode is reflected in small animal numbers from 1962 to the mid-1980th. The year 1987 marks a bifurcation point, which coincides with Spain's accession to the European Community in 1986, when new policies were adapted that promoted an intensification of industrial livestock practices (Moreno et al. 2014). Therefore, animal numbers suddenly reached exceptionally high numbers in 1988, and from then on remained at a constant high level until 2007, with minor fluctuations. The abrupt and sharp fluctuation of animal numbers has come along with attempts to alleviate an agrarian crisis until the beginning of the 1990s, such as subsidies and modernization projects of livestock (Calatrava and Sayadi 2019). Despite these attempts, we assume that the crisis threatened the extensive farms in Alpujarra de la Sierra and only larger-sized farms with pasture grounds closer to the villages and comparable high animal numbers resisted to marginalization. The latest decrease of animal numbers in Granada province can be attributed to universal socio-economic changes, accompanied by the Rural Development programs of the European Union, which have mainly supported activities in the secondary and tertiary sectors (Calatrava and Sayadi 2019). As shifting grazing pressure strongly affects vegetation cover and species composition (Alados et al. 2004), we assume that the overall high abundance of *C. galianoi* along our alpine gradients might be attributed to the increase of nature conservation measures in the area, causing reduction (Natural Park) and elimination (National Park) of traditional grazing (Verdú et al. 2000).

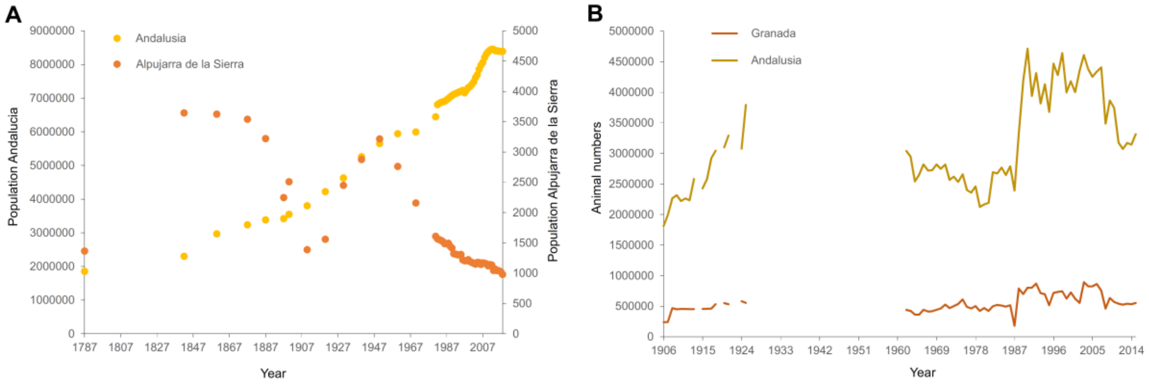

Fig. 2 A) Total human population of Andalusia and of the municipality Alpujarra de la Sierra 1787 – 2018. B) Total numbers of goats and sheep in Andalusia and in the province of Granada 1906 – 2015.

While grazing causes gradual shifts of vegetation cover, species composition, and plant growth (Alados et al. 2004), fires can eliminate the total above ground biomass (Moreno et al. 2014). Mediterranean fires often occur after the hot and dry summer period, and the effect of fires on the vegetation strongly depends on the fuel density and thus on the heat of the fire (Pausas and Fernández-Muñoz 2012, Pausas and Vallejo 1999). Small fires frequently occur in the Sierra Nevada mountain range, but, above the treeline natural fires are extremely rare today, and have probably been very rare in the past (Jiménez-Moreno et al. 2013). Since 1975, several fires have been recorded close to our study area and along our elevation gradient, but only one large fire affected the entire area in 1994 (Junta de Andalucía 2019b). Feedback effects of land-use extensification, caused by the decrease of the human population in the rural mountain areas, the installation of the protected areas in combination with the decrease of grazing pressure despite the increasing animal numbers, as well as the afforestation from the mid-20th century with resulting high calorific value, have led to a massive increase of combustible above-ground biomass (Mesa Garrido 2019, Pausas and Fernández-Muñoz 2012, Anderson et al. 2011). August 8th 1994, after a long and severe drought period, a fire was ignited in Válor valley and was brought up to the alpine areas by strong easterly winds (García 1994). The fire lasted for about 72 hours (Ramos 2020 pers. com.) and burned an area of 1500 ha (García 1994).

Disturbance

Fire frequency is high in the Mediterranean (e.g., Fulé et al. 2008, Touchan et al. 2012, Christopoulou et al. 2013), and it is supposed to increase in a further changing environment (Pausas et al. 2008, Marlon et al. 2008). Mediterranean shrub species may survive periodic fires (e.g., Keeley 1986), with vulnerability to fire depending on species and location. Here, *Cytisus galianoi*, as facultative resprouter, is probably the most competitive among the species we studied, as it is able to regenerate rapidly from below-ground organs after fire (e.g., Moreno and Oechel 1991, Calvo et al. 2002, Fernández-Santos el al. 2004). Moreover, it has been shown that fires favour seed germination (Tarrega et al. 1992, Nuñez et al. 2003), and that *Cytisus* species are clearly more favoured by fire action than *Genista* species and showed generally higher post-fire germination rates (Tarrega et al. 1992). *Astragalus* species are also known to germinate after fires (e.g. Hessl and Spackman 1995, Schwegman 1998, Weeks 2004). However, for *Astragalus schmolliae*, which is adapted to surviving fires (Rondeau 2020), a decrease in stocking density after fires has been observed (cf., Rondeau et al. 2022) and Friedlander (1980) concluded that the abundance in this species was due to the absence of fires. The latter might also apply to *A. granatensis*, which is abundant at the highest elevations, where fire has been shown to be rare in the past (Anderson et al. 2011), and is presumably also rare today due to scattered alpine vegetation. As such, the ability to regenerate after fire by stump-sprouting and seed germination indicates high fire resistance and post-fire recruitment in *G. versicolor* and particularly in *C. galianoi* (cf., Tarrega et al. 1992), and the abundance of *A. granatensis* at high elevations indicates the absence or low frequency of fires. Being able to resprout also appears to be a reasonable adaptation strategy to grazing, which is the second most important disturbance of vegetation after fire (Huntly 1991, Díaz et al. 2007).

Grazing affects plant-morphological and plant-functional traits (e.g., Briske 1996, Navarro et al. 2006), and it induces several feedback effects like changes in species composition and abundance (e.g., Alados et al. 2004, Golodets et al. 2010), in cycling and storage of nutrients (e.g. Marriott et al. 2004, Altesor et al. 2005), in the structure of above- and below-ground biomass (e.g. Wardle et al. 2004), and in the fire regime (e.g. Zimmerman and Neuenschwander 1984, Bachelet et al. 2000). As such, the reduction of grazing pressure on the vegetation, by the implementation of legal conservation measures in larger areas like National Parks, causes powerful feedback cycles to which plant species are responding (Nassl and Löffler 2015). The rural exodus in the 1950s has evoked land abandonment and extensification (e.g., Douglas et al. 1994, Calatrava and Sayadi 2019), and the decreasing economical demands on the natural environment have run parallel to the increasing concerns for nature conservation (Prados 2005). *C. galianoi* and the co-occurring species *Genista versicolor* have high grazing values, and, together with the layer of herbaceous species, represent an important fodder source for transhumance flocks during summer (Robles et al. 2009). The reduction of disturbance was followed by a rapid recovery of a dense shrub cover, which in turn enhanced the vulnerability to fires (Pausas and Fernández-Muñoz 2012, Moreno et al. 2014). Overall, it can thus be assumed that these mountain shrubs have had an important socioeconomic value.

The complex setting of different disturbances and environmental drivers is hard to disentangle in ecological studies, and there is an urgent need for approaches dealing with complex constellations of multiple drivers. Especially, studies which focus on the interactions of mechanical disturbance and fires impacts on plant performance in alpine areas are missing so far. Although studies on ecological diversity emphasize that Mediterranean species are highly resilient to disturbance (Lavorel 1999), and studies on post-fire regeneration outline the regenerative capacity of Mediterranean species (Buhk et al. 2007), our knowledge on species adaptation to multiple disturbances and changing environmental conditions is limited.

In this doctoral dissertation, we focussed on six years of plant growth during a period of relative stability after the establishment of the National Park (1999). During this period (2015 – 2020), there was no fire and a moderate grazing regime, allowing to study near-natural conditions and the environmental drivers of plant growth, for a long time. This unique geographical setting served as an ideal background to understand the climatic control of alpine plant performance against climate variability and thus as a valid background for predicting potential future changes.

4 Climatic drivers of growth

The Mediterranean climate is associated with severe summer droughts, and torrential precipitation abruptly introducing the cool, but mild and humid winter period. These conditions drive the biogeographical patterns of well-adapted species and communities which are mostly dominated by woody plants with conservative traits, such as slow growth and high sclerophylly (Sardans and Peñuelas 2013). As such, Mediterranean alpine plant life is often believed to function similarly to the plant life in the Mediterranean lowlands (Olano et al. 2013), although it is also predominantly affected by temporal snow cover during winter and the severe alpine constraints, which might play a superior role (Körner 2021). Plant performance in the alpine environment has been shown to be coupled to the overall regional climate (Bär et al. 2008), and recent studies of alpine plants in the Mediterranean have suggested that climate-driven growth patterns follow a double seasonality caused by summer droughts and winter dormancy (Olano et al. 2013). But, corresponding studies on patterns of stem diameter changes and growth mechanisms are rare for Mediterranean alpine plant species (but see Dobbert et al. 2022a). In general, knowledge is limited when it comes to climatically driven patterns of alpine shrub growth within the Mediterranean. A few studies suggest that spring climate (April – May) might determine alpine growth by high temperatures co-occurring with favourable hydric conditions (Olano et al. 2013). Regarding the effect of temperature on plants in alpine climates, the most pending question is related to explaining thermal range limits of species (Körner and Hiltbrunner 2018). As such, realized thermal niches of alpine plant species have been characterized, accounting for the seasonality that might drive plant species occurrences, and searching for species-specific thermal thresholds and their ecological justification (Löffler and Pape 2020). In the Mediterranean mountains, the coupling of temperature and moisture might play an overarching role in determining a species´ niche associated with summer droughts, low winter temperatures and highly variable spatio-temporal impact of strong winds and snow cover.

As shown in Figure 3, micro-environmental conditions (soil moisture and soil temperature) measured within the root zone of the sampled specimens reflect the semiarid Mediterranean climate regime with hot, dry summers and a drought period from May to August, rainfall from autumn to spring and related mild, humid winters (Anderson et al. 2011, Gómez-Ortiz et al. 2013). These contrasting weather conditions are caused by general atmospheric circulation patterns, such as the Northern Atlantic Oscillation (NAO) and the Western Mediterranean Oscillation (WeMO) (e.g. Martín-Vide 2006, Redolat et al. 2019). The characteristic air pressure system during the summer shows stable high pressure inversion layer climate with autochthonous weather in combination with continental Easterly streams (Jiménez-Moreno and Anderson 2012, Roberts et al. 2011). In contrast, cyclonic activity with Atlantic low air pressure corresponds with advective cool and humid weather from September to April. High year-to-year variability is a characteristic feature of this seasonal climate system corresponding with varying growth conditions (Li et al. 2006). Our micro-environmental data measured on-site reveal comparatively little variation between topographical positions, but pronounced inter-annual differences in timing of the dry period in summer (Löffler et al. 2022).

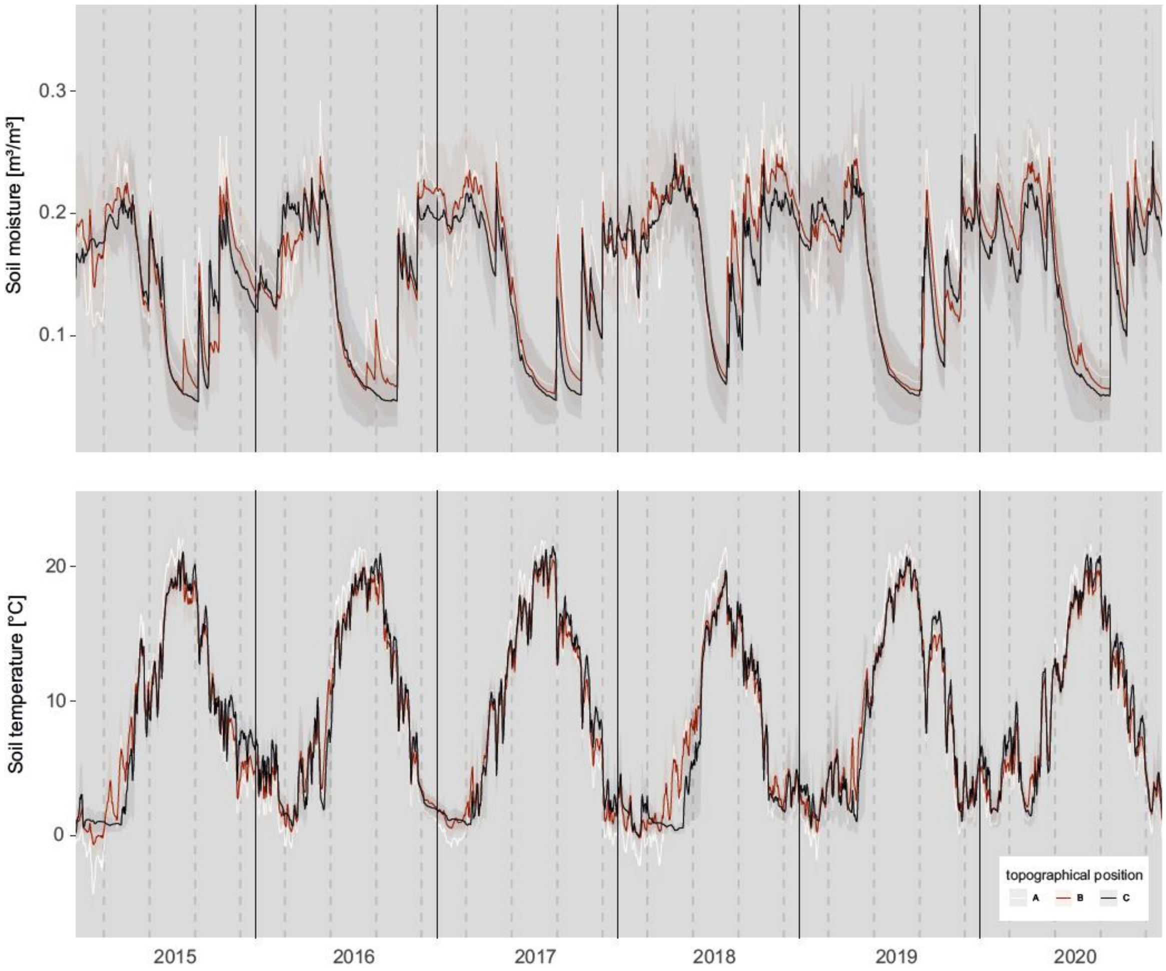

Fig. 3 Micro-environmental data from three topographical positions (A = exposed ridges, B = slopes, and C = snowbeds). The presented curves represent averaged series and transparency indicates standard deviation (modified after Löffler et al. 2022).

5 Plant species

a) *Cytisus galianoi*

In the Sierra Nevada, the oromediterranean vegetation is dominated by *Cytisus galianoi* Talavera and Gibbs (Rivas-Martínez 1996, Talavera and Gibbs 1997, Valle 2003), which is an endemic shrub species in the south of the Iberian Peninsula (Giménez et al. 2004, Melendo et al 2003), occurring frequently at all major topographical positions. From its lowest occurrence at 1700 m a.s.l., it colonizes a wide elevational range and finds its elevational limit at about 3200 m a.s.l., which is far above the elevational limit previously described in literature (Blanca et al. 2009a, Lorite 2016). *C. galianoi* is a long-living, N-fixing chamaephyte (Giménez et al. 2004, Melendo et al 2003, Macek et al. 2016) and belongs to the Fabaceae family. In addition to its green stems, deciduous leaves are formed during May/June (maximum size of 0.5 mm), when the plant is flowering, and are shed towards the end of summer (Talavera and Gibbs 1997). The species´ stems are elastic and its flexible cells shrink upon water loss while maintaining a high turgor (cf., Patakas and Noitsakis 1999), which in combination with its extensive, highly branched root system (Fernández-Santos et al. 2004) that allows to absorb water from a large volume of soil (Arndt 2000), indicates high water use efficiency. Overall, density and surface cover of *C. galianoi* differ with aspect, slope, and curvature. However, both, the species´ ability to create its own microhabitat (Pistón et al. 2016) and its green photosynthetic stems make it highly adaptable to environmental stress (Bossard and Rejmanek 1992), which is why it is abundant even at sites with harsh conditions where other species disappear. Furthermore, with its vegetative survival strategy to resprout from underground buds, just as described for *C. oromediterraneus* (Fernández-Santos et al. 2004), it is able to endure periods of high grazing pressure and fire (Fernández-Santos et al. 2004). As such, *C. galianoi* shows a relatively wide biogeographical and ecophysiological range and is well adapted to harsh climatic conditions with hot and dry summers under strong solar radiation, as well as cold and wet winters with protection by snow cover, or exposure to severe frosts without snow cover (Fig. 4).

Spring Summer

Autumn Winter

Fig. 4 Seasonal aspects of C. galianoi*. In spring*, *when chlorophyll content is high, the species´ stems appear intensely green and in summer its appearance is dominated by its yellow flowers. In autumn, it appears more brownish and in winter it is either covered by snow (slopes and snowbeds) or exposed to strong winds, low temperatures and occasional freezing conditions (ridges).*

C. galianoi has a semi-ring-porous wood with distinct annual ring boundaries consisting of thick-walled latewood cells that merge into thin-walled earlywood cells. The concentrically arranged early wood vessels, at the beginning of each annual ring, help to identify and distinguish the annual ring boundaries. Both, the first row of earlywood vessels and the intra-annual vessels, which occur in clumps and irregular bands, are surrounded by small parenchyma cells. In addition, the xylem of *C. galianoi* is crossed by narrow radial rays, mostly ranging from the round shaped pith to the outer xylem boundary (Fig. 5). Given this xylem anatomy, the difficulties described regarding identification and measurement of annual rings in Mediterranean species, which are expected to show two-split growth periods (Camarero et al. 2010), separated by drought triggered intra-annual false rings (Copenheaver et al. 2010), did not occur in our samples. This let assume that *C. galianoi* might be well adapted to droughts, and thus neither forms intra-annual false-rings, nor shows intra-annual wood-density fluctuations (de Micco et al. 2016, Rozas et al. 2011).

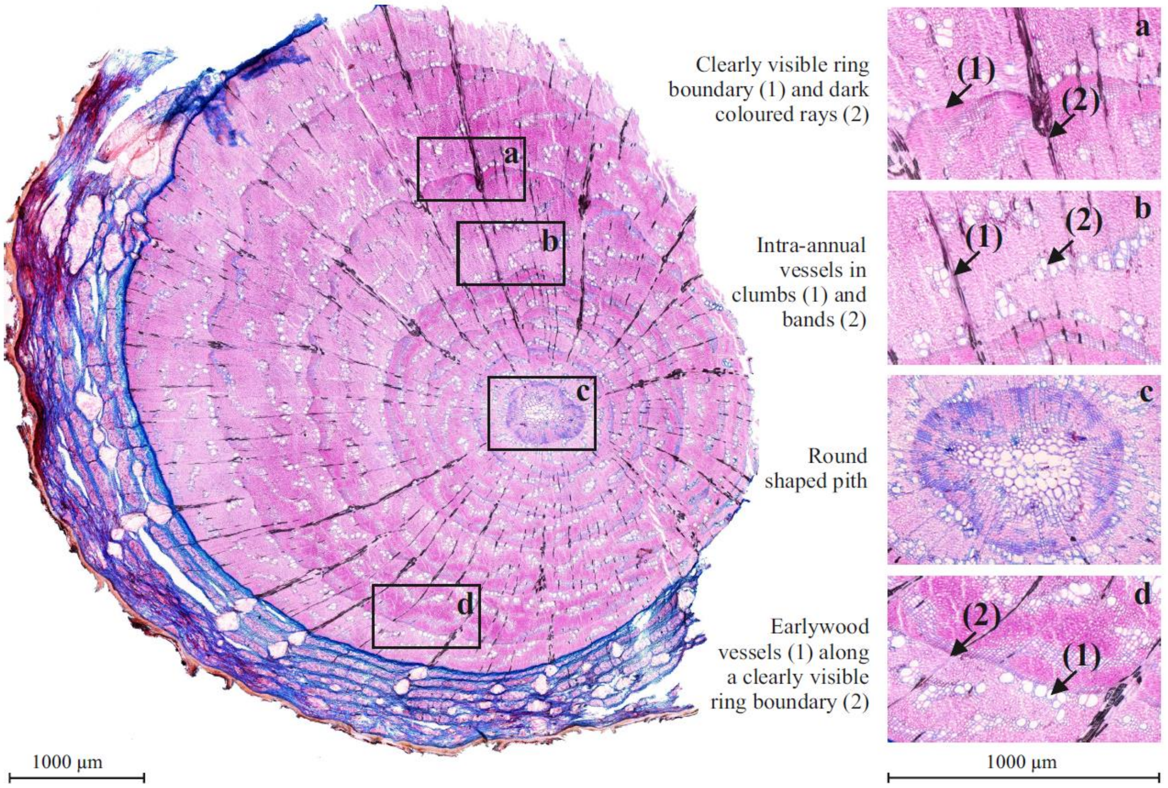

Fig. 5 Anatomical features in a base section of C. galianoi*. The species´ semi-ring porous xylem is characterized by a) clearly visible annual ring boundaries where thick-walled latewood cells merge into thin-walled earlywood cells. Narrow, dark coloured rays occur regularly and mostly range from the pith to the outer xylem boundary. b) Intra-annual vessels occur in clumps and irregular bands and are surrounded by small parenchyma cells. c) The pith is round shaped and d) the earlywood vessels are arranged along the ring boundaries.*

b) *Genista versicolor*

Within the oromediterranean vegetation, *Genista versicolor* Boiss. (Rivas-Martínez 1996, Blanca et al. 2009a), which is endemic to the South of the Iberian Peninsula (Kamari et al. 2010, Melendo et al. 2003, Giménez et al. 2004), forms dense shrub patches up to 80 cm in height and 280 cm in diameter (Löffler et al. 2022). From its lowest occurrence at 1600 m a.s.l. to its upper distributional limit at 2700 m a.s.l., the height of the shrub specimens decreases while density increases. At the same time, the abundance of the species, which is restricted to slope positions (Löffler et al. 2022), diminishes with elevation (cf. Lorite 2001). *G. versicolor* belongs to the Fabaceae family and is an N-fixing (Macek et al. 2016), long-living, cushion-forming nanophanerophyte (Melendo et al. 2003), capable of creating its own microhabitat (cf., Pistón et al. 2016). It produces a few small deciduous leaves (up to 0.5 mm) during anthesis in May/June, which are shed towards the end of summer (Blanca et al. 2009a). The green-greyish photosynthetic stems (Bossard and Rejmanek 1992) are comparatively rigid and unbending, allowing increased water uptake (cf., Schulte 1993), which is further promoted by the species´ taproot reaching deep into the soil (Fig. 6).

Spring

Summer

Autumn

Winter

Fig. 6 Seasonal aspects of G. versicolor*. In spring, when chlorophyll content is high, the species´ stems appear green-greyish and in summer its appearance is dominated by the yellow flowers. In autumn it appears more greyish-brown and in winter the species is usually covered by snow.*

G. versicolor has semi-ring-porous wood with clear annual ring boundaries distinct by radially flattened and thick-walled latewood cells that merge into thin-walled earlywood cells (Fig. 7). The concentrically arranged first row of earlywood vessels at the beginning of each annual ring help to detect the annual ring boundaries. The species´ vessels are arranged in diagonal and/or radial patterns, or occur in clusters and are surrounded by small parenchyma cells. Rays are predominantly uniseriate and upright or square and the root stele is round shaped (c.f., Crivellaro and Schweingruber 2013).

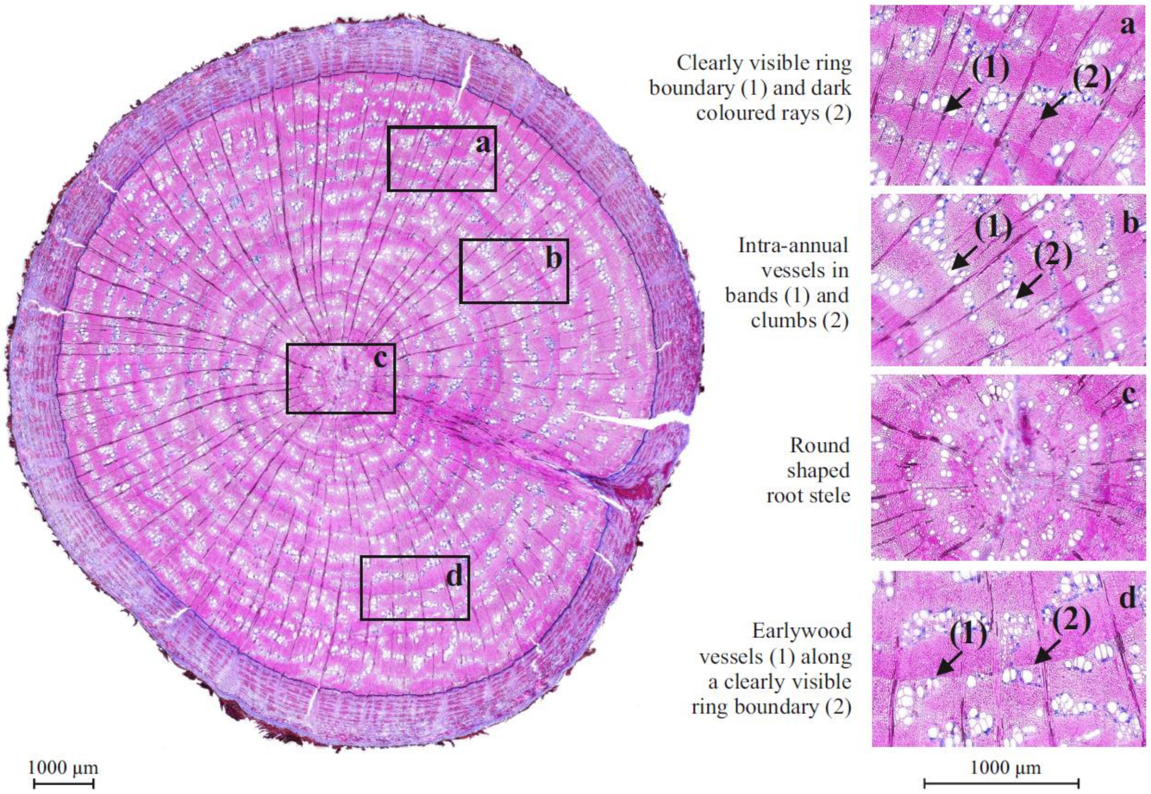

Fig. 7 Anatomical features in a root section of G. versicolor. *The species´ semi-ring porous xylem is characterized by a) clearly visible annual ring boundaries where thick-walled latewood cells merge into thin-walled earlywood cells. Narrow, dark coloured rays occur regularly and mostly range from the stele to the outer xylem boundary. b) Intra-annual vessels occur in clumps and bands and are surrounded by small parenchyma cells. c) The root stele is round shaped and d) the earlywood vessels are arranged along the ring boundaries.*

c) *Astragalus granatensis*

In our study region, *Astragalus granatensis* Lam. (Podlech 2008, Blanca et al. 2009a, Molero-Mesa 2013 pers. com.) only occurs at high elevations of the eastern gradient, where it is abundant between 2600 m a.s.l. and 2780 m a.s.l. (Fig. 1). Overall, the specimens´ height and diameter decrease with elevation, and at the highest wind-exposed ridge positions, *A. granatensis* only reaches < 25 cm height (Löffler et al. 2022). The species is a long-living, cushion-forming, Iberian-North African chamaephyte that belongs to the Fabaceae family (Molina and Izco 1986, Melendo et al. 2003, Giménez et al. 2004, Lorite et al. 2007, Podlech 2008). Its pubescent, paripinnate, spiny leaves (Blanca et al. 2009a) are usually formed twice a year, in early summer (May/June) and at the transition between autumn and winter (November/ December) (Fig. 8). Such seasonal leaf dimorphism has long been described for a variety of Mediterranean plant species (e.g., Liphschitz and Lev-Yadun 1986, Puglielli 2019) and interpreted as an adaptation strategy to the Mediterranean living conditions characterized by temperature and water stress (e.g., Guarino et al. 2005, Lianopoulou et al. 2014). Furthermore, regarding adaptation to the alpine living conditions, the species´ thorny cushion-like habitus, which has been shown to grant a remarkable resistance to intense solar radiation, persistent drought, wide-ranging temperatures as well as to mechanical disturbance due to strong winds, plays an important role as it allows the species to effectively buffer seasonal drought by dew condensation happening quite regularly in the early morning (Guarino et al. 2005), and probably also protects the plant from being browsed. Water uptake is further enhanced by the species' dual root system, consisting of a thick taproot reaching deep into the soil and a mat of finer roots near the soil surface (Guarino et al. 2005).

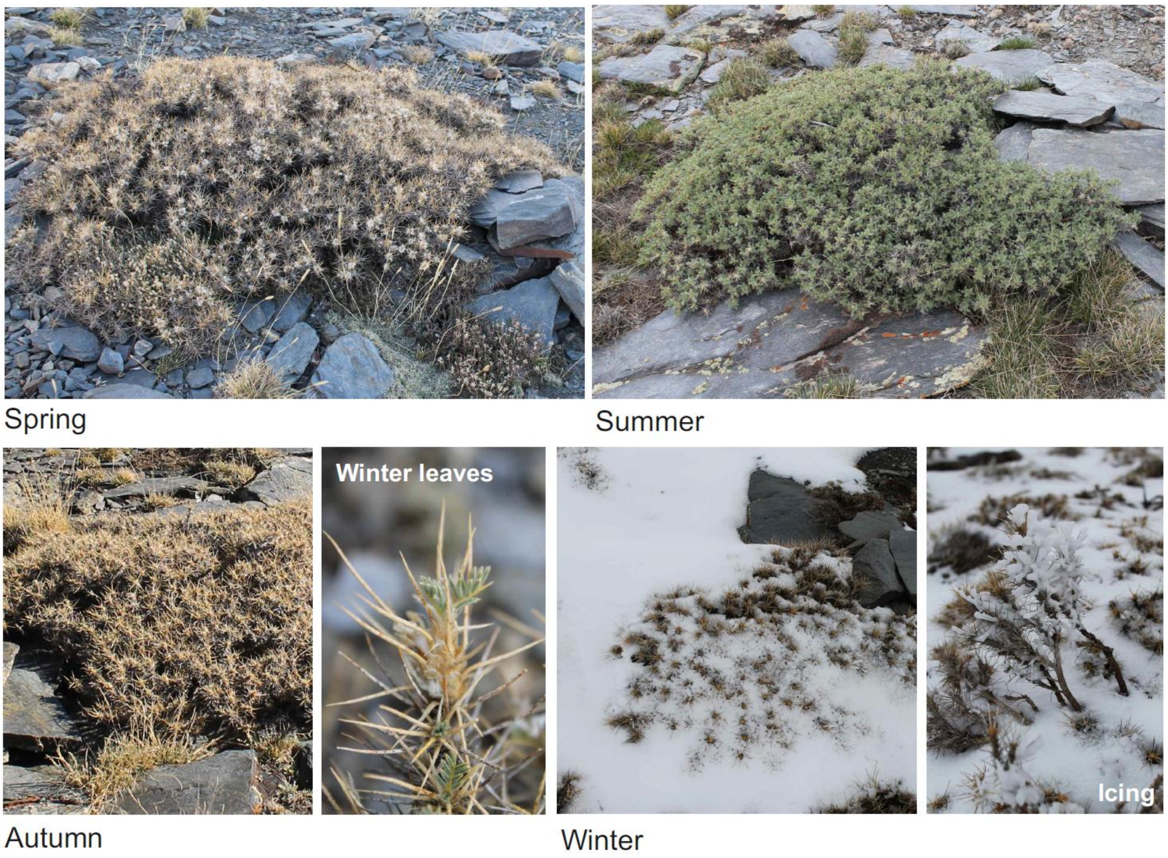

Fig. 8 Seasonal aspects of A. granatensis*. In spring, the species is leafless and at the beginning of summer its appearance is dominated by its green summer leaves (first leaf cohort), which are shed towards the end of summer. At the beginning of autumn, it appears yellowish-brown but towards the end of autumn it becomes green again when winter leaves are unfolded (second leave cohort). During winter, when the first frosts provoked leaf shedding, the species is either covered by snow (slopes) or exposed to strong winter winds, low temperatures and freezing, which in combination can lead to icing (ridges).*

A. granatensis has ring-porous to semi-ring porous wood and annual ring boundaries are distinct by marginal parenchyma bands (Fig. 9). Thick-walled vessels occur in bands or clusters, and fibers are thick- to very thick-walled. The pith is round-shaped and surrounding dimorphic cells contain dark staining substances (c.f., Crivellaro and Schweingruber 2013). The broad radial rays can be as long as ten rows of annual rings or range from the round-shaped pith to the outer xylem boundary. Both, pith and rays contain a gel-like sap, which similar to the gum described for other species of the genus *Astragalus* (e.g., Mohammadifar et al. 2006, Gorji et al. 2014, Kaya et al. 2016, Devecioğlu and Biçer 2016) exudes when twigs, stems and roots are incised. Since the amount of sap exuding is highest at the beginning of winter, we suspect that it plays an important role in osmoregulation (e.g., Braun 1984, Blackman 1991, Boughalleb et al. 2016).

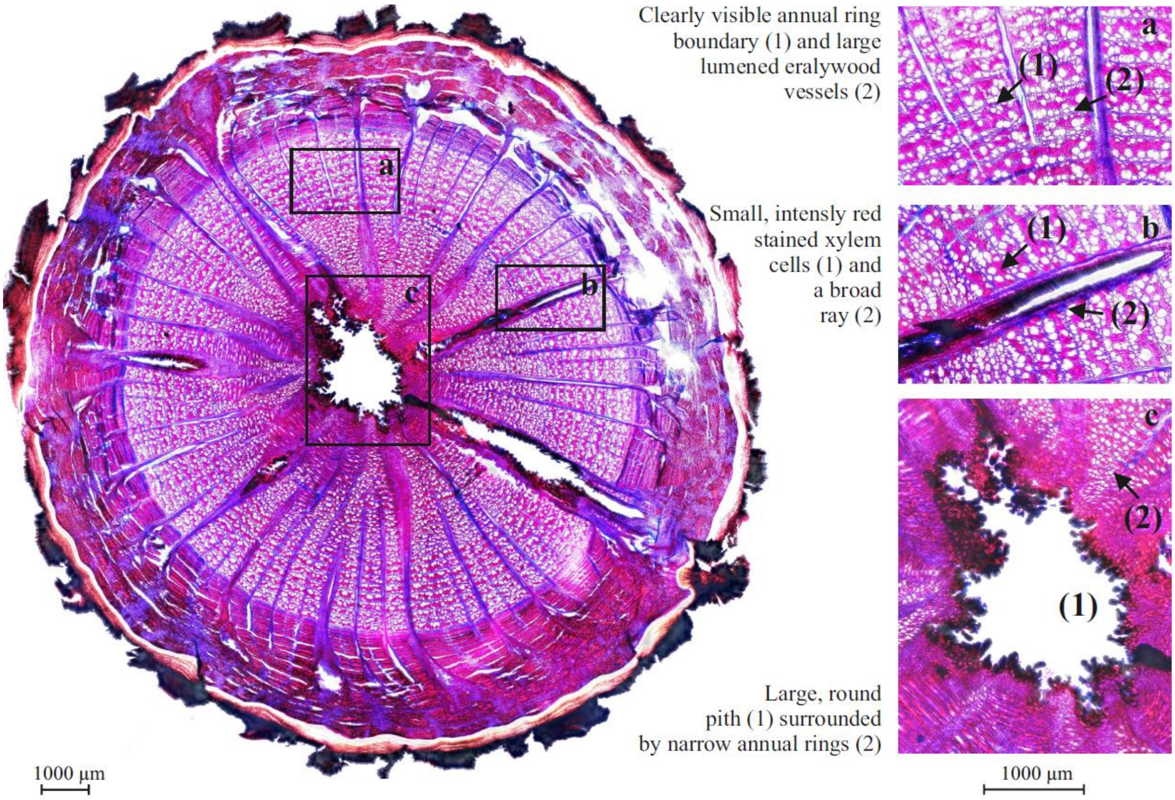

Fig. 9 Anatomical features in a stem section of A. granatensis. *The ring porous to semi-ring porous xylem is characterized by a) clearly visible ring-boundaries marked by narrow band blue-stained marginal parenchyma bands and a row of large-lumened earlywood vessels. b) The xylem consists of small red-stained thick-walled cells with single vessels, and is crossed by wide rays containing a gel like cell sap. c) The comparatively large pith is round shaped and surrounded by cells containing dark staining substances.*

6 Distribution and seasonality of alpine shrubs

The geographical distribution of our species corresponds with characteristic but complex environmental patterns, and seasonally shifting site conditions (Fig. 10). Along the elevational gradient, the dense shrub vegetation of the lower alpine environment (at 1800–2200 m a.s.l.), interspersed with individual trees and groups of *Quercus* and planted *Pinus* species, opens up and transitions into a middle alpine environment (2200–2700 m a.s.l.), dominated by a fine-meshed mosaic of scattered shrub patches, grasses, open rock and debris (Löffler et al. 2022). Above 2700 m a.s.l., vegetation gradually merges in a high-alpine environment where single low-growing shrubs co-occur with grasses in a matrix of open rock and debris (Rivas-Martínez 1981, Rivas-Martínez S., and J. Loidi, Löffler et al. 2022). In the mid-alpine environment, *Cytisus galianoi* co-occurs with *Genista versicolor* on south-facing slopes with periodic snow cover during longer winter periods (Pistón et al. 2016, Löffler et al. 2022). While *G. versicolor* is restricted to slopes, *C. galianoi* is also abundant at exposed ridge positions and in late snow beds where the patchy vegetation consists mainly of grasses and single low growing shrubs (Löffler et al. 2022). Towards higher elevations, *G. versicolor* diminishes and *C. galianoi* co-occurs with *Astragalus granatensis* (Lorite 2001), but is replaced in the latest snowbeds and at highest elevations. At the highest, most exposed ridges, where snow cover is rare and vegetation cover is patchy with open rock and debris at the surface, *A. granatnesis* remains the exclusive shrub species (Löffler et al. 2022). Alongside our three focal dwarf shrub species, we observed *Festuca clementei* being the dominant graminaceous species along the entire alpine gradient, reaching its distributional limit in the latest snowbeds and the highest, most wind-exposed hilltops (Löffler et al.

2022). This observed distributional range is far beyond the range described in literature, according to which the occurrence of *Festuca clementei* is restricted to the cryoromediterranean belt above 2700–2900 m a.s.l. (cf. Lorite 2001, Blanca et al. 2009b). Nomenclature and taxonomy of the plant species followed Blanca et al. (2009a, 2009b).

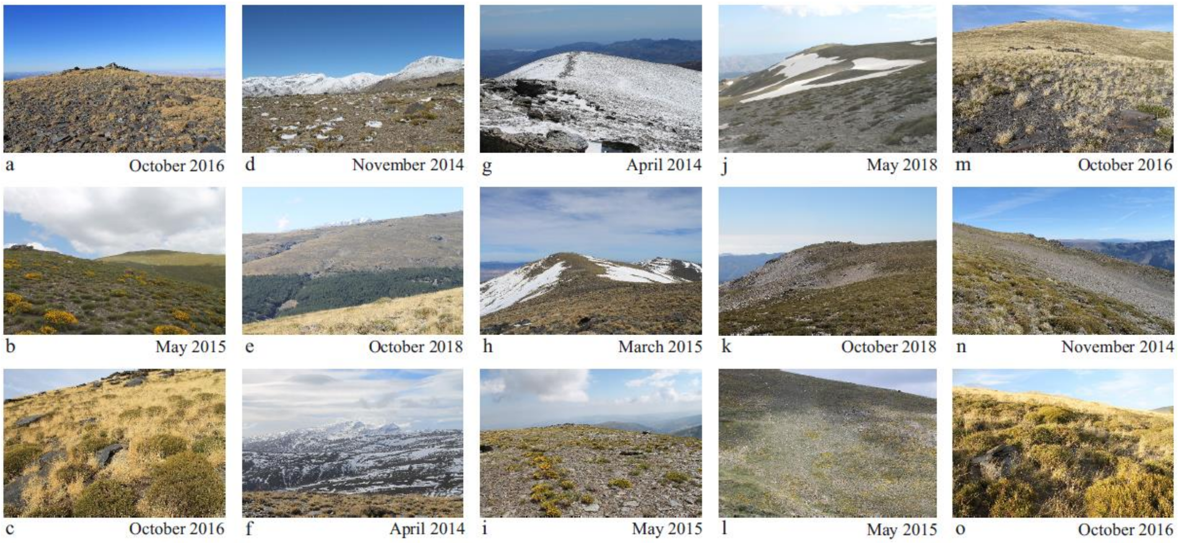

Fig. 10 Elevation and topography drive complex biogeographical patterns in our species. Vegetation cover and density increases along the elevation gradients from a) highest to b) intermediate and c) lowest elevations. During early d) winter and f) spring highest peaks usually display a complex snow pattern with decreasing intensity towards e) the treeline. Ridges are generally characterized by the absence of snow cover, causing harsh conditions also during g) April and h) March and therefore only show i) scarce vegetation cover. Aspects of snowbeds in j, l) May and k) October indicate high inter-annual climate variability. Vegetation cover changes in dependence to topography from m) hilltops and n) snowbeds with scarce cover and density to increasing density and thickness at o) slopes.

7 Shrub growth patterns

Our three studied species showed bimodal patterns of stem diameter change with high intra- and inter-annual variability, as well as pronounced differences between species and the three contrasting topographic positions (Fig. 11). By grouping and averaging our dendrometer measurements derived from individually installed dendrometers (Löffler et al. 2022), we found that changes in stem diameter of *Cytisus galianoi* during winter were characterised by moderate variability, apparently allowing early stem expansion (February) which usually peaked in May/June, suggesting that early water uptake with the resulting high turgor pressure promotes an early onset of growth processes (Albrecht et al. 2023a). Moreover, we found that both, summer and winter stem contraction were most pronounced at the ridge positions, and that *Astragalus granatensis* had a more pronounced winter stem contraction, while *C. galianoi* had more pronounced summer stem contraction, suggesting a), winter dehydration in *A. granatensis* likely to be related to frost protection and b), higher summer dehydration in *C. galianoi* likely to be linked to a more prodigal water use strategy (Albrecht et al. 2023b). Comparing patterns of stem diameter change at the slope positions, it became obvious that winter and summer stem contraction was less pronounced in *Genista versicolor*, suggesting that frost protection gets less relevant where species are protected by snow during winter, and that *G. versicolor* is well adapted to summer drought, likely by combining effective stomata control with reduced but continuous water uptake throughout the summer drought period (Albrecht et al. 2023c). Patterns of stem diameter change within snowbeds showed most pronounced differences between species, which most likely arise from highly variable snowpack distribution within the complex alpine topography (Löffler et al. 2022).

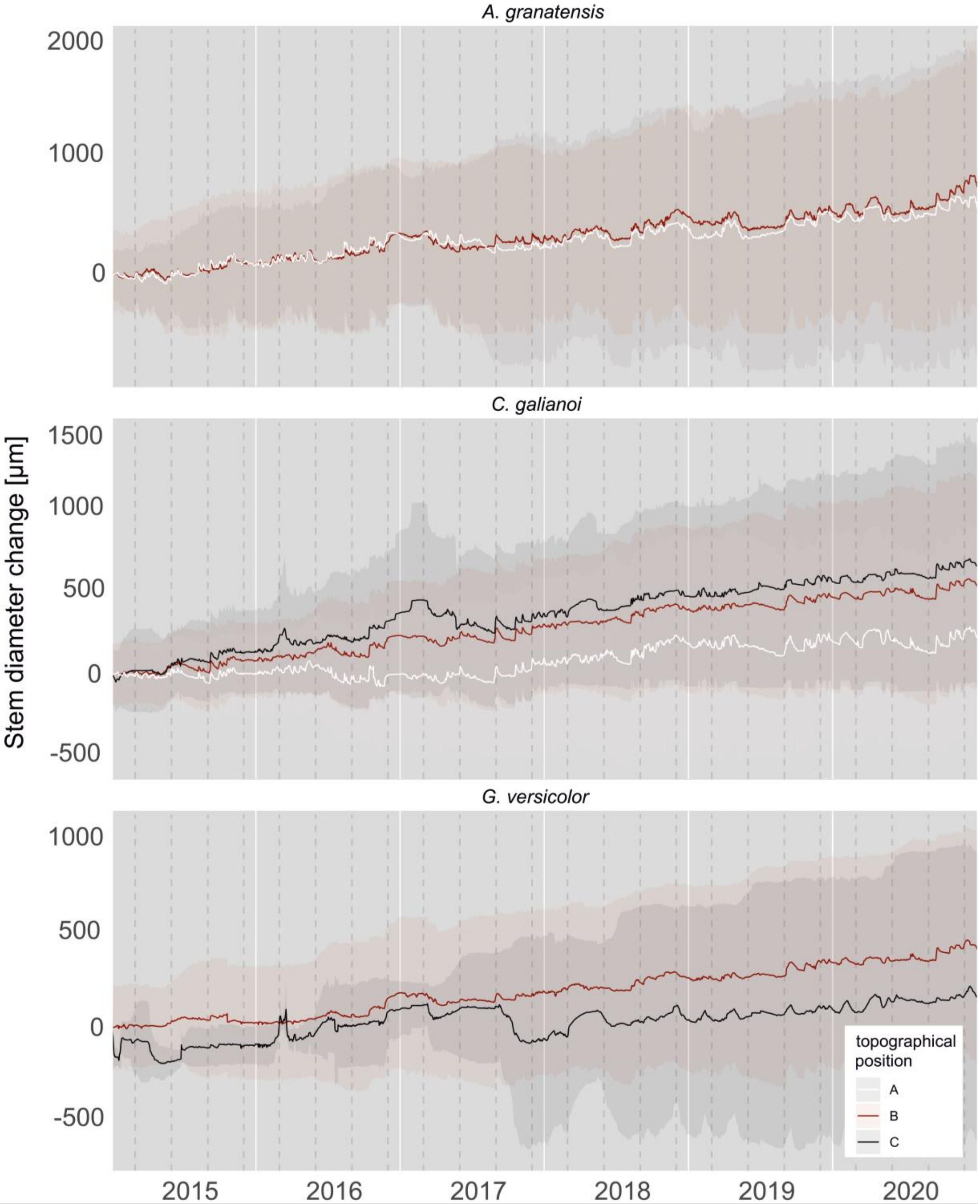

Fig. 11 Dendrometer curves representing averaged series of stem diameter change between A. granatensis, C. galianoi *and* G. versicolor *as well as between ridges (A), slopes (B) and snowbeds (C); transparency indicates standard deviation among specimens (modified after Löffler et al. 2022).*

By comparing our dendrometer measurements at the start and end of each measured year, we obtained total annual stem diameter changes shown in Figure 12 (Löffler et al. 2022). Overall, patterns of annual stem diameter change reflect the characteristic inter-annual variability of the Mediterranean climate regime and show clear differences between the contrasting topographical positions.

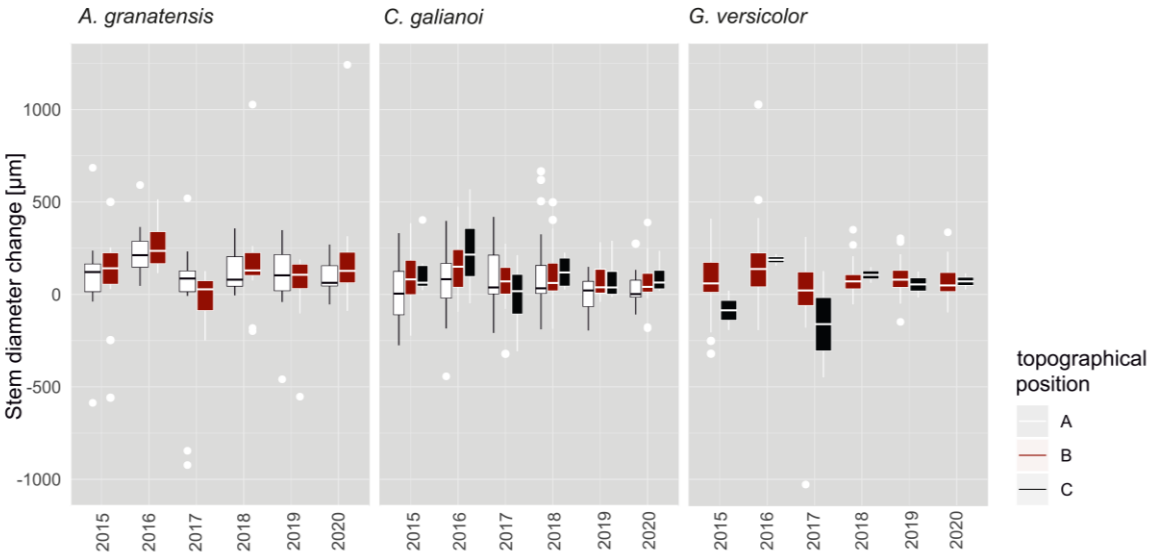

Fig. 12 Summary of annual stem diameter change (measured stem diameter at the end of the year minus measured stem diameter at the start of the year) between species as well as between ridges (A), slopes (B) and snowbeds (C) (modified after Löffler et al. 2022).

8 Complex environmental control of growth in the Mediterranean alpine shrub species *Cytisus galianoi* (Sierra Nevada, Spain)

→ Paper 1

Albrecht, E. C., S. Dobbert, R. Pape, and J. Löffler. 2023a. Unpublished Manuscript.

Author contributions

J.L. had the idea, designed the research platform, and together with E.C.A. conducted the field work and ran the long-term LTAER-ES project. S.D. wrote the statistical codes and helped with data management and figures. E.C.A. led the writing of the manuscript, analysed the data, with contributions from S.D., R.P. and J.L. This manuscript is exclusively part of only this dissertation (E.C.A.).

Abstract

Mediterranean alpine plant species are exposed to harsh environments and are required to perform with well adapted physiological strategies to withstand the dual stressors that arise from winter cold and summer drought. Consequently, bimodal growth is thought to be the dominating strategy for plant performance, which is particularly important in the face of on-going climate change. However, this growth strategy is not yet fully understood. Here, we aimed at understanding shrub growth in a widespread species, *Cytisus galianoi*. By using long-term time series of stem diameter change obtained by dendrometers, and separating water-related fluctuations in stem diameter from irreversible stem increment, we were able to disentangle growth patterns triggered by frost and drought, and relate these drivers to the timing of growth by testing the carry-over effects assumption, which addresses resource acquisition during favourable periods often far prior to the actual growth phase. Our results helped to characterize the species´ spatio-temporal plasticity and to identify the micro-environmental drivers controlling its growth processes. As such, we show the environmental control of bimodal growth in *C. galianoi*, and highlight the importance of pre-growth environmental control, leading to pronounced carry-over effects. The combination of bimodality and overall high growth plasticity likely allows the species to cover a wide geographical range across alpine areas and over a wide range of climate conditions. As such, *C. galianoi* is probably well adapted to future climate variability by taking advantage from warmer winters, and tolerating even longer summer droughts.

Key words

Climate-growth relations, adaptation strategies, growth plasticity, bimodal growth, carry-over effects, dendrometer measurements, growth physiology, dwarf shrubs, green-stems, alpine ecology, climate change

Introduction

Repercussions of climate change on plant growth

Climate change scenarios for the Mediterranean suggest warming at a rate about 20% higher than changes in the global annual mean air temperature, with summer temperatures likely increasing more than winter temperatures (Lionello and Scarascia 2018). This will result in substantial drying and warming of the Mediterranean, especially during the warm season (Giorgi and Lionello 2008). For alpine areas, climate change has been projected to reduce annual and especially spring precipitation (Bravo et al. 2008), which may limit plant growth during the main growth phase in May/June, when precipitation has been found to promote plant growth across a broad geographical area (e.g., Touchan et al. 2014, Campelo et al. 2021). Alpine species are particularly prone to experiencing changing thermal conditions, since they are exposed to steep temperature gradients occurring over short distance (Körner 2021). They are thus able to rapidly adjust their distribution range and colonize suitable habitats (e.g., Sanz-Elorza et al. 2003, Benito et al. 2011, Olano et al. 2013). However, potential responses and adaptations of Mediterranean alpine plant species might be diverging (Magaña Ugarte et al. 2019). Warmer growing seasons might result in negative growth responses of small-stature shrubs which dominate large parts of this region. Shrub growth, which is mainly constrained by seasonal droughts (Gazol and Camarero 2012a), might be modified by further moisture limitations (Pellizzari et al. 2017). Moreover, warming has been found to constrain the physiology of Mediterranean alpine species under summer drought stress (Giménez-Benavides et al. 2018). On the other hand, earlier studies have shown accelerated growth and high resource use efficiency under higher temperatures, indicating the species´ inherent advanced physiological capacity and its ability to acclimate to a warmer environment (Yang et al. 2011). Additionally, plant growth within the alpine is constrained by winter cold, so that the predicted winter warming may enhance shrub growth by reducing thermal constraints and, consequently, lengthen the growing season (Castagneri et al. 2018), associated with positive growth responses and greening of the Mediterranean alpine (Dobbert et al. 2022a). In this context, it has been noted that the response of alpine plants to climatic variability under simultaneous temperature and drought stress is complex and that models that simply assume an upwards shift as a response to higher temperatures may fail to predict future responses to climate change (Olano et al. 2013).

Alpine plant growth

Alpine species are widespread and abundant over steep ecological gradients and exposed to a huge variety of site conditions with plant performance constraint by both, low-temperature stress rising with elevation, and drought stress declining with elevation (Pescador et al. 2015, Magaña Ugarte et al. 2019). As ubiquitists, these species should perform with well-adapted physiological strategies to withstand the variety of stressors they are exposed to, including severe summer drought in addition to winter frosts (Cavieres et al. 2000, Morales et al. 2012, Gutiérrez-Girón and Gavilán 2013). However, physiologically effective drought stress and freezing stress are assumed to be rarely fatal in alpine plants (Körner 2021). Thus, plant performance must be based on drought and frost resistance strategies, which help the species survive during the dual stress periods and allow their performance under favourable conditions (cf., Mitrakos 1980). However, such mechanisms are not yet fully understood.

In low-stature alpine shrubs, meristems are adapted to the microclimate of their immediate surroundings which allows shrub growth to be partially decoupled from the free atmosphere (Körner 2012). For example, during winter, shrub meristems are often protected by snow, limiting the risk of freezing and mechanical damage (Rixen et al. 2010), while the insulating benefits of snow pack to shrub meristems may also be detrimental when late snow melt results in a shortened growing season (Pellizzari et al. 2014, 2017). In complex alpine topography along elevational and regional climatic gradients, many plant species have been shown to be restricted to their specific ecological niche (e.g., Löffler and Pape 2020, Dobbert et al. 2021a), and alpine vegetation patterns do reflect these topographical structures (e.g., Gjærevoll 1956, Billings and Bliss 1959, Holtmeier 1971, Löffler 2007, Gazol and Camarero 2012b, Leuschner and Ellenberg 2017). Thus, growth of alpine shrubs from different environments has been shown to be not only influenced by the regional climate (e.g., Bär et al. 2008, Gazol and Camarero 2012a, Li et al. 2013), but also by the local environment which has been addressed as the major driver of shrub growth (Gazol and Camarero 2012b). In this context, plastic xylogenesis has been described as a competitive advantage under the Mediterranean climate regime (cf., Camarero et al. 2010).

Accordingly, spatio-temporal plasticity of secondary growth has generally been assumed to be of particular importance in cold and dry ecosystems (c.f., Körner 2012, Pellizzari et al. 2017, Tumajer et al. 2021b), and high plasticity has been highlighted as the advantage of enabling widespread species to colonize large areas (Ghalambor et al. 2007, McLean et al. 2014).

Bimodality in growth patterns

The Mediterranean climate promotes two distinct growth peaks separated by summer quiescence, resulting in a bimodal growth pattern which may be represented by the anatomical cell structure in tree-rings (e.g., Campelo et al. 2021, Tumajer et al. 2021a). This pattern has been associated with favourable growing conditions during spring and autumn when mild temperatures and soil-water availability enhance cambial activity (e.g., Pacheco et al. 2018). This bimodal character has been found in Mediterranean lowland species and is similarly present in alpine species (Olano et al. 2013). Additionally, such bimodal growth patterns have recently been found across biomes (Dobbert et al. 2022a). Bimodality as a growth strategy likely enables shrub species to restrict their growth to phases with favourable environmental conditions (cf., Tumajer et al. 2021a). As such, bimodality is likely to enhance plant performance in the Mediterranean alpine, where winter cold and summer drought are strongly pronounced. As cambial reactivation after a dry summer is not always observed, a facultative bimodal growth has been suggested as the best way to characterize growth patterns in the Mediterranean (Battipaglia et al. 2016, Campelo et al. 2018).

Carry-over effects

Given the pronounced bimodality, it is reasonable to assume that pre-growth conditions determine growth during the active growth phases. This especially holds true for alpine plant species which, after quiescence, are facing short windows of growth opportunities under favourable conditions. Earlier studies have shown that previous year's meteorological conditions are reflected in the morphological and physiological characteristics of current-year leaves, and acclimation to changes in light intensity even occurs over multiple growing seasons (e.g., Koike et al. 1997, Jones and Thomas 2007, Ishii and Ohsugi 2011, Sumida et al. 2018). Earlywood of tree rings also contains photo-assimilates from the previous summer and autumn as well as from the current season (Helle and Schleser 2004, Kagawa et al. 2006a, 2006b, Krepkowski et al. 2013). Presupposing that all alpine plants are able to photosynthesize at sub-zero temperatures (Pisek et al. 1967, Körner 2021) and some even during severe droughts (Attia et al. 2015), it can be assumed that evergreen/green-stemmed Mediterranean alpine shrub species exhibit such carry-over effects by seasonally preceding photosynthetic activity.

Aims and Objectives

The plasticity of cambial activity and the adjustment of wood formation to fluctuations in climatic conditions may be derived from continuous dendrometer measurements (e.g., Pacheco et al. 2018). Using such time series derived from high resolution dendrometer measurements, we aimed at understanding Mediterranean alpine shrub growth in a common and widespread, green-stemmed alpine shrub species *Cytisus galianoi*. By separating water-related stem diameter changes from irreversible stem increment, we aimed to disentangle bimodal growth patterns triggered by frost and drought stress, and relate these drivers to the timing of growth by testing the carry-over effects assumption. In this way, we tried to characterize the species´ spatio-temporal growth plasticity and expected to identify environmental drivers, helping to explain growth dynamics from an ecophysiological perspective.

Material and Methods

Studied species

In this study, we focused on the dwarf shrub species *Cytisus galianoi* Talavera & Gibbs (hereafter *C. galianoi*) (Fig. S1) (taxonomy and nomenclature after Blanca et al. 2009a). *C. galianoi* is a long-living, cushion-forming chamaephyte (Melendo et al. 2003, Giménez et al. 2004, Podlech 2008) belonging to the Fabaceae family. It is an N-fixing species (Macek et al. 2016), and forms only a few small leaves during anthesis (May/June) (Talavera and Gibbs 1997, Blanca et al. 2009a). The elasticity of the above-ground biomass allows for drought resistance (cf., Patakas and Noitsakis 1999), and its green stems allow for year-round photosynthesis (cf. Bossard and Rejmanek 1992). The species is abundant in the Sierra Nevada mountain range (Spain) and endemic to the south of the Iberian Peninsula (Melendo et al. 2003, Giménez et al. 2004).

Study sites and specimens

Our focal species colonizes a broad spectrum of sites along the alpine elevational gradient up to 3200 m a.s.l. within the Mediterranean biome (Fig. S1). Accordingly, specimens are exposed to the overarching climate signal of the Mediterranean region characterized by hot and dry conditions during summer, and cool and humid conditions in autumn, winter, and spring (Roberts et al. 2011, Anderson et al. 2011, Jiménez-Moreno and Anderson 2012). The Sierra Nevada mountain range reaches its highest peak at 3479 m a.s.l. (Mulhacén) (Herrero and Polo 2016), encompassing a variety of Mediterranean alpine ecosystems (Gómez-Ortiz 2019) and forming an “island” of alpine climate and snow (Herrero and Polo 2016). Here, the growing seasons are comparatively short and plants are exposed to cold winters, high solar radiation, strong winds, and snowfall (Valle 2003). In combination with the complex alpine topography (cf., Löffler 2007) these conditions affect the spatial distribution of *C. galianoi*. Our focal species dominates the vegetation of the middle-alpine environment between 2200 and 2700 m a.s.l. (Löffler et al. 2022) and forms scattered shrub patches at exposed ridges within a matrix of open rocks, debris, and *Festuca clementei* Boiss. (Blanca et al. 2009b) that remains the dominant graminaceous species here. Above 2700 m a.s.l., where vegetation is more and more transitioning into a high-alpine environment (Löffler et al. 2022), *C. galianoi* disappears from latest snow beds.

For our long-term monitoring, we stratified-randomly selected 29 sites, following our long-term project on alpine ecosystem research (LTAER-ES; e.g., Löffler et al. 2021, Löffler et al. 2022). These sites represent the spatial variety of different environmental conditions in the area. At each site, we selected the shrub specimens to be sampled at random, with the constraint of comparable size among specimens. This approach led to a monitoring design consisting of 77 *C. galianoi* (2100 - 3175 m a.s.l.) specimens (Fig. S1) equipped with dendrometers. We recorded stem diameter changes for six full consecutive years (January 1, 2015, to December 31, 2020).

Dendrometer data and monitoring setup

To monitor radial stem diameter variations, we equipped the selected specimens with high-precision point dendrometers (type DRO; Ecomatik, Dachau/Germany), using sensors with a temperature coefficient of <0.2 µm/K which recorded data at 1 minute intervals. The dendrometers were mounted on a T-shaped aluminium bar, carefully attached to the selected stems with a UV-resistant rubber band to provide a preferably stationary system horizontally above the ground surface (approximately 1 cm above ground). To minimize the influence of hygroscopic swelling and shrinking of the bark (Zweifel and Häsler 2001), we removed the outermost layers of dead periderm (0.5 mm) at the contact point of the dendrometer pistons (cf., Dobbert et al. 2022b). Dendrometers were placed on the main stem, as close as possible to the presumed root collar, which is believed to represent the growth of the entire plant quite well (Bär et al. 2006, 2007, Ropars et al. 2017). However, the extent to which changes in radial stem diameter vary within individual specimens and between multiple stems of the same specimen has not been fully elucidated yet (Dobbert et al. 2021b). To account for this variation, we monitored a large number of specimens and ensured that selected specimens were representative of the conditions observed at each site, avoiding positions near stones and small depressions. To obtain daily mean values from our raw data set, we averaged the dendrometer data following the "daily mean approach" (Deslauriers et al. 2007). Because dendrometers measure changes in stem diameter relative to the start of the measurement cycle and not the absolute stem diameter, we normalized the annual stem diameter curves by removing the initial stem diameter, which ranged from 2358.96 µm to 10300.84 µm, from the annual curves. Finally, we checked the data for outliers, defining the interquartile range (IQR) and the 25th (Q1) and 75th (Q3) percentile (Q1/Q3 -/+ 1.5*IQR) as cut-off ranges. Since we did not find any outliers, all daily measurements per curve were retained.

Environmental conditions

To assess the drivers of the monitored radial stem diameter variations, we additionally measured micro-environmental parameters at each site and for each specimen separately using thermistors and soil moisture probes at 10 cm soil depth within the root zone of each specimen (c.f. Löffler and Pape 2020, Dobbert et al 2021b). Root zone temperatures (hereafter T_{RZ}) were recorded at 1-min intervals and stored as hourly averages using ONSET´s HOBO Loggers (type H21-002) and thermistors (type S-TMB-002) with ±0.2°C accuracy. Soil moisture conditions within the specimen’s root zone (hereafter SM_{RZ}), were measured as volumetric soil water content

(m^3/m^3) at 1-min intervals, again recorded as hourly averages, using soil moisture probes (type S-SMD-M005) with ±3% accuracy. All micro-environmental data used here were collected for the period January 1, 2015 to December 31, 2020, with additional data from 2014 used when needed. There were no missing data at the selected sites.

The mean below-ground regimes of T_{RZ} and SM_{RZ} for all monitored specimens are shown in Figs. S2 (see also Löffler et al. 2022). Consistent with the typical bimodality of the Mediterranean climate (e.g., Mitrakos 1980, Camarero et al. 2012), conditions were characterized by comparatively mild and humid conditions in spring and autumn, intermitted by harsh, cold winters with occasionally occurring frosts and periodic snow cover, and hot and dry summers with overall high solar radiation (Fig. S2).

Analysis of seasonal growth patterns

Aiming to discern the species´ seasonal growth patterns from our dendrometer curves, we defined two growth phases here, one during the first half of the year (meteorological spring) and one during the second half of the year (meteorological autumn), which are intermitted by a first phase of stem contraction during summer and a second phase during winter. This subdivision of intra-annual growth is essential, as it accounts for the bimodal rhythm of the Mediterranean climate (Mitrakos 1980). Therefore, growth-induced irreversible stem expansion (hereafter growth) was calculated semiannually. This enabled us to identify a first and a second growth phase, resulting in the total annual growth as the sum of the growth during the first and second growth phase. Mathematically, we defined growth as the cumulative maximum, or current half-year stem diameter maximum 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 is defined as equivalent to an incremental increase in stem radius when the measured radius is greater than at any point in the past (Zweifel 2016, Zweifel et al. 2021). Accordingly, growth can only take on positive values, but does not necessarily occur every year or every half year, i.e. during every growth phase. We refer to years in which there was no growth in neither the first nor the second growth phase 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. 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).

Correlation analysis and linear mixed-effects analysis

To uncover the relations between on-site environmental conditions and species’ growth patterns described above, we examined the influence of microclimate on shrub growth through correlation analysis and linear mixed-effects analysis. Using the statistical software R (R Core Team 2020), we calculated Pearson´s correlation coefficients between semi-annual irreversible stem growth and daily mean values for our environmental parameters T_{RZ} and SM_{RZ} for the years 2015 to 2020. To account for possible lagged effects of previous-year conditions on current-year growth, we included daily averages for the entire previous year 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 what was done in analyses of growth chronologies derived from ring width series (e.g., Bär et al. 2008, Weijers et al. 2018). For this purpose, we included additional micro-environmental measurements from 2014 in our calculations, i.e., measurements from before the start of our study period. To account for the variability between the observed specimens, we additionally fitted linear mixed-effects models to our data, using the lme4 R package (Bates et al. 2015). For these models, we chose semi-annual irreversible stem growth as response variable, and monthly mean values for all environmental parameters as fixed effect. The individual specimens were included as random effect.

Partial least squares regression

To complement the correlation analysis and further investigate the relationship between growth and our micro-environmental parameters we applied partial least squares regression (PLSR; Wold 1975), also known as "projection on latent structures" (Abdi 2010). With this statistical approach, we aimed to use variable selection methods to define a subset of relevant environmental conditions and their relative importance in promoting or limiting growth. PLSR, originally intended for the analysis of multidisciplinary problems (Wold 1980), has been implemented in ecological studies over the past decade (Carrascal et al. 2009, Frindte et al. 2019, Löffler and Pape 2020). Its main advantages include that it works without distributional assumptions (Wold 1980, Dijkstra 1983, Martens and Næs 1989, Vinzi et al. 2010, Frindte et al. 2019) and its applicability to data where the number of predictors exceeds the number of observations or the predictors are highly correlated, as is the case with ours. This distinguishes PLSR from classical methods such as multiple linear regression and principal component regression and makes it particularly suitable for our purposes (Geladi and Kowalski 1986, Carrascal et al. 2009, Frindte et al. 2019). In line with the approach successfully applied by Löffler and Pape (2020) to determine thermal niches of species, we aggregated our environmental data and rounded them to 0.5°C for T_{RZ} and 0.01 m^3/m^3 for SM_{RZ} values. We then counted and summed the frequency of each value occurring within the rounded time series. We performed these calculations separately for each meteorological season, yielding sets of predictor variables that we then scaled and centered. The previously calculated growth values, which turned out to be almost normally distributed, were used as associated response variable. 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. While numerous methods are available for assessing the relevance of each independent variable in the models created (overview in Mehmood et al. 2012) we found the selectivity ratio (SR) to be the most appropriate for our data (Farrés et al. 2015, Frindte et al. 2019). The SR is defined as the ratio of explained to remaining (unexplained) variance for each variable in the target projection vector. In order to achieve better contrastable results, the explained variance (SR/abs (SR +1)) was derived from the SR. The variables with the highest values represent the main explanatory variables (Rajalahti 2009). Multiplying the SR of each variable by the sign of the corresponding regression coefficient it is easy to see which variables are positively or negatively associated with the dependent variable (Rajalahti et al. 2009, Löffler and Pape 2020). In this way, we were able to clearly identify the environmental conditions that are significantly related to growth.

Linear mixed effects modelling

Finally, we aimed to explore the spatial and temporal variation in stem diameter change patterns, as well as the effects of environmental influences on this variation. Here, a modelling approach has found wide application in ecological settings in recent years to decompose the variability within grouped, complex data (Aller et al. 2019, Bolker et al. 2009, Firn et al. 2019, Henn et al. 2018, Dobbert et al. 2021a). We developed linear mixed effect models for total annual growth, as well as growth in both previously defined growth phases, which entered as response variables alongside annual stem increment (maximum stem diameter - minimum stem diameter) and the total number of growing days per year. After selecting these response variables, we grouped our data by a set of characteristics, that is, topographical position, year, and site (including both elevation and study region). Furthermore, we included the initial stem diameter at the beginning of the year, rounded to the nearest decimal, as a grouping variable. These grouping factors were included as random effects into the models. Subsequently, we investigated the percentage of variance explained by each factor, which was derived from the models using the VarCorr function (Bates et al. 2015) in R. To represent the study design within the model structure, we nested topographical position within the site parameter. The final models included no fixed effects and thus had the form Growth ~ (1 | Site/Topographical position) + (1 | Year) + (1 | Initial stem diameter) as implemented into the lmer function of the lme4 R package (Bates et al. 2015). Following this statistical exploration of spatial and temporal variability, we tested the role of microsite environmental variation within and between the grouping characteristics defined above and how this variation influenced annual growth. Here, we included seasonal means of measured environmental parameters (Tsz, Trz and SMrz) as fixed effects, creating one full model of the form Growth ~ environmental parameters + (environmental parameters | topographical position) + (environmental parameters | site) + (environmental parameters | year) + (1 | initial stem diameter), as implemented into the lmer function of the lme4 R package (Bates et al. 2015). From this model we then derived explained variance estimates (conditional, R2 c, and marginal, R2 m), as well as the partitioned variance, using the R package MuMIn (Barton 2020, Nakagawa and Schielzeth 2013). This allowed us to quantify the percentage of variance in growth, which can be explained by environmental variation between sites, years and topographical position. All environmental data were standardized (scaled by means and standard deviations) prior to model fitting to make coefficients comparable (Grace and Bollen 2005).

Results

Stem diameter changes in *C. galianoi* were of bimodal character, with the stem diameter reaching its maximum in autumn (Fig. 1). We observed pronounced variability of intra-annual and inter-annual patterns of the stem water deficit, with a generally pronounced stem contraction in summer, a less pronounced stem contraction in winter (Fig. 2), and highest growth rates in spring (April to June), co-occurring with water uptake and strongest stem expansion (Fig. 3). From the inter-annual perspective, spring growth was usually high, while autumn growth was generally of minor importance except for 2019 (Fig. 4). The strong increment in stem diameter following summer shrinkage was not mirrored by pronounced autumn growth, and only minor growth occurring after periods of summer quiescence into the winter.

As shown in figure 1, stem diameter changes in *C. galianoi* during winter suggested high water potential, which likely allowed early stem expansion as soon as February. This expansion indicated water uptake happening from DOY 100, associated with high water potential and high turgor pressure. Subsequent stem contraction after DOY 160, associated with continuously decreasing water potential and turgor pressure, and culminated at DOY 220. During autumn, pronounced continuous stem expansion started with the first rains after severe drought, and continued throughout the entire autumn season, implying stem rehydration (Fig. 2).

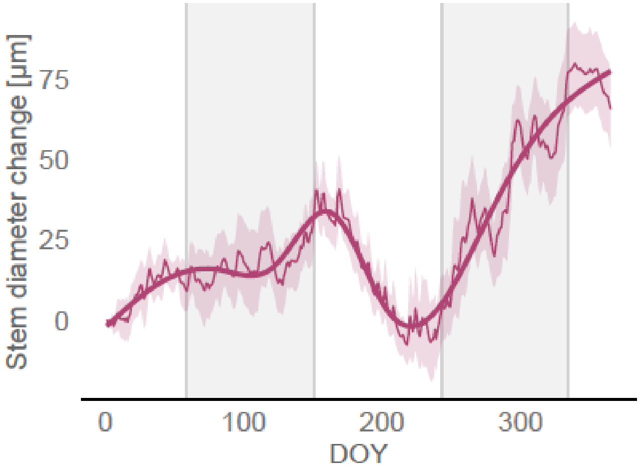

Fig. 1 Seasonal pattern of stem diameter change during the course of one year averaged over the studied period 2015 – 2020 and represented by generalized additive models (GAMs). White/grey background represents the different seasons.

Throughout the year, we found a clear synchronicity between the stem water deficit and the SM_{RZ} curves (Fig. 2). During periods of intense droughts (usually from June to August), the stem water deficit continuously rose to its maximum (at the end of August). During the following autumn months, shorter drought spells were accompanied by less severe but well pronounced stem water deficit, frequently interrupted by single precipitation events. Deeply frozen ground during single winters (2014/15, 2017/18, 2018/19) lead to low available SM_{RZ}, which was also accompanied by pronounced stem water deficits, and even single freeze-thaw cycles were visible in the stem water deficit curve. As an exception from the rule, frost-independent winter droughts (2015/16, 2019/2020) co-occurred with low water deficits. Overall, stem water deficit was low during the generally humid winters (Fig. 2).

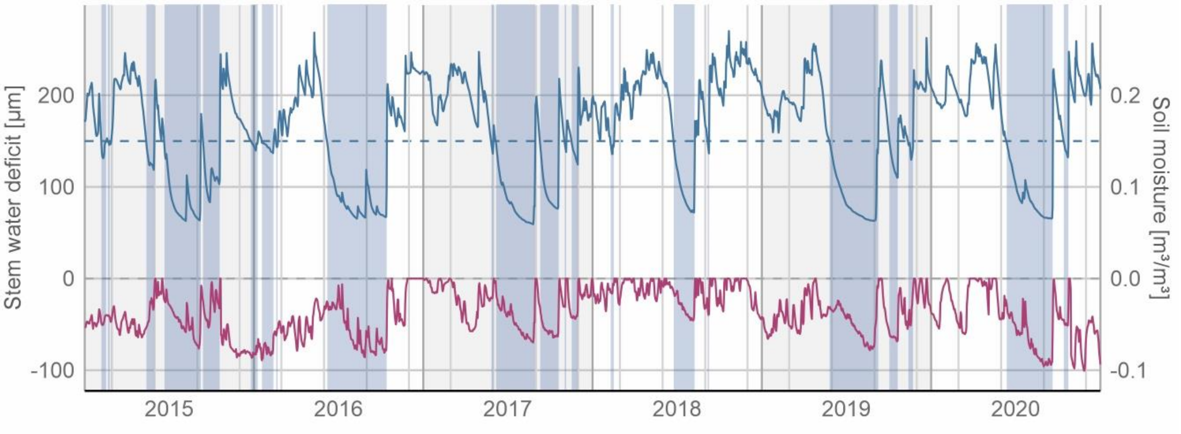

Fig. 2 Seasonal pattern of averaged stem water deficit over all positions (lower red curve) related to minimum, average, and maximum soil moisture (upper blue curve). Summer and winter drought periods were defined as SM_{RZ} *< 0.15 m³/m³ (vertical light blue bands).*

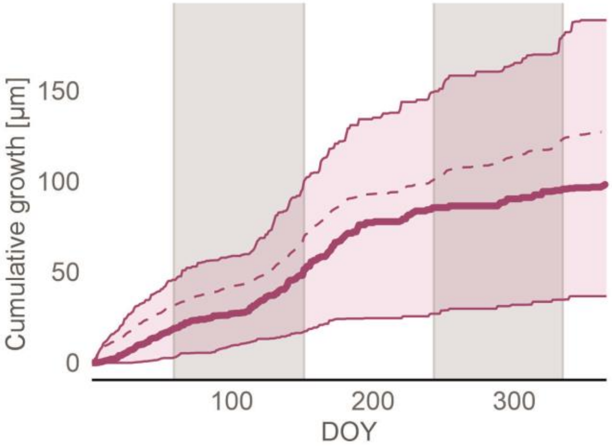

Fig. 3 Cumulative curve of stem diameter change (growth) in C. galianoi, *shown as median (solid line), average (dashed line) and the 25% and 75% quartiles (shaded) for the years 2015 – 2020.*

As shown in figures 4 and S2, spring growth rates were highest in 2015 following a late short winter with severe frost in January and February, but lowest in 2019 after a long, dry, and mild winter with a short late frost spell. Furthermore, autumn growth was highest in 2016 and 2018, when summer was followed by a continuous humid autumn. Our time-series data of stem diameter changes in combination with the timing of growth show high variability of growth patterns between the individual specimens (Fig. S3). These growth patterns varied inter- and intra-annually, and there were several environmental constraints that coincided with different patterns in growth timing (Figs. S2, S4). Growth onset in spring usually coincided with thawing soils in February/March. It was delayed after severe winter frosts followed by early spring drought (2015, 2016, 2019), but occurred early after humid winters characterized by high SM_{RZ} in early spring (2017, 2018). Growth resumption after summer drought usually occurred in September/October, well after the first autumn rains in August. It was delayed by severe drought spells in autumn (September) in combination with a long summer drought (e.g., 2019). Immediate growth resumption, however, occurred after a short summer drought combined with an early onset of humid conditions (August) (e.g., 2018).

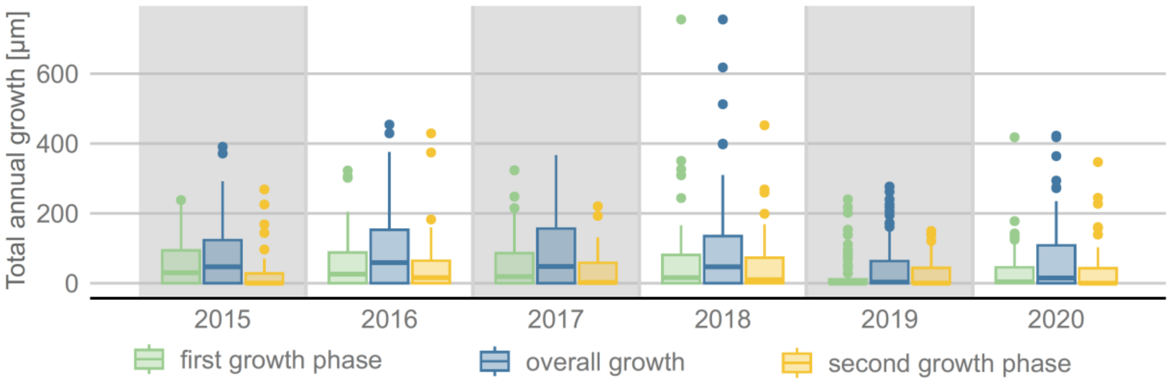

Fig. 4 Boxplot showing the distribution of total annual growth as well as growth during the first and the second growth phases in C. galianoi.

Our PLSR results for both growth phases and all positions (Fig. 5) showed that growth of *C. galianoi* was promoted by comparatively mild temperature thresholds during the previous year's winter (winter T_{RZ} 2°C for the first growth phase, and winter T_{RZ} 4°C for the second growth phase). In the second growth phase, growth was additionally promoted by mild conditions during the pre-growth summer (T_{RZ} 10-18°C). Overall, growth of *C. galianoi* was promoted by relatively warm conditions (spring T_{RZ} of 6-14°C for the first growth phase and autumn T_{RZ} of 9°C for the second growth phase). There was hardly any SM_{RZ} threshold for species performance in both growth phases.

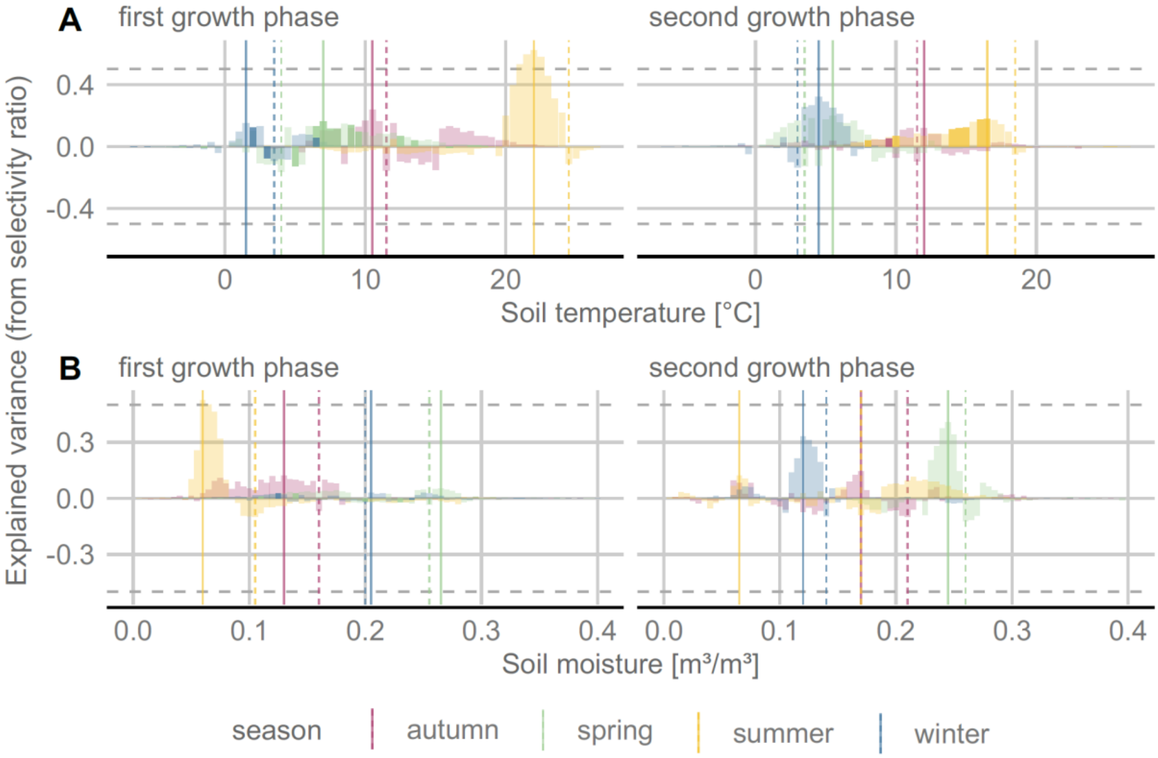

Fig. 5 Partial least squares regression (PLSR) calculated for soil temperature (T_{RZ}, A) and soil moisture (SM_{RZ}, B) for C. galianoi, *pooled for all positions and for all seasons. Colors represent seasons, with solid-color areas representing values designated as significant (p<0.05) and shaded areas representing no significance. Solid lines underline the strongest*

positive and dashed lines the strongest negative correlations, regardless of significance. For the first growth phase, the analysis is based on pre-growth summer, autumn and winter and the current spring conditions, whereas for the second growth phase on previous winter, spring, summer, and the current autumn conditions.

Our correlation analyses and linear mixed effects models confirmed that pre-growth conditions were crucial for growth in *C. galianoi* during both growth phases (Figs. S5, S6). During the first growth phase, our species performed best when T_{RZ} was high during the previous year (March – November) and SM_{RZ} during pre-growth autumn to winter (previous year August - current year February) was low. During the winter, low T_{RZ} and low SM_{RZ} (particularly during February) were promotive. Furthermore, at the beginning (March) and at the end (May/June) of the first growth phase, low T_{RZ} and high SM_{RZ} were promotive, whereas during the middle of the first growing phase (April), high T_{RZ} and low SM_{RZ} were promotive. During the second growth phase, our species performed best when the previous year autumn to winter SM_{RZ} (previous year November – January) was low. During the middle of the first growth phase (April), low SM_{RZ}, but at the end (May/June) of the first growth phase high SM_{RZ} promoted growth. Low pre-growth spring to summer T_{RZ} (March – August) promoted autumn growth. Furthermore, during the actual second growth phase, high SM_{RZ} and low T_{RZ} in autumn (October – November) were promotive.

Linear mixed effect models revealed the relative effect of spatial and temporal variability between sites, topographical positions, and years on overall growth, with these variables, together with the initial stem diameter, accounting for up to 56% of the explained variance (Fig. 6). Despite of the highly complex topography found in the studied area, the variance in topographical position only partially explained the observed differences in growth patterns. Instead, variation in climate and environmental variation associated with the elevational gradient, as well as the overall regional climate signal reflected in the site variable, had somewhat higher explanatory power. The initial stem diameter at the start of the study period played a significant role for all growth variables, except for the second growth phase. Growth variance between the years was low in all growth variables (Fig. 6). Low variability in growth response to microsite environmental conditions during the first and the second growth phase was contrasted by relatively high variability in growth response for overall (annual) growth, with autumn SM_{RZ} and T_{RZ} being of major importance for growth variability at the sites (elevation and region) (Fig. 7). Through linear mixed effects modelling, we were able to attribute 79.83% of variance in total annual growth to temporal and spatial environmental variation (Fig. 7), leaving 20.17% of growth variance unexplained. We identified soil moisture, related to seasonal summer drought and winter soil freezing, as the strongest contributors to the variation of overall growth, and in contrast, none of these potential drivers during the single growth phases. As such, growth variance during the first growth phase was to a lesser extend explained by the variance in the environmental data (Fig. 7).

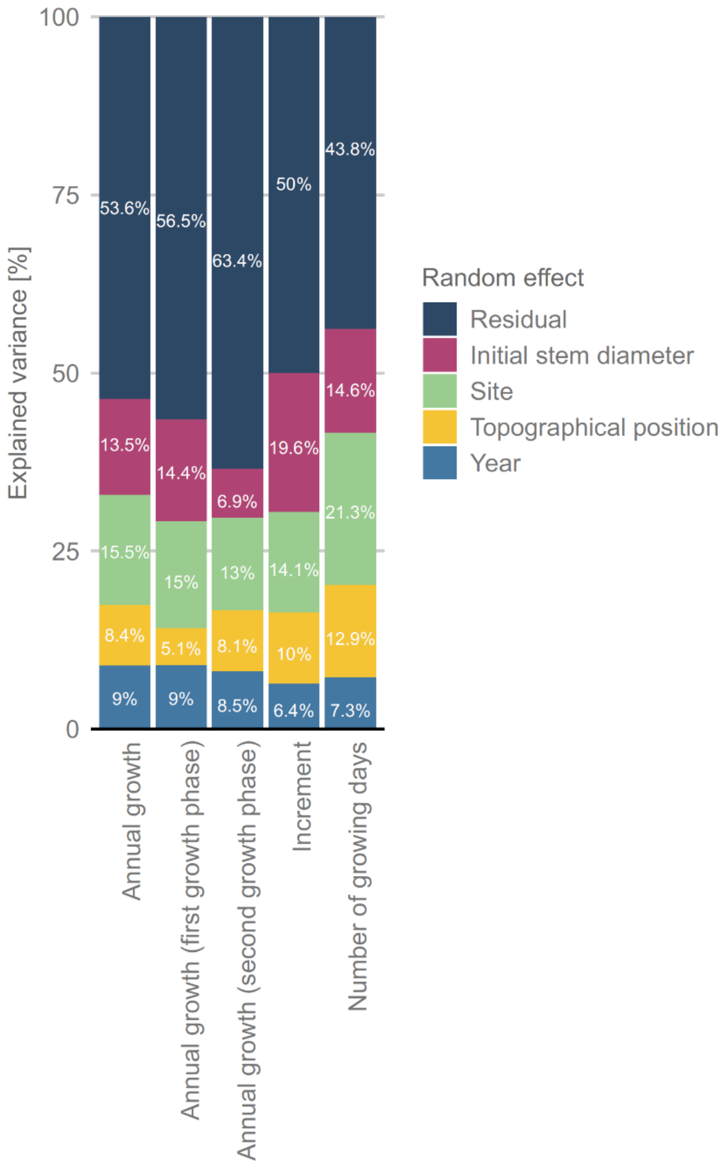

Fig. 6 Variance explained as derived from linear mixed effect models for C. galianoi. *Partitioned variance in growth parameters explained by variation in spatial and temporal grouping variables. For each growth parameter (annual growth, growth in first growth phase, growth in second growth phase, stem increment, number of growing days) one model was fitted including all data. The models included no fixed effects and thus had the form Growth ~ (1 | Site/Topographical position) + (1 | Year) + (1 | Initial stem diameter), as implemented into the lmer function of the lme4 R package (Bates et al. 2015).*

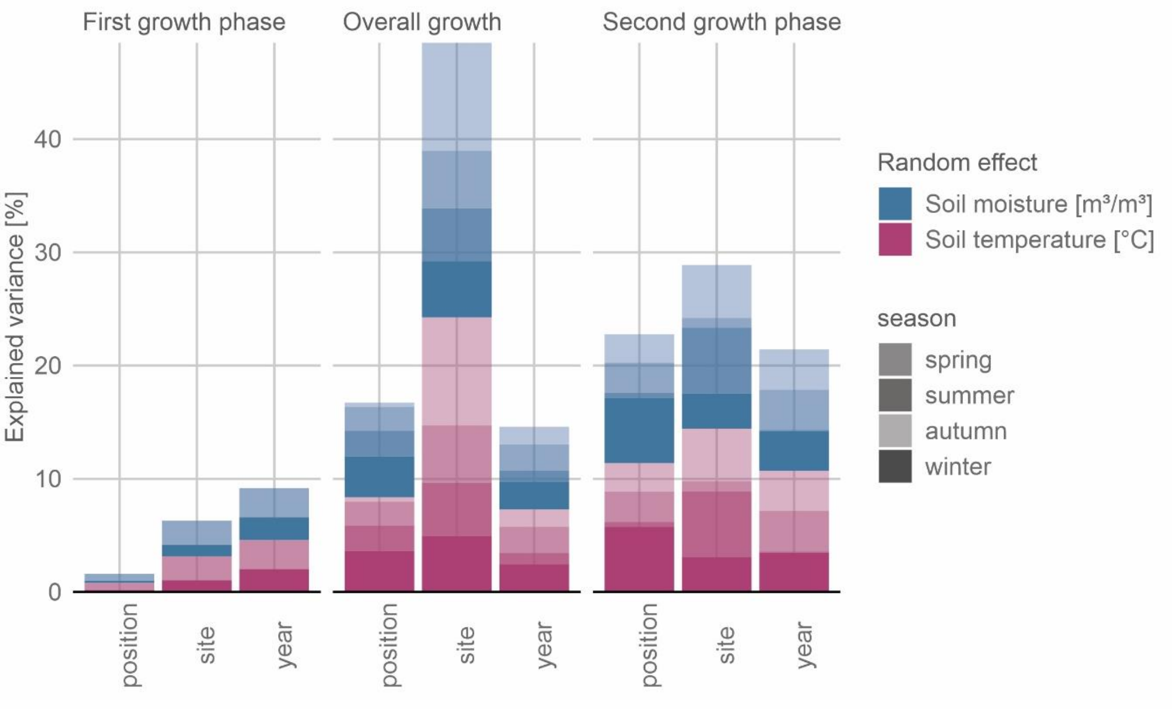

Fig. 7 Variance explained in overall annual growth, growth during the first growth phase, and growth during the second growth phase based on variation in seasonally aggregated environmental conditions (T_{RZ}, SM_{RZ}) between topographical position, site (including region and elevation) and year. All results are derived from a singular model of the form Growth ~ environmental parameters + (environmental parameters | position) + (environmental parameters | Site) + (environmental parameters | Year) + (1 | Initial stem diameter), as implemented into the lmer function of the lme4 R package (Bates et al. 2015).

Discussion

Bimodality

Growth bimodality has been reported for other shrub species (Tumajer et al. 2021a, 2021b) and has been addressed as an important factor in maintaining the ecological balance of dry Mediterranean ecosystems inhabiting stressful sites (Gazol and Camarero 2012a, Génova et al. 2013, Sánchez-Salguero and Camarero 2020, Valeriano et al. 2023). However, it has been assumed that bimodality may be limited to lowland plant growth (Magaña Ugarte et al. 2019, Szymczak et al. 2020), but as suggested by Olano et al. (2013), our results confirm recent findings of bimodal growth patterns in alpine shrubs from the Tundra and Mediterranean biome (Dobbert et al. 2022a). In *C. galianoi*, we found periods of growth quiescence driven by winter cold and summer drought, similar to growth patterns that have been observed in Mediterranean trees (Mitrakos 1980). These bimodal patterns arise from growth under favourable warm and humid conditions during spring and autumn, but reduced growth rates in summer, and short winter dormancy (Cherubini et al. 2003). In our alpine species, we found additional winter stem contraction when frozen ground occurred. Similar processes were found in arctic-alpine shrubs and interpreted as a mechanism to protect the plant from embolism under frost droughts (Dobbert et al. 2022b). At the same time, summer stem contraction was stronger than winter stem contraction, suggesting cambium activity to be possible during winter based on a higher stem water potential.

Summer stem contraction in our species was a function of drought severity. Summer drought stress has been regarded as the main constraint for plant performance and survival in the Mediterranean, and comprises the simultaneous effect of elevated temperatures, high irradiance, and water scarcity (Larcher 2000, Magaña Ugarte et al. 2019). Growth bimodality has been suggested as an adaptation enabling shrub species to withstand the dual climatic stress induced by the climatic regime (Camarero et al. 2010, Tumajer et al. 2021a).

Similar to most Mediterranean woody plants, growth in our species was highest during spring (Pellizzari et al. 2017, Alday et al. 2020, Camarero et al. 2021). Such pronounced spring growth has been related to annual ring formation during this first growth phase (Camarero et al. 2010, Valeriano et al. 2023). Furthermore, we found a pronounced water-related stem diameter increment in autumn, yet only minor growth rates during this time. Such contrasting figures of bimodality in stem diameter change and actual growth have not yet been disentangled before (Valeriano et al. 2023), and it has been questioned in earlier studies, whether autumn radial increment is actual radial growth or stem swelling due to rehydration of stem tissues after summer drought (Mäkinen et al. 2008, Zweifel et al. 2016). Our results show that both, swelling and growth, simultaneously occur, but in *C. galianoi*, post-summer rehydration is stronger than growth, likely due to its elastic cells allowing the species to tolerate severe dehydration, while maintaining high water potential (cf., Patakas and Noitsakis 1999).

We found complex environmental controls of growth during the first growth phase with high short-term variability of significant driver constellations: a) Early spring growth activity regardless of high freeze-thaw activity suggests that our species can be physiologically active down to 0°C (cf., Oribe and Kubo 1997). b) High temperatures in the middle of the first growth phase allow for maximum photosynthetic activity supported by the new leaf cohort under cloudless high-pressure weather conditions when solar radiation is heading towards solstice (cf., Starr 2001, Starr and Oberbauer 2003, Peri et al. 2011). c) Late spring with cool and humid conditions likely promotes a high water potential when plants have leaves (cf., Gucci et al. 1997, Jones 1998). The latter finding is in agreement with previous studies from the Mediterranean, which show a predominant and coherent growth response to May – June precipitation (Campelo et al. 2006, 2009, 2021, Vila et al. 2008, Gutiérrez et al. 2011, Touchan et al. 2011, 2014). During the second growth phase, humid and cool autumn conditions are likely associated with a lower risk of transpiration loss, and may allow for constant high turgor pressure in the plants.

Spring and autumn precipitation have been identified as drivers for growth (de Luis et al. 2007, 2009, Touchan 2012, Pellizzari et al. 2017), making soil water available and thus reactivating the cambium (e.g., Campelo et al. 2018, Alday et al. 2020, Tumajer 2021a). Therefore, it has generally been assumed that bimodal growth is triggered by climatic drivers (Camarero et al. 2010, Vieira et al. 2013, Pacheco et al. 2016, 2018, Campelo et al. 2021, Tumajer et al. 2021a, Valeriano et al. 2023), but the extent to which it depends on these climate drivers or rather on plant internal processes (i.e., de Micco et al. 2016) is unclear. Our results confirm the environmental control of bimodal growth in *C. galianoi*, but critically highlight the importance of pre-growth environmental control, especially winter conditions for major spring growth. We assume that our alpine species adapts to frost and drought taking advantage from evergreen stems for photosynthetic activity under extreme temperatures, while reducing transpiration loss (Bossard and Rejmanek 1992). Resources accumulated during pre-growth assimilation likely lead to carry-over effects, helping the plant to perform even under unfavourable conditions during the active growth phase, facilitated by the ability to store and mobilize carbohydrates (cf., Palacio et al. 2007) in order to decouple growth from carbon uptake (cf., Iwasa and Kubo 1997, Wyka 1999, Meloche and Diggle 2003). Even for the minor autumn growth, pre-growth_conditions were of major importance. Growth was likely promoted by long-term storage of assimilates from both, cloudless high-pressure winters during the previous year (cf., Wyka and Oleksyn 2014), and mild pre-growth summers (cf., Attia et al. 2015). Overall, our study suggests, that at least for our alpine species, the concept of bimodality needs to be rethought, and common assumptions on the actuality of driver – growth relations have to be used with caution.

Plasticity

The variance of site and position had the highest explanatory power on the variance in the number of growing days in our linear mixed effects models, suggesting environmental adjustment of the length of growth along the elevational and/or snow-cover gradients. Previous studies have shown such adjustments in alpine shrubs (Dobbert et al. 2021a) and trees (Royce and Barbour 2001, Linares et al. 2012, Kraus et al. 2016). However, the role of growth length and growth rate for total growth remains uncertain.

The variance of the initial stem diameter had the highest explanatory power on the variance of stem increment in our study. The high elasticity of stem cells, which may shrink upon water loss while maintaining high turgor (cf., Patakas and Noitsakis 1999) might indicate elastic stems at variable stem diameters, and thus potentially for all ages. This specific trait is of physiological advantage under the dual climatic stress in the Mediterranean alpine (Tumajer et al. 2021a). The variance of the initial stem diameter had a very low explanatory power on the variance of growth during the second growth phase, which may be again explained as to the influence of autumn conditions on xylogenesis being episodic and dependent on site and climate conditions (Camarero et al. 2010, Valeriano et al. 2023), and as such indicate a high plasticity of autumn growth. In turn, the variance of the initial stem diameter had a higher explanatory power on the variance of growth during the first growth phase, suggesting that the species may profit from larger stems and overall stature, when water supply is sufficient. The role of plant size and potential growth rate in affecting productivity under stress are not well resolved (Blum 1997), and size per se is unlikely to be the cause of the higher explained variance during spring. Difference in plant size may be associated with the difference in its surface-volume ratio, which should lead to differential water availability and thus, to differences in resource allocation (Bloom et al. 1995, Zotz et al. 2001).

The temporal, inter-annual variance (“year”, Fig. 6) had the lowest explanatory power of all our random effects on the variance in growth. This suggests that high year-to-year variability of climatic constraints for growth in *C. galianoi* is followed by adjusted growth responses, i.e. in the timing and magnitude of growth sustaining the general bimodal growth and stress-coping strategies. Such a temporal plasticity associated with high climatic variability has been attributed to the Mediterranean climate, where the pace of secondary growth must be adjusted to a broad array of climatic conditions (Camarero et al. 2010).

The variance of position and site had also minor explanatory power for the growth variance. This was in contrast to similar studies of arctic-alpine shrub species, which showed stronger spatial coupling of growth patterns to their ecological niches (Löffler and Pape 2020, Dobbert et al. 2021a). The emergent growth patterns of our species from a huge variation of different sites along multiple geographical gradients suggest bimodality with major spring growth and long-term carry-over effects to be a successful strategy in the entire Mediterranean alpine. Such strong adaptation to the spatial heterogeneity can be attributed as spatial plasticity to environmental variance, as has been elaborated in previous studies (Pacheco et al. 2018, Tumajer et al. 2021b, Valeriano et al. 2023).

Conclusion

The combined strategies of bimodality and adaptation to the environment by relocating the assimilation phase to periods with harmless (i.e., low) transpiration losses together with its high growth plasticity likely allows *C. galianoi* to exist over a wide geographical range in the Mediterranean alpine and over a wide range of temporal fluctuations of the weather and climate regime. As such, *C. galianoi* is probably well adapted to future climate variability by taking advantage from warmer winters, and tolerating even longer summer droughts.

Data Availability

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

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Literature Cited

Abdi, H. 2010. Partial least squares regression and projection on latent structure regression (PLSRegression). WIREs Computational Statistics 2:97–106.

Alday, J. G., J. J. Camarero, J. Revilla, and V. Resco de Dios. 2020. Similar diurnal, seasonal and annual rhythms in radial root expansion across two coexisting Mediterranean oak species. Tree Physiology 40:956–968.

Aller, A. E., J. S. Eklöf, M. Gullström, U. Kloiber, H. W. Linderholm, and L. M Nordlund. 2019. Temporal variability of a protected multispecific tropical seagrass meadow in response to environmental change. Environmental Monitoring and Assessment 191(12):774.

Anderson, R. S., G. Jiménez-Moreno, J. S. Carrión, and C. Pérez-Martínez. 2011. Postglacial history of alpine vegetation, fire, and climate from Laguna de Río Seco, Sierra Navada, southern Spain. Quaternary Science Reviews 30:1615–1629.

Attia, Z., J. C. Domec, R. Oren, D. A. Way, and M. Moshelion. 2015. Growth and physiological responses of isohydric and anisohydric poplars to drought. Journal of Experimental Botany 66:4373–4381.

Bär, A., A. Bräuning, and J. Löffler. 2006. Dendroecology of dwarf shrubs in the high mountains of Norway – A methodological approach. Dendrochronologia 24:17–27.

Bär, A., A. Bräuning, and J. Löffler. 2007. Ring-width chronologies of the alpine dwarf shrub *Empetrum hermaphroditum* from the Norwegian mountains. IAWA Journal 28:325–338.

Bär, A., R. Pape, A. Bräuning, and J. Löffler. 2008. Growth-ring variations of dwarf shrubs reflect regional climate signals in alpine environments rather than topoclimatic differences. Journal of Biogeography 35:625–636.

Barton, K. 2020. MuMIn: Multi-model inference. (https://CRAN.R-project.org/package=MuMIn).

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Battipaglia, G., V. DeMicco, W. A. Brand, M. Saurer, G. Aronne, P. Linke, and P. Cherubini 2013. Drought impact on water use eciency and intra-annual density fluctuations in Erica arborea on Elba (Italy). Plant, Cell & Environment 37:382–391.

Benito, B., J. Lorite, and J. Peñas. 2011. Simulating potential effects of climatic warming on altitudinal patterns of key species in Mediterranean-alpine ecosystems. Climatic Change 108:471–483.

Billings, W. D., and L. C. Bliss, L. 1959. An alpine snowbank environment and its effects on vegetation, plant development, and productivity. Ecology 40:388–397.

Blanca, G., B. Cabezudo, M. Cueto, C. Fernández López, C. Morales Torres. 2009a. Flora Vascular de Andalucía Oriental. Consejería de Medio Ambiente. Junta de Andalucía 2:334–356.

Blanca, G., B. Cabezudo, M. Cueto, C. Fernández López and C. Morales Torres. 2009b. Flora Vascular de Andalucía Oriental. Consejería de Medio Ambiente. Junta de Andalucía 1:306.

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

Blum, A. 1997. Constitutive traits affecting plant performance under stress. Pages 131-135 *in* G. O. Edmeades, M. Banziger, H. R. Mickelson, and C. B. Pena-Valdivia, editors. Developing drought- and low N-tolerant maize. Proceedings of a Symposium, El Batan, 25–29 Mar 1996. Mexico, DF (Mexico). Cimmyt.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M. H. H. Stevens, and J. -S. -S. White. 2009. Generalized linear mixed models: A practical guide for ecology and evolution. Trends in Ecology and Evolution 24:127–135.

Bossard, C. C., and M. Rejmanek. 1992. Why have green stems? Functional Ecology 6:197–205.

Bravo, D. N., M. B. Araújo, T. Lasanta, and J. I. L. Moreno. 2008. Climate change in Mediterranean mountains during the 21st century. Ambio 37:280–285.

Camarero, J. J., J. M. Olano and A. Parras. 2010. Plastic bimodal xylogenesis in conifers from continental Mediterranean climates. New Phytologist 185:471–480.

Camarero, J. J., J. M. Olano, S. J. A. Alfaro, B. Fernández-Marín, J. M. Becerril, and J. I. García-Plazaola. 2012. Photoprotection mechanisms in Quercus ilex under contrasting climatic conditions. Flora-Morphology, Distribution, Functional Ecology of Plants 207:557–564.

Camarero, J. J., C. Valeriano, A. Gazol, M. Colangelo, and R. Sánchez-Salguero. 2021. Climate differently impacts the growth of coexisting trees and shrubs under semi-arid mediterranean conditions. Forests 12:381.

Campelo, F., C. Nabais, H. Freitas, E. Gutiérrez. 2006. Climatic significance of tree-ring width and intra-annual density fluctuations in *Pinus pinea* from a dry Mediterranean area in Portugal. Annals of Forest Science 64:229–238.

Campelo, F., C. Nabais, I. García-González, P. Cherubini, E. Gutiérrez, and H. Freitas. 2009. Dendrochronology of *Quercus ilex* L. and its potential use for climate reconstruction in the Mediterranean region. Canadian Journal of Forest Research 39:2486–2493.

Campelo, F., E. Gutiérrez, M. Ribas, R. Sánchez-Salguero, C. Nabais, and J. J. Camarero. 2018. The facultative bimodal growth pattern in *Quercus ilex* – a simple model to predict sub-seasonal and inter-annual growth. Dendrochronologia, 49:77–88.

Campelo, F., M. Ribas, and E. Gutiérrez. 2021. Plastic bimodal growth in a Mediterranean mixed-forest of *Quercus ilex* and *Pinus halepensis*. Dendrochronologia 67:125836.

Carrascal, L. M., I. Galván, and O. Gordo. 2009. Partial least squares regression as an alternative to current regression methods used in ecology. Oikos 118:681–690.

Castagneri, D., G. Battipaglia, G. v. Arx, A. Pacheco, and M. Carrer. 2018. Tree-ring anatomy and carbon isotope ratio show both direct and legacy effects of climate on bimodal xylem formation in *Pinus pinea*. Tree Physiology 38:1098–1109.

Cavieres L, A. Peñaloza, and M. Arroyo. 2000. Altitudinal vegetation belts in the high-Andes of Central Chile (33°S). Revista Chilena de Historia Natural 73:331–344.

Cherubini, P., B. L. Gartner, R. Tognetti, O. U. Bräker, W. Schoch, and J. L. Innes. 2003. Identification, measurement and interpretation of tree rings in woody species from Mediterranean climates. Biological Reviews 78:119–148.

de Jong, S. 1993. SIMPLS: an alternative approach to partial least squares regression. Chemometrics and Intelligent Laboratory Systems 18:251–263.

de Luis, M., J. Gričar, K. Čufar, and J. Raventós. 2007. Seasonal dynamics of wood formation in *Pinus halepensis* from dry and semi-arid ecosystems in Spain. IAWA Journal 28:389–404.

de Luis, M., K. Novak, K. Čufar, and J. Raventós. 2009. Size mediated climate–growth relationships in *Pinus halepensis* and *Pinus pinea*. Trees, 23:1065–1073.

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

Deslauriers, A., S. Rossi, and T. Anfodillo. 2007. Dendrometer and intra-annual tree growth: what kind of information can be inferred? Dendrochronologia 25:113–124.

Dijkstra, T. 1983. Some comments on maximum likelihood and partial least squares methods. Journal of Econometrics 22:67–90.

Dobbert, S., E. C. Albrecht, R. Pape, and J. Löffler. 2022a. Alpine shrub growth follows bimodal seasonal patterns across biomes–unexpected environmental controls. Communications Biology 5:1–12.

Dobbert, S., R. Pape, and J. Löffler. 2021a. How does spatial heterogeneity affect inter-and intraspecific growth patterns in tundra shrubs? Journal of Ecology 109:4115–4131.

Dobbert, S., R. Pape, and J. Löffler. 2021b. Contrasting growth response of evergreen and deciduous arctic-alpine shrub species to climate variability. Ecosphere 12(8):e03688.

Dobbert, S., R. Pape, and J. Löffler. 2022b. The application of dendrometers to alpine dwarf shrubs–a case study to investigate stem growth responses to environmental conditions. Biogeosciences 19:1933–1958.

Farrés, M., S. Platikanov, S. Tsakovski, and R. Tauler. 2015. Comparison of the variable importance in projection (VIP) and of the selectivity ratio (SR) methods for variable selection and interpretation. Journal of Chemometrics 29:528–536.

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

Frindte, K., R. Pape, K. Werner, J. Löffler, and C. Knief. 2019. Temperature and soil moisture control microbial community composition in an arctic-alpine ecosystem along elevational and micro-topographic gradients. ISME Journal 13:2031–2043.

Gazol, A., and J. J. Camarero. 2012a. Mediterranean dwarf shrubs and coexisting trees present different radial-growth synchronies and responses to climate. Plant Ecology 213:1687–1698.

Gazol, A., and J. J. Camarero. 2012b. The performance of Mediterranean subshrubs depends more on microsite than on regional climate conditions. Journal of Vegetation Science 23:1062–1070.

Geladi, P., and B. R. Kowalski. 1986. Partial leastsquares regression: a tutorial. Analytica Chimica Acta 185:1–17.

Génova, M., J. Sánchez-Espejo, F. Domínguez-Lozano, J. C. Moreno-Saiz. 2013. Dendrochronological study of the endangered shrub *Vella pseudocytisus* subsp. *paui* (Brassicaceae): implications for its recovery and conservation. Anales del Jardín Botánico de Madrid 70:178–186.

Ghalambor, C. K., J. K. McKay, S. P. Carroll, and D. N. Reznick. 2007. Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. Functional Ecology 21:394–407.

Giménez, E., M. Melendo, F. Valle, F. Gómez-Mercado, and E. Cano. 2004. Endemic flora biodiversity in the south of the Iberian Peninsula: altitudinal distribution, life forms and dispersal modes. Biodiversity and Conservation 13:2641–2660.

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

Giorgi, F. and Lionello, P. 2008. Climate change projections for the Mediterranean region. Glob. Planet. Change 63, 90–104.

Gjærevoll, O. 1956. The plant communities of the Scandinavian alpine snow-beds. Det Kunglige Norske videnskabers selskaps skrifter 1:1–405.

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

Grace, J. B., and K. A. Bollen. 2005. Interpreting the results from multiple regression and structural equation models. Bulletin of the Ecological Society of America 86:283–295.

Gucci, R., L. Lombardini, and M. Tattini. 1997. Analysis of leaf water relations in leaves of two olive (*Olea europaea*) cultivars differing in tolerance to salinity. Tree Physiology 17:13–21.

Gutiérrez, E., F. Campelo, J. J. Camarero, M. Ribas, E. Muntán, C. Nabais, and H. Freitas. 2011. Climate controls act at different scales on the seasonal pattern of *Quercus ilex* L. stem radial increments in NE Spain. Trees 25:637–646.

Gutiérrez-Girón A, and R.G. Gavilán. 2013. Plant functional strategies and environmental constraints in Mediterranean high mountain grasslands in central Spain. Plant Ecology and Diversity 6:435–446.

Helle G., G. H. Schleser. 2004. Beyond CO_2-fixation by Rubisco – an interpretation of $^{13}C/^{12}C$ variations in tree rings from novel intra-seasonal studies on broad-leaf trees. Plant, Cell and Environment 27:367–380.

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

Herrero, J., and M. J. Polo. 2016. Evaposublimation from the snow in the Mediterranean mountains of Sierra Nevada (Spain). The Cryosphere 10:2981–2998.

Holtmeier, F. K. 1971. Der Einfluss der orographischen Situation auf die Windverhältnisse im Spiegel der Vegetation dargestellt an Beispielen aus dem Val Maroz (Bergell), aus dem Oberengadin und vom Pru del Vent (Puschlav). Erdkunde 25:178–195.

Ishii, H., and Y. Ohsugi. 2011. Light acclimation potential and carry-over effects vary among three evergreen tree species with contrasting patterns of leaf emergence and maturation. Tree Physiology 31:819–830.

Iwasa, Y., and T. Kubo.1997. Optimal size of storage for recovery after unpredictable disturbances. Evolutionary Ecology 11:41–65.

Jiménez-Moreno, G. and R. S. Anderson. 2012. Holocene vegetation and climate change recorded in alpine bog sediments from the Borreguiles de la Virgen, Sierra Nevada, southern Spain. Quaternary Research 77:44–53.

Jones, H. G. 1998. Stomatal control of photosynthesis and transpiration. Journal of Experimental Botany 49:387–398.

Jones, T. A. and S. C. Thomas. 2007. Leaf-level acclimation to gap formation in mature *Acer saccharum* trees. Tree Physiology 27:281–290.

Kagawa, A., A. Sugimoto, and T. C. Maximov. 2006a. $^{13}CO_2$ pulse-labelling of photoassimilates reveals carbon allocation within and between tree rings. Plant, Cell & Environment 29:1571–1584.

Kagawa, A., A. Sugimoto, and T. C. Maximov. 2006b. Seasonal course of translocation, storage and remobilization of ^{13}C pulse-labeled photoassimilate in naturally growing *Larix gmelinii* saplings. New Phytologist 171:793–804.

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

Körner, C. 2012. Treelines will be understood once the functional difference between a tree and a shrub is. Ambio 41:197–206.

Körner, C. 2021. Alpine plant life: functional plant ecology of high mountain ecosystems. Springer Nature, Cham, Switzerland.

Kraus, C., C. Zang, and A. Menzel. 2016. Elevational response in leaf and xylem phenology reveals different prolongation of growing period of common beech and Norway spruce under warming conditions in the Bavarian Alps. European Journal of Forest Research 135:1011–1023.

Krepkowski, J., A. Gebrekirstos, O. Shibistova, and A. Bräuning. 2013. Stable carbon isotope labeling reveals different carry-over effects between functional types of tropical trees in an Ethiopian mountain forest. New Phytologist 199:431–440.

Kucheryavskiy, S. 2020. mdatools – R package for chemometrics. Chemometrics and Intelligent Laboratory Systems 198:103937.

Larcher, W. 2000. Temperature stress and survival ability of Mediterranean sclerophyllous plants. Plant Biosyst 134:279–295.

Leuschner, C., and H. Ellenberg. 2017. Ecology of Central European Non-Forest Vegetation: Coastal to Alpine, Natural to Man-Made Habitats: Vegetation Ecology of Central Europe, Volume II:271–431. Springer Nature, Cham, Switzeland.

Li, Z., G. Liu, B. Fu, Q. Zhang, K. Ma, and N. Pederson. 2013. The growth-ring variations of alpine shrub *Rhododendron przewalskii* reflect regional climate signals in the alpine environment of Miyaluo Town in Western Sichuan Province, China. Acta Ecologica Sinica 33:23–31.

Linares, J. C., F. Covelo, J. A. Carreira, and J. Á. Merino. 2012. Phenological and water-use patterns underlying maximum growing season length at the highest elevations: implications under climate change. Tree Physiology 32:161–170.

Lionello, P., and L. Scarascia. 2018. The relation between climate change in the Mediterranean region and global warming. Regional Environmental Change 18:1481–1493.

Löffler, J. 2007. The influence of micro-climate, snow cover, and soil moisture on ecosystem functioning in high mountains. Journal of Geographical Sciences 17:3–19.

Löffler, J., and R. Pape. 2020. Thermal niche predictors of alpine plant species. Ecology 101:e02891.

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

Löffler, J., S. Dobbert, R. Pape, and D. Wundram. 2021. Dendrometer measurements of arctic-alpine dwarf shrubs and micro-environmental drivers of plant growth - Dataset from long-term alpine ecosystem research in central Norway. Erdkunde 75:DP311201.

Mäkinen, H., J. W. Seo, P. Nöjd, U. Schmitt, and R. Jalkanen. 2008. Seasonal dynamics of wood formation: a comparison between pinning, microcoring and dendrometer measurements. European Journal of Forest Research 127:235–245.

Macek, P., I. Prieto, J. Macková, N. Pistón, and F. I. Pugnaire. 2016. Functional plant types drive plant interactions in a Mediterranean mountain range. Frontiers in Plant Science 7:662.

Magaña Ugarte, R., A. Escudero, and R. G. Gavilán. 2019. Metabolic and physiological responses of Mediterranean high-mountain and alpine plants to combined abiotic stresses. Physiologia Plantarum 165:403–412.

Martens, H., and T. Næs. 1989. Multivariate calibration. John Wiley and Sons, Chichester, UK.

McLean, E. H., S. M. Prober, W. D. Stock, D. A. Steane, B. M. Potts, R. E. Vaillancourt, and M. Byrne. 2014. Plasticity of functional traits varies clinically along a rainfall gradient in *Eucalyptus tricarpa*. Plant, Cell and Environment 37:1440–1451.

Mehmood, T., K. H. Liland, L. Snipen, and S. Sæbø. 2012. A review of variable selection methods in Partial Least Squares Regression. Chemometrics and Intelligent Laboratory Systems 118:62–69.

Melendo, M., E. Giménez, E. Cano, F. Gómez-Mercado, and F. Valle. 2003. The endemic flora in the south of the Iberian Peninsula: taxonomic composition, biological spectrum, pollination, reproduction mode and dispersal. Flora 198:260–276.

Meloche, C. G., and P. K. Diggle. 2003. The pattern of carbon allocation supporting growth of preformed shoot primordia in *Acomastylis rossii* (Rosaceae). American Journal of Botany 90:1313–1320.

Mitrakos, K. 1980. A theory for Mediterranean plant life. Acta Oecologica, Oecologia Plantarum (France).

Morales, A. I. G. C., J. M. O. Mendoza, M. E. Gozalbo, and J. J. C. Martínez. 2012. Arboreal and prostrate conifers coexisting in Mediterranean high mountains differ in their climatic responses. Dendrochronologia 30:279–286.

Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining R2 from generalized linear mixed-effects models. Methods in Ecology and Evolution 4:133–142.

Olano, J. M., I. Almería, M. Eugenio, and G. von Arx. 2013. Under pressure: how a Mediterranean high-mountain forb coordinates growth and hydraulic xylem anatomy in response to temperature and water constraints. Functional Ecology 27:1295–1303.

Oribe, Y., and T. Kubo. 1997. Effect of heat on cambial reactivation during winter dormancy in evergreen and deciduous conifers. Tree Physiology 17:81–87.

Pacheco, A., J. J. Camarero, and M. Carrer. 2016. Linking wood anatomy and xylogenesis allows pinpointing of climate and drought influences on growth of coexisting conifers in continental Mediterranean climate. Tree Physiology 36:502–512.

Pacheco, A., J. J. Camarero, M. Ribas, A. Gazol, E. Gutierrez, and M. Carrer. 2018. Disentangling the climate-driven bimodal growth pattern in coastal and continental Mediterranean pine stands. Science of the Total Environment 615:1518–1526.

Palacio, S., M. Maestro, and G. Montserrat-Martí. 2007. Seasonal dynamics of non-structural carbohydrates in two species of Mediterranean sub-shrubs with different leaf phenology. Environmental and Experimental Botany 59:34–42.

Patakas, A., and B. Nortsakis. 1999. Mechanisms involved in diurnal changes of osmotic potential in grapevines under drought conditions. Journal of Plant Physiology 154:767–774.

Pellizzari, E., J. J. Camarero, A. Gazol, E. Granda, R. Shetti, M. Wilmking, P. Moiseev, M. Pividori, and M. Carrer. 2017. Diverging shrub and tree growth from the Polar to the Mediterranean biomes across the European continent. Global Change Biology 23:3169–3180.

Pellizzari, E., M., Pividori, and M. Carrer. 2014. Winter precipitation effect in a mid-latitude temperature-limited environment: the case of common juniper at high elevation in the Alps. Environmental Research Letters 9:104021.

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

Pescador, D. S., F. de Bello, F. Valladares, and A. Escudero. 2015. Plant trait variation along an altitudinal gradient in mediterranean high mountain grasslands: controlling the species turnover effect. PLoS One 10(3):e0118876.

Pisek A, W. Larcher, and R. Unterholzner. 1967. Kardinale Temperaturbereiche der Photosynthese und Grenztemperaturen des Lebens der Blätter verschiedener Spermatophyten. I. Temperaturminimum der Nettoassimilation, Gefrier-und Frostschadensbereiche der Blätter. Flora, Abt. B 157:239–264.

Podlech, D. 2008. The genus *Astragalus* L. (Fabaceae) in Europe with exclusion of the former Soviet Union. Feddes Repertorium 119:310–387.

R Core Team. 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

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

Rixen, C., C. Schwoerer, S. Wipf. 2010. Winter climate change at different temporal scales in *Vaccinium myrtillus*, an Arctic and alpine dwarf shrub. Polar Research 29:85–94.

Roberts, N., D. Brayshaw, C. Kuzucuolu, R. Perez, and L. Sadori. 2011. The mid-Holocene climatic transition in the Mediterranean: causes and consequences. Holocene 21:3–13.

Ropars, P., S. Angers-Blondin, M. Gagnon, I. H. Myers-Smith, E. Lévesque, and S. Boudreau. 2017. Different parts, different stories: climate sensitivity of growth is stronger in root collars vs. stems in tundra shrubs. Global Change Biology 23:3281–3291.

Royce, E. B., and M. G. Barbour 2001. Mediterranean climate effects. II. Conifer growth phenology across a Sierra Nevada ecotone. American Journal of Botany 88:919–932.

Sánchez-Salguero, R., and J. J. Camarero. 2020. Greater sensitivity to hotter droughts underlies juniper dieback and mortality in Mediterranean shrublands. Science of the Total Environment 721:137599.

Sanz-Elorza, M., E. D. Dana, A. González and E. Sobrino. 2003. Changes in the High-mountain Vegetation of the Central Iberian Peninsula as a Probable Sign of Global Warming. Annals of Botany 92:273–280.

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

Starr, G., and S. F. Oberbauer. 2003. Photosynthesis of arctic evergreens under snow: implications for tundra ecosystem carbon balance. Ecology 84:1415–1420.

Sumida, A., T. Watanabe, and T. Miyaura. 2018. Interannual variability of leaf area index of an evergreen conifer stand was affected by carry-over effects from recent climate conditions. Scientific Reports 8:1–11.

Szymczak, S., M. Häusser, E. Garel, S. Santoni, F. Huneau, I. Knerr, K. Trachte, J. Bendix, and A. Bräuning, 2020. How do Mediterranean pine trees respond to drought and precipitation events along an elevation gradient? Forests 11:758.

Talavera, S. and P. Gibbs. 1997. *Cytisus purgans* auct. (Leguminosae – Papilionoideae) comprises four distinct species. Botanical Journal of the Linnean Society 125:331–342.

Touchan, R., K. J. Anchukaitis, D. M. Meko, M. Sabir, S. Attalah, and A. Aloui. 2011. Spatiotemporal drought variability in northwestern Africa over the last nine centuries. Climate Dynamics 37:237–252.

Touchan, R., V. V. Shishov, D. M. Meko, I. Nouiri, and A. Grachev. 2012. Process based model sheds light on climate sensitivity of Mediterranean tree-ring width. Biogeosciences 9:965–972.

Touchan, R., K. J. Anchukaitis, V. V. Shishov, F. Sivrikaya, J. Attieh, M. Ketmen, J. Stephan, I. Mitsopoulos, A. Christou, and D. M. Meko. 2014. Spatial patterns of eastern Mediterranean climate influence on tree growth. Holocene 24:381–392.

Tumajer, J., V. V. Shishov, V. A. Ilyin, and J. J. Camarero. 2021a. Intra-annual growth dynamics of Mediterranean pines and junipers determines their climatic adaptability. Agricultural and Forest Meteorology 311:108685.

Tumajer, J., A. Buras, J. J. Camarero, M. Carrer, R. Shetti, M. Wilmking, J. Altman, G. Sangüesa-Barreda, and J. Lehejček. 2021b. Growing faster, longer or both? Modelling plastic response of *Juniperus communis* growth phenology to climate change. Global Ecology and Biogeography 30:2229–2244.

Valeriano, C., E. Gutiérrez, M. Colangelo, A. Gazol, R. Sánchez-Salguero, J. Tumajer, V. Shishov, J. A. Bonet, J. Martínez de Aragón, R. Ibáñez, M. Valerio, and J. J. Camarero. 2023. Seasonal precipitation and continentality drive bimodal growth in Mediterranean forests. Dendrochronologia 78:126057.

Valle, F., editor. 2003. Mapa de Series de Vegetación de Andalucía. Editorial Rueda, S.I., Madrid.

Vila, B., M. Vennetier, C. Ripert, O. Chandioux, E. Liang, F. Guibal, and F. Torre. 2008. Has global change induced divergent trends in radial growth of *Pinus sylvestris* and *Pinus halepensis* at their bioclimatic limit? The example of the Sainte-Baume forest (south-east France). Annals of Forest Science 65:709–709.

Vieira, J., S. Rossi, F. Campelo, H. Freitas, and C. Nabais. 2013. Seasonal and daily cycles of stem radial variation of *Pinus pinaster* in a drought-prone environment. Agriculture and Forest Meteorology 180:173–181.

Vinzi, E. V. 2010. Handbook of partial least squares. Concepts, methods and applications. Springer, Berlin, Germany and London, UK.

Weijers, S., N. Beckers, and J. Löffler. 2018. Recent spring warming limits near-treeline deciduous and evergreen alpine dwarf shrub growth. Ecosphere 9(6):e02328.

Wold, H. 1975. Soft modelling by latent variables: The Non-Linear Iterative Partial Least Squares (NIPALS) approach. Journal of Applied Probability 12:117–142.

Wold, H. 1980. Evaluation of econometric models. Academic Press, New York, USA.

Wold, S. 1978. Cross-validatory estimation of the number of components in factor and principal components models. Technometrics 20:397–405.

Wyka, T. 1999. Carbohydrate storage and use in an alpine population of the perennial herb *Oxytropis sericea*. Oecologia 120:198–208.

Wyka, T. P., and J. Oleksyn. 2014. Photosynthetic ecophysiology of evergreen leaves in the woody angiosperms – a review. Dendrobiology 72:3–27.

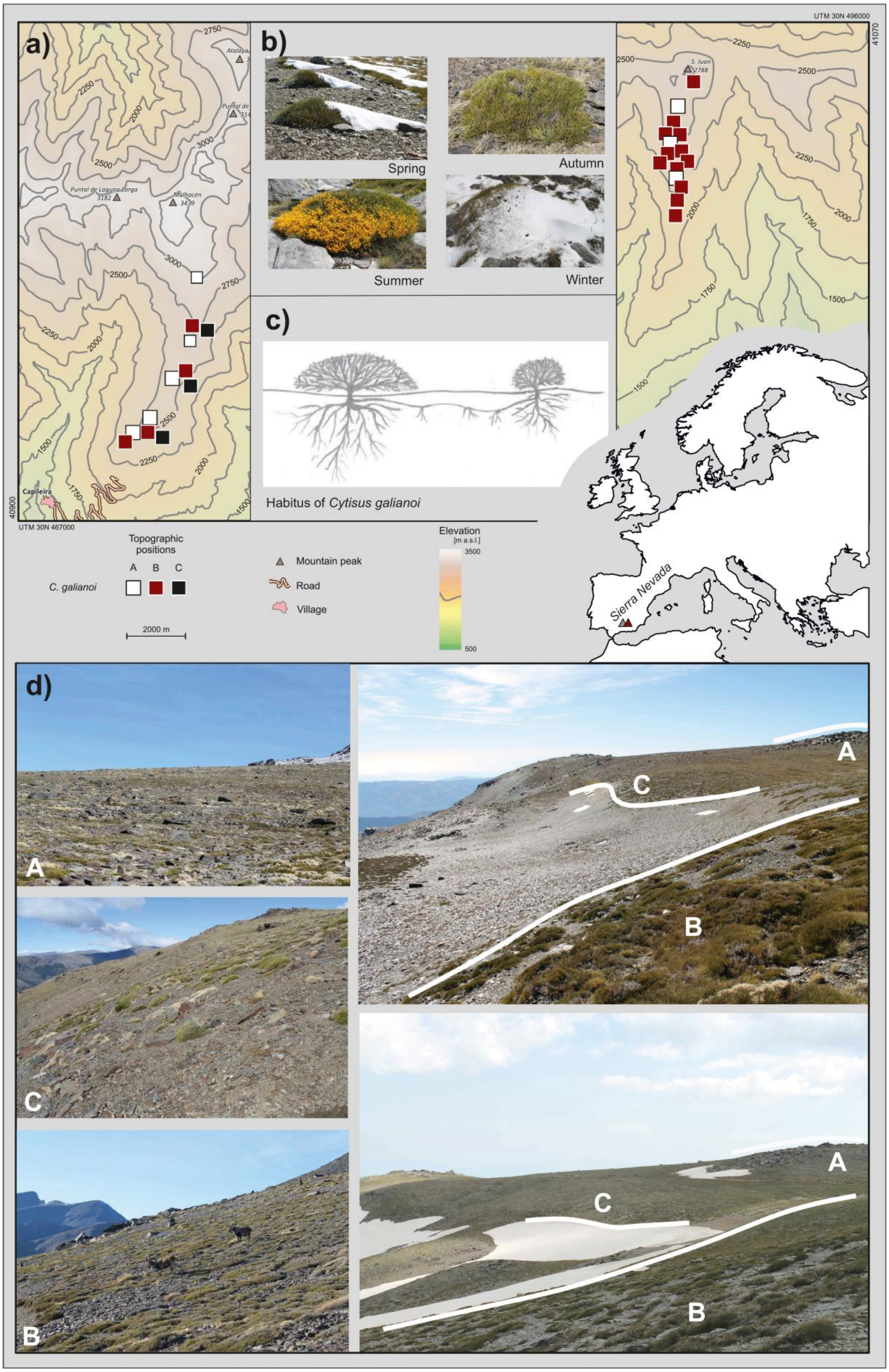
Yang, Y., G. Wang, K. Klanderud, L. Yang. 2011. Responses in leaf functional traits and resource allocation of a dominant alpine sedge (*Kobresia pygmaea*) to climate warming in the Qinghai-Tibetan plateau permafrost region. Plant and Soil 349:377–387.

Zotz, G., P. Hietz, and G. Schmidt. 2001. Small plants, large plants: the importance of plant size for the physiological ecology of vascular epiphytes. Journal of Experimental Botany 52:2051–2056.

Zweifel, R. 2016. Radial stem variations - a source of tree physiological information not fully exploited yet. Plant, Cell and Environment 39:231–232.

Zweifel, R., and R. Häsler. 2001. Dynamics of water storage in mature subalpine Picea abies: temporal and spatial patterns of change in stem radius. Tree Physiology 21:561–569.

Zweifel, R., F. Sterck, S. Braun, N. Buchmann, W. Eugster, A. Gessler, M. Häni, R. L. Peters, L. Walthert, M. Wilhelm, K. Ziemińska, and S. Etzold. 2021. Why trees grow at night. New Phytologist 231:2174–2185.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S. Juan 2788
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Mountain peak
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Village
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Fig. S1 a) Map of study area in the Sierra Nevada (Spain) and location of selected study sites, b) photos of the seasonal aspect of our focal species C. galianoi*, c) sketch of its above- and below-ground habitus, d) photos of the alpine environment showing A = ridges, B = slopes, and C = Snow beds.*

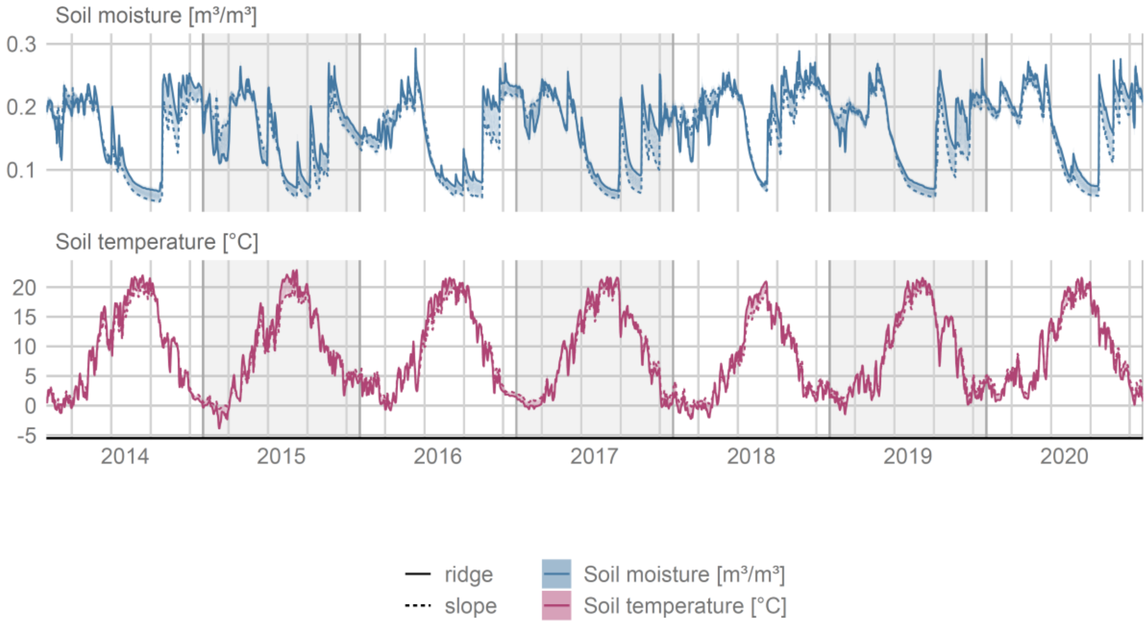

Fig. S2 Illustration of micro-environmental data. Root zone temperature (ST_{RZ}), root zone soil moisture (SM_{RZ}) regimes (daily means, derived from hourly measurements) averaged over ridge and slope sites, with shaded areas indicating standard deviation.

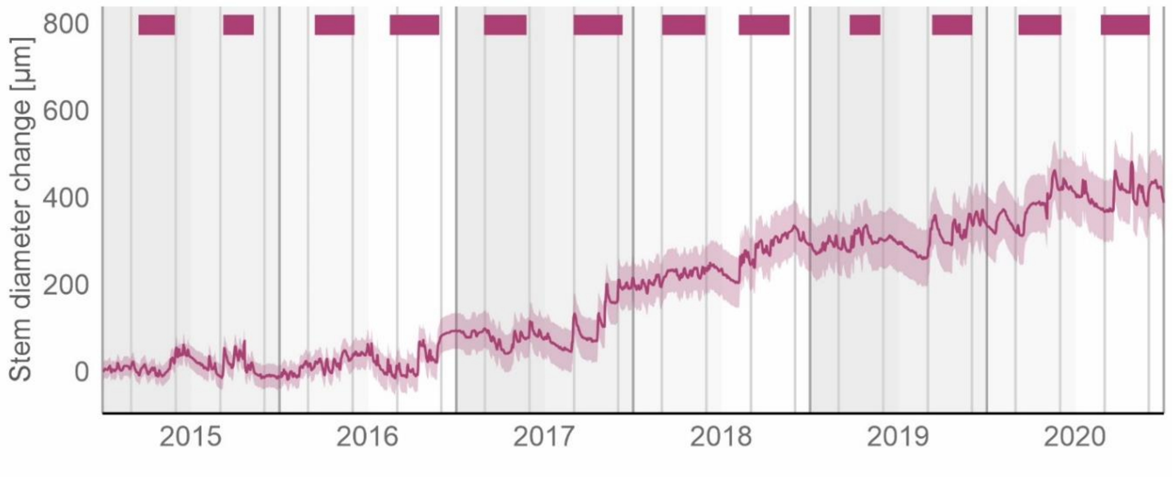

Fig. S3 Time-series of mean (solid line) and SD (shaded) stem diameter changes from all C. galianoi *specimens as derived from dendrometer measurements pooled for all positions, and phases of irreversible stem increment (growth) as shown in Fig. S4.*

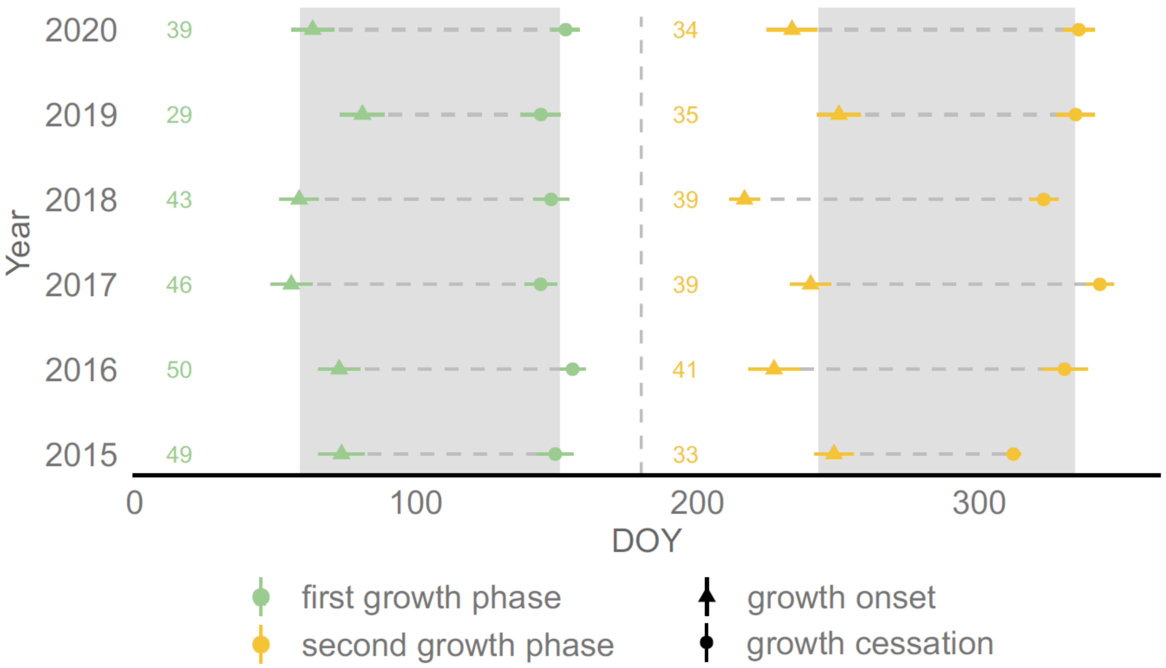

Fig. S4 Average Growth onset and cessation in C. galianoi *for the first and second growth phases in 2015 – 2020, derived from stem diameter curves and pooled for all positions, ridges and slopes. Numbers indicate the number of specimens growing.*

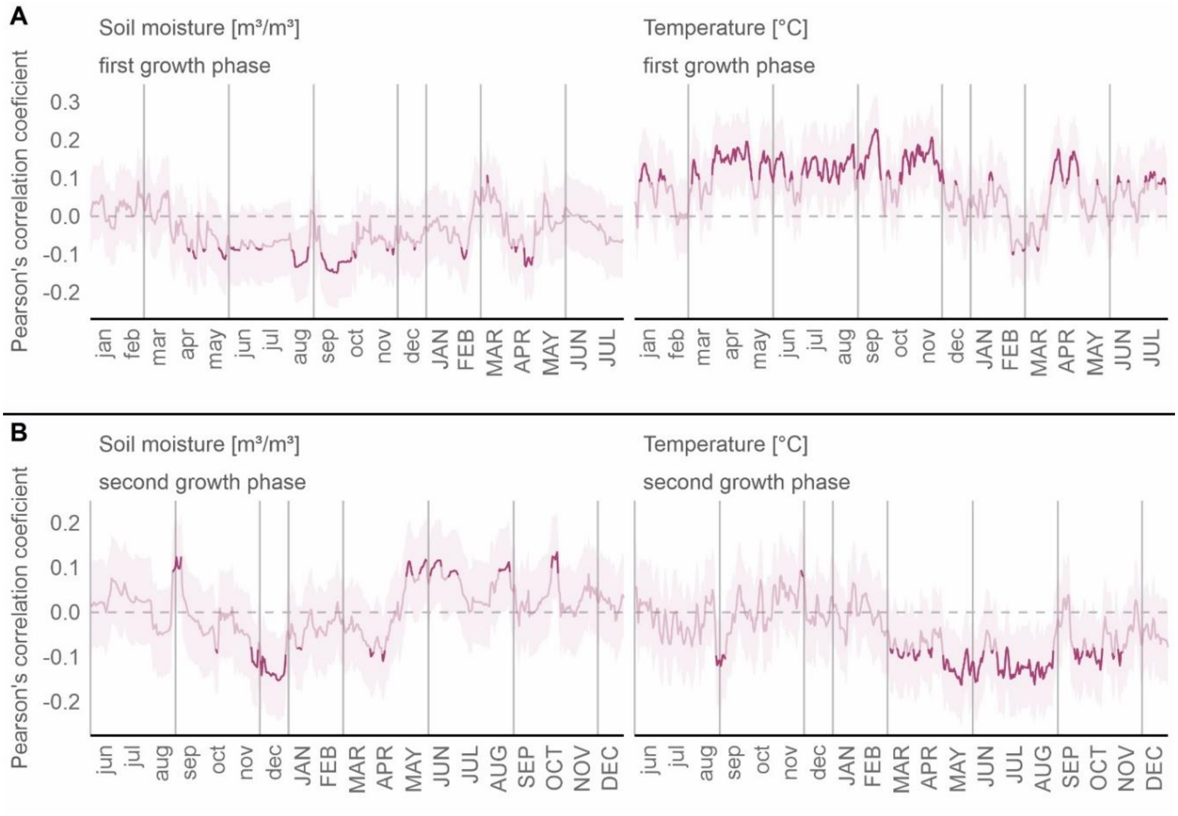

Fig. S5 Pearson's correlation coefficients calculated between first (A) and second (B) growth phase as derived from the dendrometer curves and daily soil moisture ($SM_{RZ)}$ and soil temperature ($T_{RZ)}$ data, measured at the individual sites. Transparency indicates non significance.

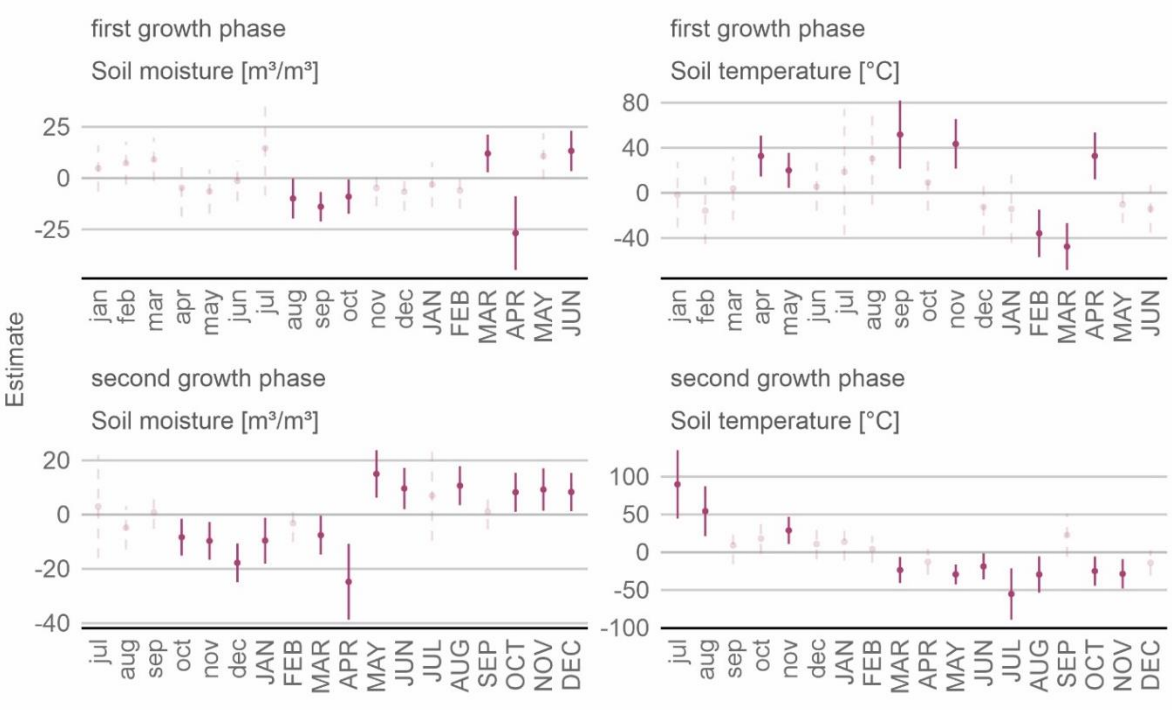

Fig. S6 Linear mixed effects analysis for growth during the first and second growth phase as derived from the dendrometer curves (dependent variable) and monthly environmental data (means) as fixed effects. Individual specimens entered as random effects. Transparency indicates non significance. Abbreviations of months from the previous year are in lowercase letters and those of the current year are given in capitals.

9 Patterns, timing, and environmental drivers of growth in two physiologically distinct (green-stemmed vs. dimorphic) Mediterranean alpine shrub species in the Sierra Nevada (Spain)

→ **Paper 2**

Albrecht, E. C., S. Dobbert, R. Pape, and J. Löffler. 2023b. Unpublished Manuscript.

Author contributions

J.L. had the idea, designed the research platform, and together with E.C.A. conducted the field work and ran the long-term LTAER-ES project. S.D. wrote the statistical codes and helped with data management and figures. E.C.A. led the writing of the manuscript, analysed the data, with contributions from S.D., R.P. and J.L. This manuscript is exclusively part of only this dissertation (E.C.A.).

Abstract

Cold-adapted alpine plant species are thought to be particularly sensitive to climate warming and are likely to be most affected in the Mediterranean biome, where their performance is, apart from winter cold, additionally constrained by summer drought. Growth in the Mediterranean is driven by a bimodal mild and humid climate, reaching its maximum during spring. Little is known about the capacity to make use of drought and frost adaptive strategies, and the critical time scale relevant for plant growth is insufficiently reflected when characterizing the environmental drivers of growth. We aimed at a better understanding of alpine shrub growth looking at two species with distinctly different traits. By separating growth from water-related stem diameter changes, we expected to identify bimodal growth patterns, with water-related timing of growth, and drought- and frost-related environmental limitations. Implementing (moving window) correlation analyses, linear mixed effects models and partial least squares regression on our time series of dendrometer-based stem diameter changes and corresponding soil temperature and soil moisture data, we found pre-growth environmental drivers to be most relevant for fitness and growth of both species, albeit with contrasting mechanisms. There was a strong temporal decoupling of the growth process from photosynthetic opportunities. In *Cytisus galianoi*, high photosynthetic rates during winter likely allow for high spring growth, while in *Astragalus granatensis*, high photosynthetic rates during short-term summer solstice likely allow for high autumn growth. As such, resource acquisition is optimized during phases when the species´ traits and growth strategies allow for physiological activity at high gain and low costs, with the result of species-specific time windows of maximum growth. Our study overall contributes to the debate on plant adaptive capacity in alpine environments under future climate variability.

Key words

Climate-growth relations, adaptation strategies, dendrometer measurements, growth physiology, *Cytisus galianoi*, *Astragalus granatensis,* dwarf shrubs, alpine ecology, climate change, ecohydrology, drought adaptive capacity, frost resistance

Introduction

Climate change is expected to affect productivity and performance of woody plants across biomes (e.g., Forbes et al. 2010, Myers-Smith et al. 2020) and to induce changes in vegetation structure with a profound impact on the global carbon cycle (e.g., Graven et al. 2013, Pan et al. 2011, Körner 2021). However, little is known about the temporal, spatial, and interspecific differences in cambium dynamics (Tumajer et al. 2021), including the seasonal heterogeneity and spatial variability of growth trends observed in the past decades (IPCC 2021). Patterns and underlying processes remain poorly understood (Gamm et al. 2018, AMAP 2021). Therefore, increasing our knowledge on plant species' adaptive capacity is critical, especially for predicting their future performance (e.g., Cotto et al. 2017, Magaña Ugarte et al. 2019). Cold-adapted alpine plant species are thought to be particularly sensitive to changing conditions (e.g., Körner 2021), and are likely to be most affected in the Mediterranean biome, where alpine plant performance is constrained by both, summer drought and winter cold (Morales et al. 2012, Pescador et al. 2015, Giménez - Benavides et al. 2018). Warmer (Giorgi and Lionello 2008, Gazol and Camarero 2012) and longer (Castagneri et al. 2018, Hanewinkel et al. 2013) growing seasons may affect the species´ performance and cause shifts in their growth patterns, thus modifying their distributional range (Bravo et al. 2008, Dobbert et al. 2022a). Analyses of spatio-temporal growth patterns and their environmental drivers may be the key to a better understanding of the species´ adaptive capacity to a warmer future climate.

Generally, growth patterns of woody plants from the Mediterranean biome depart from the unimodal growth pattern in woody plants from cold regions (e.g., Rossi et al. 2008, Treml et al. 2015). Cambium activity in the Mediterranean has been shown to be bimodal, with two growth peaks in spring and autumn separated by reduced summer growth and short winter dormancy (e.g., Castagneri et al. 2018, Pacheco et al. 2018, Alday et al. 2020, Tumajer et al. 2021). This bimodality has been interpreted as a response to the separation of favorable conditions before and after summer drought (de Luis et al. 2007, Camarero et al. 2010). Such partitioning of growth may also be present in Mediterranean alpine plants (Olano et al. 2013, Dobbert et al. 2022a). It is believed that growth in the Mediterranean is driven by mild and humid spring and autumn conditions with maximized growth during these phases (e.g., Mitrakos 1980, de Luis et al. 2009, Camarero et al. 2010, Rammig et al. 2010, García-Cervigón et al. 2012, Olano et al. 2013) and spring being the major growth period (e.g., Körner 2012, Pasho et al. 2012, Gričar et al. 2015, Pellizzari et al. 2017, Alday et al. 2020, Camarero et al. 2021).

Thermal constraints are associated with plant growth, and extreme temperatures and their timing trigger threshold responses, such as mortality (Körner 2016). Besides the period of major plant physiological activity, winter conditions such as low soil temperatures, frozen ground, and limited soil water availability, all of which mediated by snow, have been recognized to play a major role in driving vegetation patterns, plant growth and other ecosystem properties (Pauli et al. 2013, Petty et al. 2015, Choler 2018, Niittynen and Luoto 2018). Alpine plants employ different strategies to cope with frost and several frost survival mechanisms have evolved in woody alpine plants: tolerance to extracellular freezing and freeze dehydration, lifecycles that allow species to escape frost, and freeze-avoidance mechanisms (Neuner 2014). Osmoregulation is associated with cellular dehydration, helping plants to avoid frost damage, using the cold acclimation approach to deal with low temperature stress, which allows plants to survive freezing via accumulation of cryoprotective polypeptides and osmolytes (Essiamah and Eschrich 1985, Kozlowski and Pallardy 2002, Ritonga and Chen 2020). Moreover, water availability is one of the most limiting factors for plant growth (Meinzer et al. 2006, Battipaglia et al. 2014, Szymczak et al. 2020), and besides 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, while the drought avoidance strategy relies on delayed initiation of water scarcity in plant tissues, and the drought tolerance strategy is a result of coordinated physiological and biochemical alterations at the cellular and molecular levels (Chaves et al. 2003, Chen and Wang 2009). Little is known about the adaptive capacity to make use of such strategies in the Mediterranean alpine. Still, the critical time scale relevant for plant growth is insufficiently reflected when characterizing the environmental drivers of plant growth and the species' overall ecological niche (Löffler and Pape 2020).

Here, we aimed at a better understanding of alpine shrub growth by comparing two species with distinctly different traits, *C. galianoi* (green-stemmed) and *A. granatensis* (dimorphic). By separating growth from water-related stem diameter changes, we expected to find bimodal growth patterns, with water-related timing of growth, as well as drought- and frost-related environmental limitations of alpine shrub growth. In accordance with the Mediterranean climate regime, mild and humid spring and autumn conditions likely promote plant growth.

Material and Methods

Studied species

In this study, we focused on two dwarf shrub species, *Cytisus galianoi* Talavera & Gibbs (hereafter *C. galianoi*) and *Astragalus granatensis* Lam. (hereafter *A. granatensis*) (Fig. 1; taxonomy and nomenclature after Blanca et al. 2009a). Both are long-living, cushion-forming chamaephytes (Melendo et al. 2003, Giménez et al. 2004, Podlech 2008) belonging to the Fabaceae family. They are abundant across the Sierra Nevada mountain range (Spain), but differ in distribution and are of distinctly different habitus. While *C. galianoi* is endemic to the south of the Iberian Peninsula (Melendo et al. 2003, Giménez et al. 2004), *A. granatensis* is also found in the Atlas Mountains in North Africa (Molina and Izco 1986, Lorite et al. 2007, Podlech 2008). Moreover, *C. galianoi* has green stems with only a few small leaves formed during anthesis (May/June) (Talavera and Gibbs 1997, Blanca et al. 2009a), while *A. granatensis* has pubescent, paripinnate, spiny leaves (Blanca et al. 2009a), that we often observed being formed twice a year, at the beginning of summer (May/June) and at the beginning of winter (November/December). Accordingly, we here consider *C. galianoi* as a green-stemmed species with summer leaves, and *A. granatensis* as a deciduous species with summer and winter leaves, i.e. with seasonal dimorphism. Both, evergreen stems and seasonal dimorphism, have been described for many Mediterranean plant species (e.g., Liphschitz and Lev-Yadun 1986, Bossard and Rejmanek 1992, Puglielli 2019) and are regarded as adaptation strategies to the Mediterranean living conditions (e.g., Westman 1981, Christodoulakis and Fasseas 1991, Aronne and de Micco 2001, Lianopoulou et al. 2014). This probably also applies to the gel-like sap that we observed in the intracellular space of the xylem of *A. granatensis*, which, similar to the gum described for other species of the genus *Astragalus* (e.g., Mohammadifar et al. 2006, Gorji et al. 2014, Kaya et al. 2016, Devecioğlu and Biçer 2016), exudes when twigs, stems, and roots are incised. The amount of gum exuding is highest at the beginning of winter, suggesting that it plays an important role in frost protection through osmoregulation (e.g., Braun 1984, Blackman 1991, Boughalleb et al. 2016). In addition, the species xylem anatomy and hydraulic architecture (Fig. S1) provide indications on its strategy or ability to cope with drought and frost (Sperry and Tyree 1988, Sperry 1993) and also its ability to repair drought-induced embolism (Ganthaler and Mayr 2015, Brodersen and McElrone 2013).

Study sites and specimens

Our study focused on alpine sites along an extended transect (2200 – 2800 m a.s.l.) on the southern slope of the Spanish Sierra Nevada (Fig. 1) within the Mediterranean biome. These sites are characterized by the overarching climate signal of the Mediterranean region, which is determined by hot and dry conditions in summer (Roberts et al. 2011, Anderson et al. 2011, Jiménez-Moreno and Anderson 2012), and cool and humid conditions in autumn, winter, and spring (Roberts et al. 2011). The Sierra Nevada mountain range reaches its highest peak at 3479 m a.s.l. (Mulhacén) (Herrero and Polo 2016) and is characterized by alpine climate and snow (Herrero and Polo 2016), including comparatively short growing seasons, cold winters, high solar radiation, strong winds, and snowfall (Valle 2003). In combination with the complex alpine topography these conditions affect the spatial distribution of our focal species: *C. galianoi* dominates the vegetation of the middle-alpine environment between 2200 and 2700 m a.s.l. (Löffler et al. 2022). Above 2700 m a.s.l., where vegetation is more and more transitioning into a high-alpine environment (Löffler et al. 2022), *C. galianoi* disappears from latest snow beds, whereas *A. granatensis* dominates the hilltops at about 2800 m a.s.l.

We selected sites on exposed ridges only, following our long-term project on alpine ecosystem research (LTAER-ES; e.g., Löffler et al. 2021, Löffler et al. 2022). At these sites, high air temperatures (max. 25.30°C) with a high solar radiation input (max. 1153.80 W/m^2) prevail in summer, while strong winds (max. 70.00 m/s) lead to snow drifts in winter, leaving the ridges with discontinuous snow cover, leading to low temperatures and freezing soils (min. -16.10°C). Thus, our study sites represent the most extreme conditions in the area. On each of these sites, we carefully selected shrub specimens of comparable size. This approach led to a monitoring design consisting of 16 *C. galianoi* (2300 - 2700 m a.s.l.) and 10 *A. granatensis* (2700 - 2800 m a.s.l.) specimens (Fig. 1), which we monitored for six full consecutive years (January 1, 2015, to December 31, 2020).

Dendrometer data, monitoring setup and environmental data collection

To monitor radial stem diameter variations, we equipped the main stem of randomly selected 26 specimens with high-precision point dendrometers (type DRO; Ecomatik, Dachau/Germany), using sensors with a temperature coefficient of <0.2 μm/K to record data at 1-minute intervals. The dendrometers were carefully attached to the selected stems with a UV-resistant rubber band on a stationary system provided by a T-shaped aluminium bar placed horizontally above the ground surface (approximately 1 cm above ground) (Fig. 1). To minimize the influence of hygroscopic swelling and shrinking of the bark (Zweifel and Häsler 2001), we removed the outermost layers of dead periderm (0.5 mm) at the contact point of the dendrometer pistons (cf., Dobbert et al. 2022b). The dendrometers were placed as close as possible to the presumed root collar on the main stem, which is believed to at least partially represent the growth of entire plant (Bär et al. 2006, 2007, Ropars et al. 2017). However, the extent to which changes in radial stem diameter vary within individual specimens and between multiple stems of the same specimen has not been fully elucidated yet (Dobbert et al. 2021). To account for this variation, we monitored a large number of specimens and ensured that selected specimens were representative of the conditions observed at each site, avoiding positions near stones and small depressions. To obtain daily mean values from our raw data set, we averaged the 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 µm to 12948.8 µm for *A. granatensis* and from 3633.5 µm to 10240.5 µm for *C. galianoi*, from the curves. This is necessary because dendrometers measure changes in stem diameter relative to the start of the measurement cycle and not the absolute stem diameter. Finally, we checked the data for outliers, defining the interquartile range (IQR) and the 25th (Q1) and 75th (Q3) percentile (Q1/Q3 -/+ 1.5*IQR) as cut-off ranges. Since we did not find any outliers, all daily measurements per curve were retained.

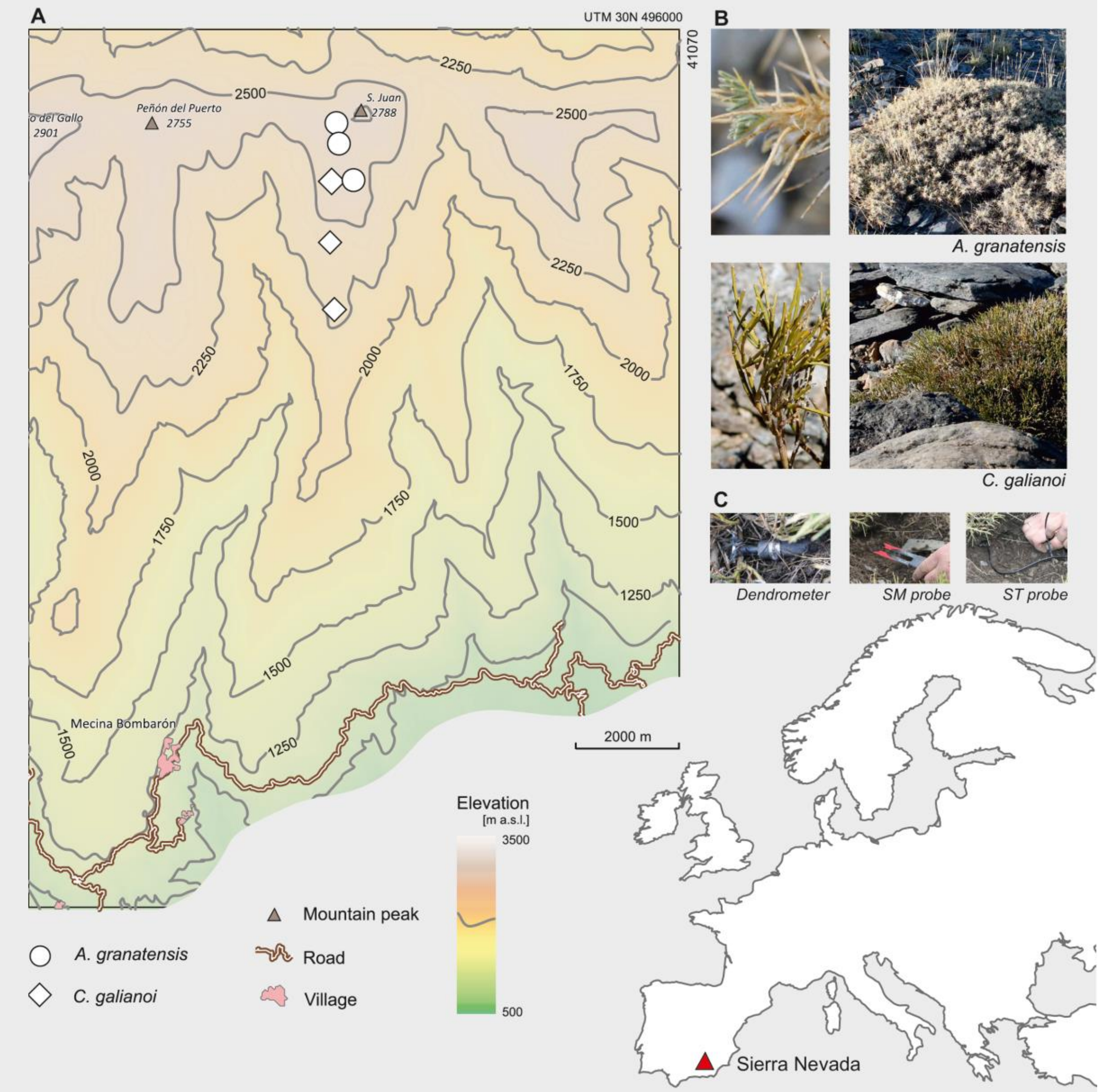

Fig. 1 Study area in the Sierra Nevada (Spain) and exact location of selected study sites (A). Photos show our two focal species A. granatensis *and* C. galianoi *(B) as well as our monitoring set up with a mounted point-dendrometer, soil moisture probe and soil temperature probe (C).*

Environmental conditions

To assess the potential drivers of the monitored radial stem diameter variations, we additionally measured micro-environmental parameters at each site and for each specimen separately. Therefore, we installed thermistors and soil moisture probes at 10 cm soil depth within the root zone of each specimen (c.f. Löffler and Pape 2020, Dobbert et al 2021). Root zone temperatures (T_{RZ}) were recorded at 1-min intervals and stored as hourly averages using ONSET´s HOBO Loggers (type H21-002) and thermistors (type S-TMB-002) with ±0.2°C accuracy. To capture soil moisture conditions within the specimen's root zone (SM_{RZ}), we measured the volumetric soil water content (m^3/m^3) at 1-min intervals, which were recorded as hourly means using soil moisture probes (type S-SMD-M005) with ±3% accuracy. Complementary, 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 ±10 W/m^2 accuracy at 1 cm above the ground surface. All micro-environmental data were collected for the period January 1, 2015 to December 31, 2020, with additional data from 2014 used as needed. There were no missing data at the selected sites.

The mean below-ground regimes of T_{RZ} and SM_{RZ} for all monitored specimens as well as the near ground GR_{SZ} regime at 2692 m a.s.l. are shown in Figs. S2, S3, S4 and in Tab. S1 (see also Löffler et al. 2022). Consistent with the typical bimodality of the Mediterranean climate (e.g., Mitrakos 1980, Camarero et al. 2012), conditions at our ridge sites were characterized by comparatively mild and humid conditions in spring and autumn, intermitted by harsh, cold winters with occasionally occurring frosts and periodic snow cover, and hot and dry summers with overall high solar radiation (Figs. S2, S3). T_{RZ} began to rise in March/April, usually exceeding 10°C in June and 20°C in July/August in most years. SM_{RZ} also started to increase in March/April in most years and reached its first peak in May (approx. 0.25 m^3/m^3). Subsequently, SM_{RZ} decreased until August, whereas autumn precipitation led to a second peek in September/October (approx. 0.20 m^3/m^3). Overall, both T_{RZ} and SM_{RZ} were slightly lower for the *A. granatensis* sites than for the *C. galianoi* sites, with lowest annual mean temperatures measured in 2018 and highest in 2017 (Tab. S1). The year 2018 stands out because of an overall short summer drought that was followed by a comparatively long and humid autumn (Fig. S2). In contrast, the autumn in 2019 was comparatively dry, but followed by a humid winter without frost. In drier winters, on the other hand, we observed severe ground frost, as evident in January/February 2015 and 2018, a phenomenon also observed at a research station at 3005 m a.s.l. in the summit area of the Sierra Nevada (Oliva et al. 2014).

Analysis of seasonal growth patterns

Aiming to discern the species´ seasonal growth patterns from our dendrometer curves, we calculated growth semiannually, defining two growth phases: one during the first half of the year (first growth phase) and one during the second half of the year (second growth phase). These phases of radial stem increment are intermitted by two phases of stem contraction, one during summer (drought period) and one during winter (cold period). This subdivision of intra-annual growth is essential, as it accounts for the bimodal rhythm of the Mediterranean climate (Mitrakos 1980), which is known to induce bimodal growth patterns in several Mediterranean lowland shrub and tree species (e.g., Camarero et al. 2010), which might also occur in Mediterranean alpine species (Olano et al. 2013). Therefore, growth-induced irreversible stem expansion (hereafter growth), was defined as the cumulative maximum, or current half-year stem diameter maximum 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 is defined as equivalent to an incremental increase in stem radius when the measured radius is greater than at any point in the past (Zweifel 2016, Zweifel et al. 2021). Accordingly, growth does not necessarily occur every year or every half year, i.e. during every growth phase. We refer to years in which there was no overall 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. At this point it is worth mentioning that since both the first and second 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).

Correlation analysis and linear mixed-effects analysis

To uncover the relations between on-site environmental conditions and species’ growth patterns described above, we conducted a correlation analysis and linear mixed-effects analysis. Using the statistical software R (R Core Team 2020), we calculated Pearson´s correlation coefficients between semi-annual irreversible stem growth and daily mean values for our environmental parameters T_{RZ} and SM_{RZ} for the years 2015 to 2020. To account for possible lagged effects of previous-year conditions on current-year growth, we included daily averages for the entire previous year 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 ring width series (e.g., Bär et al. 2008, Weijers et al. 2018). For this purpose, we included additional micro-environmental 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 semi-annual irreversible stem growth as response variable, and monthly mean values for all environmental parameters as fixed effect. The individual specimens were included as random effect to account for differences at the individual sites.

Furthermore, we aimed to uncover additional temporal patterns of climate-growth relations. Therefore, we calculated lagged moving window correlations for our two species using Pearson's correlation coefficient for each individual dendrometer curve and the corresponding environmental parameters (daily means). Here, we averaged our daily T_{RZ} and SM_{RZ} values over previous time windows ranging in length from one to 180 days and correlated these values with the measured dendrometer data. We additionally ran these correlations for moving window widths from 180 to 365 days, however, this addition provided no further information. Since we observed inter-annual variations in these patterns in our data, we performed correlations for the entire study period from 2015 to 2020. Hereby, we were able to shed light on the temporal patterns and the year-to-year variations within these patterns.

Overall, for the comparison of 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. Averages were calculated for visualization purposes only.

Partial least squares regression analysis

Finally, we applied partial least squares regression (PLSR; Wold 1975), also known as "projection on latent structures" (Abdi 2010), to our dataset to complement the correlation analysis. Here, we used variable selection methods to identify relevant environmental conditions and their relative importance promoting or limiting growth. PLSR, originally intended for the analysis of multidisciplinary problems (Wold 1980), has been implemented in ecological studies over the past decade (Carrascal et al. 2009, Frindte et al. 2019, Löffler and Pape 2020). The method is applicable to data where the number of predictors exceeds the number of observations or the predictors are highly correlated, as is the case with ours. This makes PLSR particularly suitable for our purposes (Geladi and Kowalski 1986, Carrascal et al. 2009, Frindte et al. 2019). We aggregated our environmental data and rounded them to 0.5°C for T_{RZ} and 0.01 m^3/m^3 for SM_{RZ} values (Löffler and Pape 2020). We then counted and summed the frequency of each value occurring within the rounded time series. We performed these calculations separately for each meteorological season, yielding sets of predictor variables that we then scaled and centered. The previously calculated growth values, which turned out to be almost normally distributed (Fig. S5), entered the analysis as associated response variable. 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. Numerous methods are available for assessing the relevance of each independent variable in the models created (overview in Mehmood et al. 2012). Based on assessments by Farrés et al. (2015) and Frindte et al. (2019) we found the selectivity ratio (SR), which is defined as the ratio of explained to remaining (unexplained) variance for each variable in the target projection vector, to be the most appropriate for our data.

To achieve better contrastable results, the explained variance (SR/abs (SR +1)) was derived from the SR (Rajalahti 2009). Finally, we multiplied the SR of each variable by the sign of the corresponding regression coefficient to identify which variables are positively or negatively associated with the dependent variable (Rajalahti et al. 2009, Löffler and Pape 2020). In this way, we were able to clearly identify the environmental conditions that are significantly related to annual growth.

Results

Our results reveal differences and similarities between our two distinct alpine shrub species in a) intra-annual growth patterns, b) timing of growth, and c) environmental drivers of growth.

a) Patterns of stem diameter change and growth

Overall, we observed bimodal patterns of annual stem diameter change in our two focal species with pronounced stem contraction in summer and less pronounced stem contraction in winter (Figs. 2, S6). At the same time, species-specific, intra-annual and inter-annual variability in these patterns was high. *C. galianoi* showed a stronger bimodality than *A. granatensis,* with the latter showing a right-skewed pattern of stem diameter change (Fig. 2). In *C. galianoi*, summer stem contraction usually started in May/June and continued until August/September, while in *A. granatensis*, stem contraction usually peaked at the end of June and its stem diameter increased slightly throughout the summer drought (Figs. 2, S6). Growth patterns were similarly contrasting between the two species, with *C. galianoi* achieving highest growth rates in spring, whereas *A. granatensis* achieved highest growth rates in autumn, when growth coincided with the most pronounced stem diameter increase (Figs. 2, S7, S8).

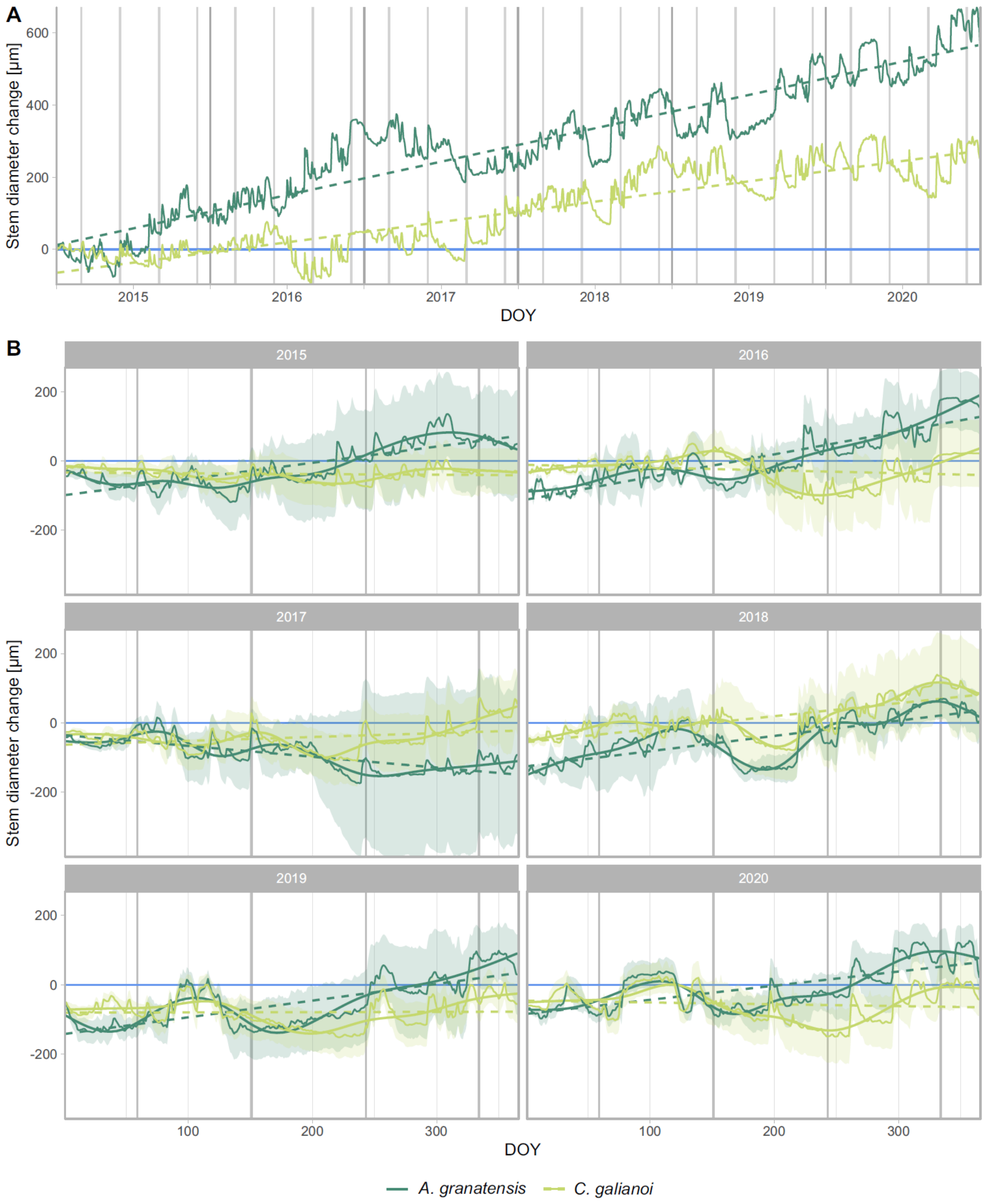

Fig. 2 Averaged stem diameter change relative to the start of the measuring period (A) and averaged annual stem diameter variations (+/- SE) relative to the previous year's maximum (B). Dashed straight lines represent linear trends and solid lines represent generalized additive splines that roughly illustrate the intra-annual growth pattern.

b) Timing of growth

Growth onset of the first growth phase in *C. galianoi* usually occurred in February/March, while in *A. granatensis*, it occurred in late March/April with high inter-annual variability (Figs. 3, Tab. S2). In both species, the onset was exceptionally delayed in individual years (2019 for *C. galianoi*, 2015 for *A. granatensis*), while it was exceptionally early in 2016 for *A. granatensis*. Cessation of the first growth phase mostly occurred by the end of May in *C. galianoi*, while it was highly variable in *A. granatensis* (mid of April to end of May). Growth onset of the second growth phase usually occurred in September/October for *C. galianoi*, and in the middle of August for *A. granatensis* (Figs. 3, Tab. S2). In *C. galianoi*, we discovered a highly variable timing of growth resumption, which was exceptionally delayed in 2016 and 2019, but occurred early in 2018 (Figs. 3, S2). Growth cessation usually occurred in November/December in both species. Overall, the inter-annual variability of the duration of the two growth phases was high, but the growth rates in both species were decoupled from the duration of the growth phases (Tab. S2, Fig. S8).

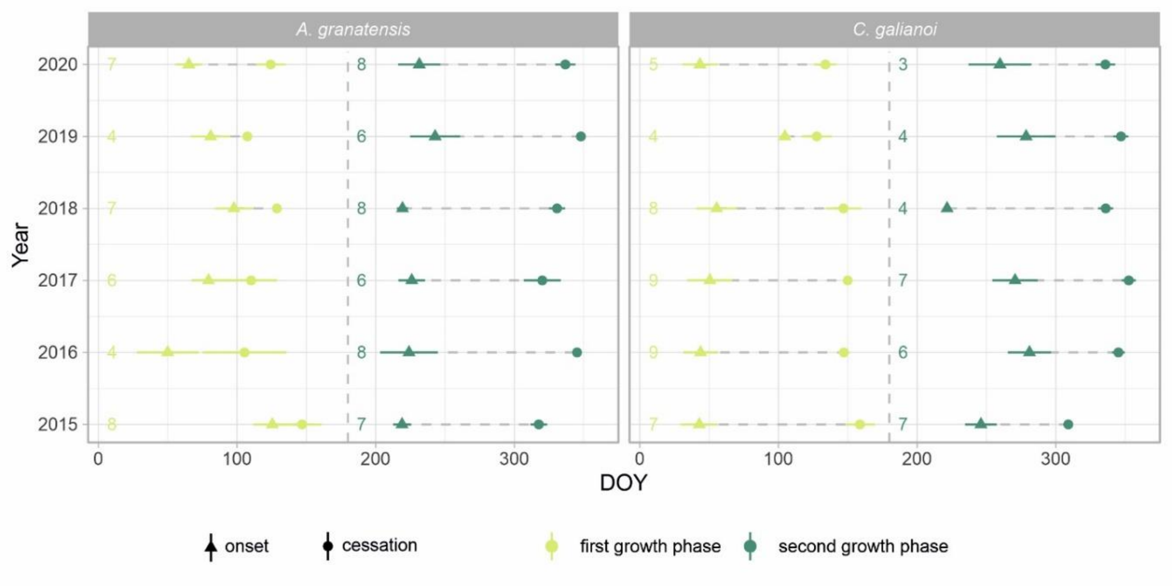

Fig. 3 Growth onset and cessation in A. granatensis *and* C. galianoi *for the first and second growth phases in 2015 – 2020, derived from stem diameter curves and averaged across all sites studied. Numbers indicate the number of specimens which showed growth during the respective phases and solid lines show the standard deviation.*

c) Environmental drivers of growth

Both, growth differences between species, and between the growth phases had complex environmental controls. Growth in *C. galianoi* was generally promoted by high T_{RZ} associated with humid winters, while growth in *A. granatensis* was generally promoted by winter cold and summer heat, as well as autumn humidity (Fig. 4).

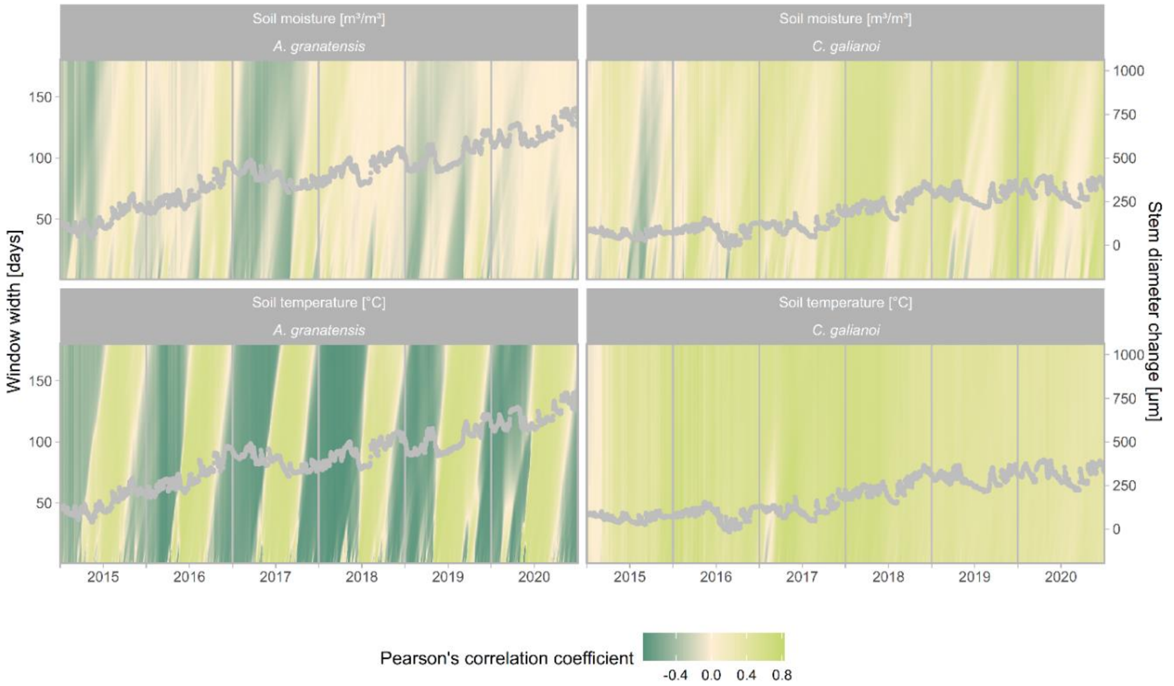

Fig. 4 Moving window correlation for daily stem diameter change and daily measurements of environmental data. Correlations were performed for window widths ranging from 3 to 180 days (right-aligned), revealing temporal patterns of radial stem diameter change and microenvironment relations. Additionally, radial stem diameter change is indicated in grey for direct comparison.

During the first growth phase, *C. galianoi* was promoted by previous-year high T_{RZ} from April to November, while *A. granatensis* was promoted by previous-year high T_{RZ} during July/August and low T_{RZ} from previous year December to March (Figs. 5, S9). There was no robust previous-year SM_{RZ} control in *C. galianoi*, but previous-year July SM_{RZ} drove growth in *A. granatensis* (Figs. 5, S9). Besides pre-growth conditions, high April T_{RZ} were beneficial in both species, and particularly in *C. galianoi* (Figs. 5, S9). We further found positive correlations with March and May/June SM_{RZ} in *C. galianoi* (Figs. 5, S9), while growth in *A. granatensis* was positively correlated with June SM_{RZ}, only.

The second growth phase was mostly decoupled from conditions during the previous year for *C. galianoi*. In the majority of our *A. granatensis* specimens, pre-growth T_{RZ} control indicated that winter cold and summer heat were significant drivers (Figs. 5, S9). There was also no pre-growth SM_{RZ} control in *A. granatensis*. Once growth resumed, there was no robust T_{RZ} control in both species which were rather controlled by SM_{RZ}, with *C. galianoi* being driven by SM_{RZ} during August/September, while *A. granatensis* was driven by SM_{RZ} during October/November.

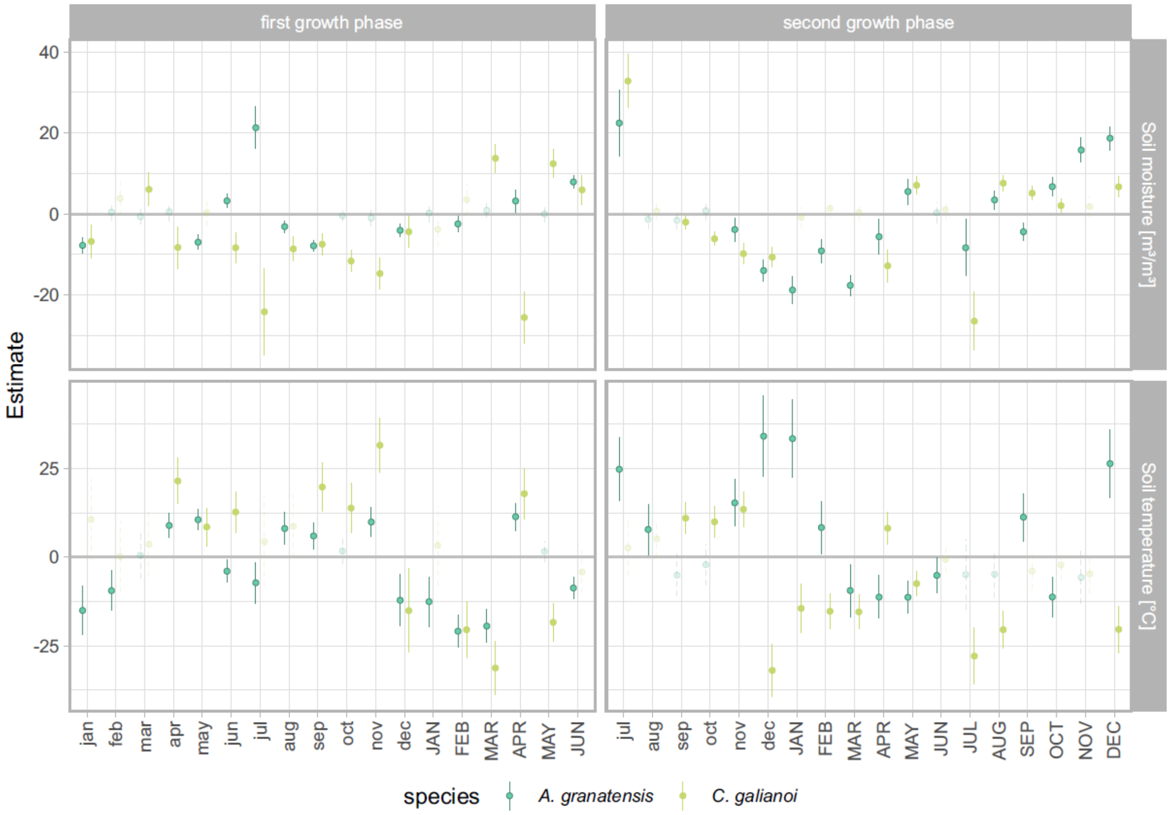

Fig. 5 Linear mixed effects analysis for growth during the first and second growth phase as derived from the dendrometer curves (dependent variable) and monthly environmental data (means) as fixed effects. Individual specimens entered as random effects. Transparency indicates non significance. Abbreviations of months from the previous year are in lowercase letters and those of the current year are given in capitals.

Finally, the PLSR revealed quantitative thermal and hydric conditions under which our two species performed best, or were impeded, respectively (Fig. 6).

During the first growth phase, both species were promoted by previous year´s summer temperatures (T_{RZ} of 22.5°C for *C. galianoi*, 19.0°C for *A. granatensis*) co-occurring with minimum soil moisture. Growth of *C. galianoi* was impeded by sub-zero pre-winter temperatures (T_{RZ} of -2.5°C), and *A. granatensis* was promoted by sub-zero pre-winter temperatures (T_{RZ} of -5.0°C to -1.0°C), respectively. Inversely, growth of *C. galianoi* was impeded by spring T_{RZ} at 0.0°C, and *A. granatensis* was impeded at T_{RZ} 2.0 to 3.0°C, respectively. Growth in *C. galianoi* was also driven by unfrozen ground (SM_{RZ} 0.26 m^3/m^3), and *A. granatensis* was impeded by SM_{RZ} 0.22 m^3/m^3 in winter, but in spring promoted by 0.25 to 0.26 m^3/m^3.

Growth of *C. galianoi* during the second growth phase showed no significant thermal drivers, while *A. granatensis* showed growth impediment at winter T_{RZ} of 2.0°C, but growth promotion at summer T_{RZ} of 21.0°C, and favoured humid springs at 0.22 to 0.25 m^3/m^3. *C. galianoi* was impeded at summer SM_{RZ} of 0.08 to 0.12 m^3/m^3. *A. granatensis* was impeded at winter SM_{RZ} of 0.22 m^3/m^3, but promoted at summer SM_{RZ} of 0.05 m^3/m^3. During autumn, *A. granatensis* was impeded at 14.0°C and promoted by SM_{RZ} of 0.22 to 0.023 m^3/m^3.

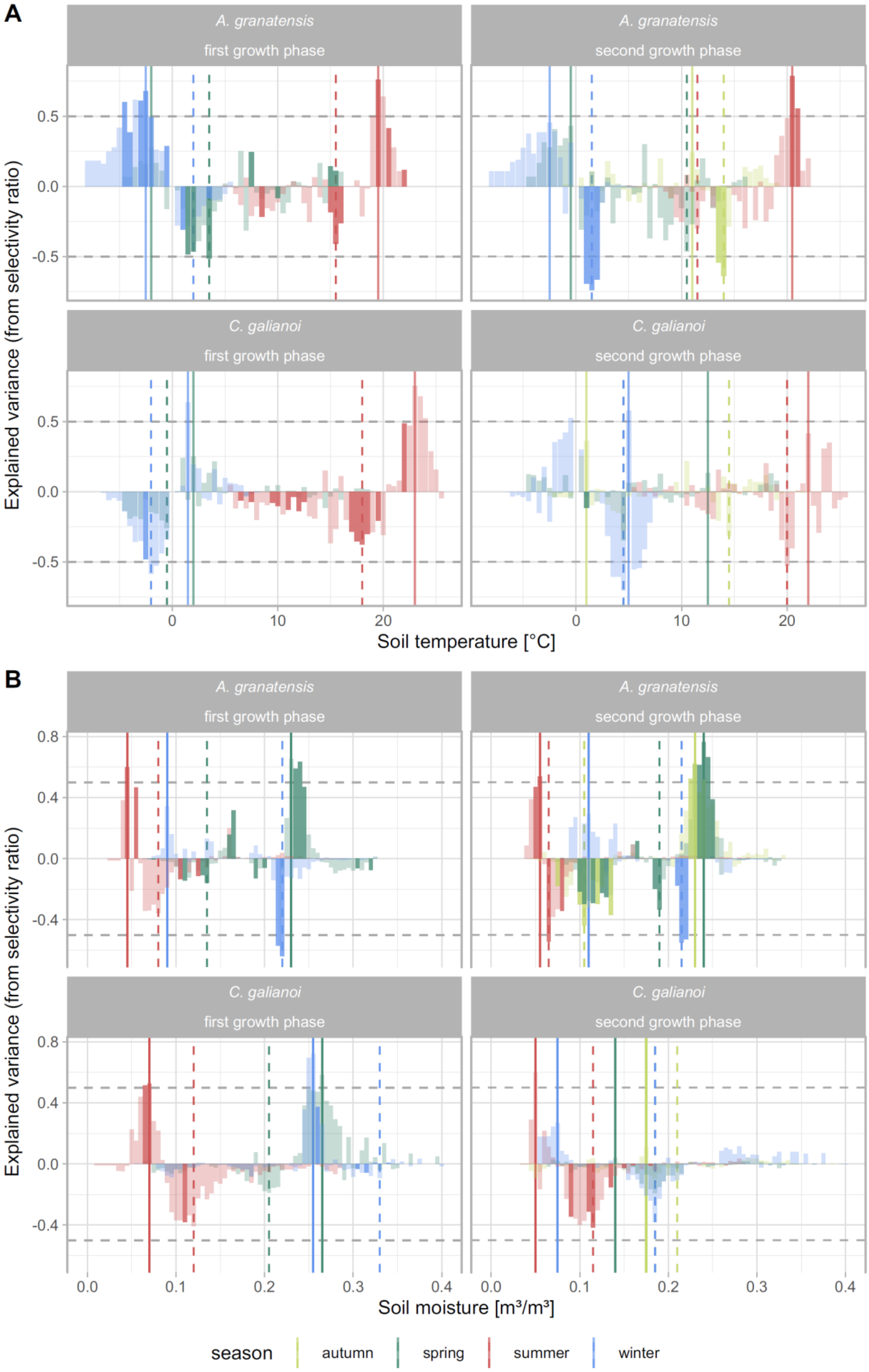
A
A. granatensis
first growth phase
A. granatensis
second growth phase
C. galianoi
first growth phase
C. galianoi
second growth phase
Explained variance (from selectivity ratio)
0.5
0.0
-0.5
0
10
20
Soil temperature [°C]
B
0.8
0.4
0.0
-0.4
0.0
0.1
0.2
0.3
0.4
Soil moisture [m³/m³]
season
autumn
spring
summer
winter

Fig. 6 Partial least squares regression (PLSR) calculated for soil temperature (T_{RZ}, A) and soil moisture (SM_{RZ}, B) for A. granatensis *and* C. galianoi *and all seasons. Colors represent seasons, with solid-color areas representing significant values and shaded areas representing no significance. Solid lines underline the strongest positive and dashed lines the strongest negative correlations, regardless of significance. For the first growth phase, the analysis is based on pre-growth summer, autumn and winter, and the current spring conditions, whereas for the second growth phase on pre-growth winter, spring and summer, and the current autumn conditions.*

Discussion

a) Growth patterns

Distinguishing between irreversible growth, and reversible water-induced shrinking and swelling of the stem (Zweifel et al. 2005, Zweifel 2016) helped us to deduce the species´ water use strategies from the overall stem diameter changes and to understand their contrasting growth patterns. We observed similar bimodal patterns of stem diameter change in our two distinct alpine shrub species. However, these stem diameter changes did not always correspond to their growth patterns, but rather reflected differences in summer-heat and winter-cold induced droughts and corresponding dehydration and rehydration patterns.

Summer drought led to stem contraction in our two species which interrupted the growth process, accompanied by water-related stem shrinkage (cf., Zweifel et al. 2016). This summer stem contraction and dehydration pattern in *C. galianoi* suggests drought tolerance at the cost of reduced performance during autumn (cf. Bacelar et al. 2012), when rehydration is prioritized to increase the water potential prior to growth resumption, but with the advantage of benefiting from carbon fixation in winter and maximizing growth at high water potential in spring (cf., Bossard and Rejmanek 1992). The species´ ability to uptake low daily dew precipitation (cf., Mooney at al. 1980, Kidron 1999) is compensated by relatively high transpiration loss, which is regulated by anisohydry of its photosynthetically active green stems (cf., Bossard and Rejmanek 1992) resulting in long-term shrinkage at high water potential. 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 the summer (cf. 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 (Mauseth 2000, Borchert and Pockmann 2005, Giffits and Males 2017), controlled by isohydric summer leafs, results in the long-term steady increase of its water potential.

Furthermore, ground frost led to different patterns of winter stem contraction in our shrub species at the exposed snow-free ridges. In *C. galianoi*, only minor winter stem contraction occurred, which suggests high frost tolerance of its tissue (cf., Lindfors et al. 2019), 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 (cf., Liphschitz and Lev-Yadun 1986, Gimeno et al. 2012, Bienau et al. 2014, Blok et al. 2015). In *A. granatensis*, winter stem contraction suggests that the species is able to induce water efflux by osmoregulation (cf., Essiamah and Eschrich 1985, Boughalleb et al. 2016, Schenk et al. 2021) in order to protect cells from frost damage.

b) *Timing of growth*

The timing of both growth phases differed strongly between the two species, and especially growth onset in spring and growth resumption in autumn were contrasting.

Early onset of spring growth in *C. galianoi* is plausible when considering its general advantages of green-stems (Bossard and Rejmanek 1992), low stature (Körner 1998, 2016) and frost tolerance (Neuner 2014, Muffler et al. 2016). In contrast, the late and variable onset of spring growth despite early stem diameter increase in *A. granatensis* suggests that after winter dehydration, water uptake is osmotical, and thus retarded during the leafless period. The timing of the spring growth cessation in *C. galianoi* was most likely drought triggered, while in *A. granatensis* growth ceased when vessel formation completed.

The discrepancy in the timing of growth resumption during autumn between both species is likely linked to differences in the species´ drought resistance strategies. In *C. galianoi*, using the drought tolerance strategy, photosynthetically active stems might be the key trade to achieve positive net photosynthetic rates (cf., Bossard and Rejmanek 1992). With its green stems, the species exhibits pronounced anisohydry, and tolerates the variation in plant water potential as a result of weak stem stomata regulation (cf., Jones 1998, Tardieu and Simonneau 1998). Thus, the species still achieves high photosynthetic rates even under increasing water stress (Attia et al 2015). However, due to continued carbon uptake, *C. galianoi* is more susceptible to damage from prolonged droughts (Attia et al. 2015). This ultimately may reduce photosynthetic rates, lead to decelerated rehydration, and explains the delayed growth resumption. In *A. granatensis*, using the drought avoidance strategy, summer leaves are probably hypostomatic and xerophytic, both of which have been shown to effectively protect the plant during summer drought (Westman 1981, Christodoulakis 1989, Puglielli 2019). These leaf traits might allow regulating transpiration-induced water loss and thus minimize fluctuations in tissue water potential (Franks et al. 2007), as is typical for isohydric plants (Attia et al. 2015). As such, early growth resumption after the summer drought is coherent, when the osmotic potential is high and allows for rapid water uptake, and as such, explains immediate growth resumption. The synchronous timing of the autumn growth cessation in both species was triggered by the onset of winter cold (cf., Weiser 1970, Carbon et al. 2020), with limited stomata conductance (Starr 2001) in *C. galianoi* and shedding of the second leaf cohort in *A. granatensis* as a result.

We found the timing of spring and autumn growth in both species variable and independent of the length of the growing phases. As such, the impact of intensity and duration of the environmental drivers on plant performance is likely relative to the species´ traits and ecophysiological strategies. High spring growth rates in *C. galianoi* likely resulted from the formation of earlywood cells and vessels which were mainly promoted by pre-growth winter conditions (cf., Gimeno et al. 2012, Camarero et al. 2013), whereas autumn latewood formation had low rates. In contrast, as a deciduous, ring-porous to semi-ring-porous species, *A. granatensis* relies on new conductive tissue in spring to replace the previous year non-functioning xylem (Essiamah and Eschrich 1986), and as such shows only minor growth rates from vessel formation during spring (Marcati et al. 2006), and high growth rates from xylem formation during autumn.

c) *Environmental drivers of growth*

We found that for both co-existing species pre-growth environmental drivers were most relevant for fitness and growth, with contrasting mechanisms. Additionally, there was a strong temporal decoupling of the growth process from its photosynthetic constraints. To our knowledge, such an interdependency has not been shown before.

Promotion of spring growth of *C. galianoi* by previous year high T_{RZ} (April to November) suggests growth advantages from maximized previous year´s photosynthesis. Promotion of *A. granatensis* was driven by high T_{RZ} during previous year's August, only. As such, both species were promoted by warm and dry previous summers, with *A. granatensis* benefitting from July precipitation, which in contrast was detrimental in *C. galianoi*. These findings suggest that a drought avoiding species benefits from occasional summer rain, while a drought tolerating species might experience embolism due to rain-enforced stomata opening (cf., Lens et al. 2013). We found that growth of *C. galianoi* during the first growth phase was impeded by subzero temperatures during the previous winter (T_{RZ} of -2.5°C). This suggests that *C. galianoi* can cope with relatively low (but above zero) temperatures and is thus well adapted to the environmental constraints at the exposed snow-free ridge. Here, the species profits from unfrozen ground during the winter, when its green stems allow for additional photosynthetic opportunities (cf., Bossard and Rejmanek 1992, Oribe and Kubo 1997, Wyka and Oleksyn 2014). We argue that *C. galianoi* benefits from increased synthesis of carbohydrates during the period of reduced respiration (cf., Gimeno et al. 2012, Camarero et al. 2013), when low soil temperatures promote the storage of carbohydrates in root parenchyma (cf., Sperling et al. 2017). As such, the major importance of spring growth is most likely due to continued carbon gain throughout the winter, with N-fixation playing an additional role (cf., Wheeler et al. 1979, Larsen et al. 2012). In contrast, our findings regarding growth promotion by sub-zero pre-winter T_{RZ} in *A. granatensis* suggests growth onset depending on winter chilling, a phenomenon described in the context of bud break (e.g., Heide 1993, Pop et al. 2000, Campoy et al. 2019), and spring growth being heterotrophic, as known from leaf formation in deciduous trees (e.g., Crang et al. 2018). The preference of *C. galianoi* to humid conditions at the beginning of the first growing season suggests that the species can benefit from early defrost water, whereas its preference to humidity at the end of the first growing period suggests that the species benefits from early summer rains which provide sustained water supply well into the summer, being essential for the species´ tolerance to desiccate. The preference to humidity at the end of the first growing period in *A. granatensis* suggests high water demand during leaf unfolding. Spring growth impediment at low temperatures may reduce stomata conductance in *C. galianoi* and hinder vascularization in *A. granatensis*, whereas growth promotion under high April T_{RZ} may rather reflect unlimited vessel formation during the middle of the first growth phase. This is consistent with various studies from cold regions (e.g., Starr 2001, Bär et al. 2008, Franklin 2012, Olano et al. 2013, Dobbert et al. 2022b), and helps understand the superior role of early growth on alpine plant species (Callaway et al. 2002).

During the second growth phase, there was a minor pre-growth control by summer drought in *C. galianoi*, but winter cold and summer heat were significant drivers in *A. granatensis*. This is plausible for *C. galianoi*, which tolerates drought with the disadvantage of reduced photosynthetic capacity hampering autumn growth, and also for *A. granatensis*, which avoids droughts with the benefit of maximized photosynthetic capacity supporting autumn growth. Our interpretation is supported by the literature, where anisohydric species have been shown to achieve high photosynthetic rates under water stress, but continued carbon uptake and sustained activity made them vulnerable to drought induced damage, whereas isohydic species showed 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 moisture signal during August/September, while *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, as the latter has been shown to be effective after prolonged droughts when seasonal but predictable rainfalls occur (Guo et al. 2020). Such a rapid switch is probably supported by its extensive root system, which enables to benefit from pre-growing season water supply (cf., Bossard and Rejmanek 1992). In contrast, we assume that *A. granatensis*, being leafless after summer, is influenced by its environmental constraints only when heterotrophic growth gradually ceases, and the second leaf cohort is unfolded with new photosynthetic opportunities.

Contrasting the literature (de Luis et al. 2009, Camarero et al. 2010, Rammig et al. 2010, García-Cervigón et al. 2012, Olano et al. 2013), the decoupling of growth from the environmental drivers during phases of actual growth pinpoints dependency of growth on resources attained prior to growth. In *C. galianoi*, high photosynthetic rates during winter allow for high spring growth, while in *A. granatensis* high photosynthetic rates during short-term summer solstice allow for high autumn growth. As such, resource acquisition is rather optimized during phases when the species´ traits and growth strategies allow for physiological activity at high gain and low costs, with the result of species-specific windows of maximum growth (and heterotrophic growth in *A. granatensis*).

Conclusion

Our approach helped us understand general physiological patters of growth, their timing, and their environmental drivers. For both species, we deciphered the phenology of stem diameter changes and were able to distinguish between growth and water-related swelling and shrinking. Our major result on the decoupling of growth from resource acquisition may contribute to the debate on plant adaptive capacity in alpine environments under future climate variability (Olano et al. 2013, Lionello et al. 2014, Dobbert et al. 2022a).

Data Availability

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

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Literature Cited

Abdi, H. 2010. Partial least squares regression and projection on latent structure regression (PLSRegression). WIREs Computational Statistics 2:97–106.

Alday, J. G., J. J. Camarero, J. Revilla, and V. Resco de Dios. 2020. Similar diurnal, seasonal and annual rhythms in radial root expansion across two coexisting Mediterranean oak species. Tree Physiology 40:956–968.

AMAP. Arctic Climate Change Update. 2021. Key Trends and Impacts. Arctic Monitoring and Assessment Programme.

Anderson, R. S., G. Jiménez-Moreno, J. S. Carrión, and C. Pérez-Martínez. 2011. Postglacial history of alpine vegetation, fire, and climate from Laguna de Río Seco, Sierra Navada, southern Spain. Quaternary Science Reviews 30:1615–1629.

Aronne, G., and V. de Micco. 2001. Seasonal dimorphism in the Mediterranean *Cistus incanus* L. subsp. incanus. Annals of Botany 87:789–794.

Attia, Z., J. C. Domec, R. Oren, D. A. Way, and M. Moshelion. 2015. Growth and physiological responses of isohydric and anisohydric poplars to drought. Journal of Experimental Botany 66:4373–4381.

Bär, A., A. Bräuning, and J. Löffler. 2006. Dendroecology of dwarf shrubs in the high mountains of Norway – A methodological approach. Dendrochronologia 24:17–27.

Bär, A., A. Bräuning, and J. Löffler. 2007. Ring-width chronologies of the alpine dwarf shrub *Empetrum hermaphroditum* from the Norwegian mountains. IAWA Journal 28:325–338.

Bär, A., R. Pape, A. Bräuning, and J. Löffler. 2008. Growth-ring variations of dwarf shrubs reflect regional climate signals in alpine environments rather than topoclimatic differences. Journal of Biogeography 35:625–636.

Bacelar, E. L., J. M. Moutinho-Pereira, B. M. Gonçalves, C. V. Brito, J. Gomes-Laranjo, H. M. Ferreira, and C. M. Correia. 2012. Water use strategies of plants under drought conditions. Pages 145–170 *in* R. Arcoca, editor. Plant responses to drought stress: from morphological to molecular features. Springer, Heidelberg, Germany.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Battipaglia, G., V. de Micco, W. A. Brand, M. Saurer, G. Aronne, P. Linke, and P. Cherubini. 2013. Drought impact on water use eciency and intra-annual density fluctuations in *Erica arborea* on Elba (Italy). Plant, Cell and Environment 37:382–391.

Bienau, M. J., D. Hattermann, M. Kröncke, L. Kretz, A. Otte, W. L. Eiserhardt, A. Milbau, B. J. Graae, W. Durka, and R. L. Eckstein. 2015. Snow cover consistently affects growth and reproduction of *Empetrum hermaphroditum* across latitudinal and local climatic gradients. Alpine Botany 124:115–129.

Blackman, V. H. 1991. Osmotic pressure, root pressure, and exudation. New Phytologist 20:106–115.

Blanca, G., B. Cabezudo, M. Cueto, C. Fernández López and C. Morales Torres. 2009b. Flora Vascular de Andalucía Oriental. Consejería de Medio Ambiente. Junta de Andalucía 1:306.

Blanca, G., B. Cabezudo, M. Cueto, C. Fernández López, C. Morales Torres. 2009a. Flora Vascular de Andalucía Oriental. Consejería de Medio Ambiente. Junta de Andalucía 2:334.

Blok, D., S. Weijers, J. M. Welker, E. J. Cooper, A. Michelsen, J. Löffler, and B. Elberling. 2015. Deepened winter snow increases stem growth and alters stem δ13C and δ15N in evergreen dwarf shrub *Cassiope tetragona* in high-arctic Svalbard tundra. Environmental Research Letters 10(4):044008.

Borchert, R., and W. T. Pockman. 2005. Water storage capacitance and xylem tension in isolated branches of temperate and tropical trees. Tree Physiology 25:457–466.

Bossard, C. C., and M. Rejmanek. 1992. Why have green stems? Functional Ecology 197–205.

Boughalleb, F., R. Abdellaoui, N. Ben Brahim, and M. Neffati. 2016. Growth, photosynthesis, water use efficiency, and osmoregulation of the wild species *Astragalus gombiformis* Pomel. Under water deficit. Brazilian Journal of Botany 39:147–156.

Braun, H. J. 1984. The significance of the accessory tissues of the hydrosystem for osmotic water shifting as the second principle of water ascent, with some thoughts concerning the evolution of trees. IAWA Journal 5:275–294.

Bravo, D. N., M. B. Araújo, T. Lasanta, and J. I. L. Moreno. 2008. Climate change in Mediterranean mountains during the 21st century. Ambio 37:280–285.

Brodersen, C. R., and A. J. Mc Elrone. 2013. Maintenance of xylem network transport capacity: a review of embolism repair in vascular plants. Frontiers in Plant Science 4:108.

Cabon, A., R. L. Peters, P. Fonti, J. Martínez-Vilalta, and M. Cáceres. 2020. Temperature and water potential co-limit stem cambial activity along a steep elevational gradient. New Phytologist 226:1325–1340.

Callaway R.M., R. W. Brooker, P. Choler, Z. Kikvidze, C. J. Lortiek, R. Michalet, L. Paolini, F. I. Pugnaireq, B. Newingham, E. T. Aschehoug, C. Armasq, D. Kikodze, and B. J. Cook. 2002. Positive interactions among alpine plants increase with stress. Nature 417:844–848.

Camarero, J. J., J. M. Olano and A. Parras. 2010. Plastic bimodal xylogenesis in conifers from continental Mediterranean climates. New Phytologist 185:471–480.

Camarero, J. J., J. M. Olano, S. J. A. Alfaro, B. Fernández-Marín, J. M. Becerril, and J. I. García-Plazaola. 2012. Photoprotection mechanisms in *Quercus ilex* under contrasting climatic conditions. Flora-Morphology, Distribution, Functional Ecology of Plants 207:557–564.

Camarero, J. J., S. Palacio, and G. Montserrat-Martí. 2013. Contrasting seasonal overlaps between primary and secondary growth are linked to wood anatomy in Mediterranean sub-shrubs. Plant Biology 15:798–807.

Camarero, J. J., C. Valeriano, A. Gazol, M. Colangelo, and R. Sánchez-Salguero. 2021. Climate differently impacts the growth of coexisting trees and shrubs under semi-arid Mediterranean conditions. Forests 12:381.

Campoy, J. A., R. Darbyshire, E. Dirlewanger, J. Quero-García, and B. Wenden. 2019. Yield potential definition of the chilling requirement reveals likely underestimation of the risk of climate change on winter chill accumulation. International Journal of Biometeorology 63:183–192.

Carrascal, L. M., I. Galván, and O. Gordo. 2009. Partial least squares regression as an alternative to current regression methods used in ecology. Oikos 118:681–690.

Castagneri, D., G. Battipaglia, G. v. Arx, A. Pacheco, and M. Carrer. 2018. Tree-ring anatomy and carbon isotope ratio show both direct and legacy effects of climate on bimodal xylem formation in *Pinus pinea*. Tree Physiology 38:1098–1109.

Chaves, M. M., J. P. Maroco, and J. S. Pereira. 2003. Understanding plant responses to drought-from genes to the whole plant. Functional Plant Biology 30:239–264.

Chen, L., and R. Z. Wang. 2009. Anatomical and physiological divergences and compensatory effects in two *Leymus chinensis* (Poaceae) ecotypes in northeast China. Agriculture, Ecosystems and Environment 134:46–52.

Choler, P. 2018. Winter soil temperature dependence of alpine plant distribution: Implications for anticipating vegetation changes under a warming climate. Perspectives in Plant Ecology, Evolution and Systematics 30:6–15.

Christodoulakis, N. S. 1989. An anatomical study of seasonal dimorphism in the leaves of *Phlomis fruticose*. Annals of Botany 63:389–394.

Christodoulakis, N. S., and C. Fasseas. 1991. Seasonal dimorphism of *Phlomis fruticosa* under controlled. Acta Œcologica 12:323–330.

Cotto, O., J. Wessely, D. Georges, G. Klonner, M. Schmid, S. Dullinger, W. Thuiller and F. Guillaume. 2017. A dynamic eco-evolutionary model predicts slow response of alpine plants to climate warming. Nature Communications 8:15399.

Crang, R. F. E., S. Lyons-Sobaski, and R. Wise. 2018. Plant anatomy: a concept-based approach to the structure of seed plants. Springer, Cham, Switzerland.

de Jong, S. 1993. SIMPLS: an alternative approach to partial least squares regression. Chemometrics and Intelligent Laboratory Systems 18:251–263.

de Luis, M., J. Gričar, K. Čufar, and J. Raventós. 2007. Seasonal dynamics of wood formation in *Pinus halepensis* from dry and semi-arid ecosystems in Spain. IAWA Journal 28:389–404.

de Luis, M., K. Novak, K. Čufar, and J. Raventós. 2009. Size mediated climate–growth relationships in *Pinus halepensis* and *Pinus pinea*. Trees 23:1065–1073.

Deslauriers, A., S. Rossi, and T. Anfodillo. 2007. Dendrometer and intra-annual tree growth: what kind of information can be inferred? Dendrochronologia 25:113–124.

Devecioğlu, A. G., and Y. Biçer. 2016. The effects of tragacanth addition on the thermal and mechanical properties of lightweight concretes mixed with expanded clay. Periodica Polytechnica Civil Engineering 60:45–50.

Dijkstra, T. 1983. Some comments on maximum likelihood and partial least squares methods. Journal of Econometrics 22:67–90.

Dobbert, S., E. C. Albrecht, R. Pape, and J. Löffler. 2022a. Alpine shrub growth follows bimodal seasonal patterns across biomes–unexpected environmental controls. Communications Biology 5:1–12.

Dobbert, S., R. Pape, and J. Löffler. 2021. Contrasting growth response of evergreen and deciduous arctic-alpine shrub species to climate variability. Ecosphere 12(8):e03688.

Dobbert, S., R. Pape, and J. Löffler. 2022b. The application of dendrometers to alpine dwarf shrubs–a case study to investigate stem growth responses to environmental conditions. Biogeosciences 19:1933–1958.

Essiamah, S., and W. Eschrich. 1985. Changes of starch content in the storage tissues of deciduous trees during winter and spring. IAWA Journal 6:97–106.

Essiamah, S., and W. Eschrich. 1986. Water uptake in deciduous trees during winter and the role of conducting tissues in spring reactivation. IAWA Journal 71:31–38.

Farrés, M., S. Platikanov, S. Tsakovski, and R. Tauler. 2015. Comparison of the variable importance in projection (VIP) and of the selectivity ratio (SR) methods for variable selection and interpretation. Journal of Chemometrics 29:528–536.

Forbes, B. C., M. Macias-Fauria, and P. Zetterberg. 2010. Russian arctic warming and “greening” are closely tracked by tundra shrub willows. Global Change Biology 16:1542–1554.

Franklin, R. S. 2012. Growth response of the alpine shrub, *Linanthus pungens*, to snowpack and temperature at a rock glacier site in the eastern Sierra Nevada of California, USA. Quaternary International 30:1e14.

Franks, P. J., P. L. Drake, and R. H. Froend. 2007. Anisohydric but isohydrodynamic: seasonally constant plant water potential gradient explained by a stomatal control mechanism incorporating variable plant hydraulic conductance. Plant, Cell and Environment 30:19–30.

Frindte, K., R. Pape, K. Werner, J. Löffler, and C. Knief. 2019. Temperature and soil moisture control microbial community composition in an arctic-alpine ecosystem along elevational and micro-topographic gradients. ISME Journal 13:2031–2043.

Gamm, C. M., P. F. Sullivan, A. Buchwal, R. J. Dial, A. B. Young, D. A. Watts, S. M. P. Cahoon, J. M. Welker, and E. Post. 2018. Declining growth of deciduous shrubs in the warming climate of continental western Greenland. Journal of Ecology 106:640–654.

Ganthaler, A., and S. Mayr. 2015. Dwarf shrub hydraulics: two Vaccinium species (*Vaccinium myrtillus*, *Vaccinium vitis-idaea*) of the European Alps compared. Physiologia Plantarum 155:424–434.

García-Cervigón, A. I., J. M. Olano Mendoza, M. E. Gozalbo, and J. J. Camarero Martínez. 2012. Arboreal and prostrate conifers coexisting in Mediterranean high mountains differ in their climatic responses. Dendrochronologia 30:279–286.

Gazol, A., and J. J. Camarero. 2012. Mediterranean dwarf shrubs and coexisting trees present different radial-growth synchronies and responses to climate. Plant Ecology 213:1687–1698.

Geladi, P., and B. R. Kowalski. 1986. Partial least-squares regression: a tutorial. Analytica Chimica Acta 185:1–17.

Giménez, E., M. Melendo, F. Valle, F. Gómez-Mercado, and E. Cano. 2004. Endemic flora biodiversity in the south of the Iberian Peninsula: altitudinal distribution, life forms and dispersal modes. Biodiversity and Conservation 13:2641–2660.

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

Gimeno, T. E., J. J. Camarero, E. Granda, B. Pías, and F. Valladares. 2012. Enhanced growth of *Juniperus thurifera* under a warmer climate is explained by a positive carbon gain under cold and drought. Tree Physiology 32:326–336.

Giorgi, F., and P. Lionello. 2008. Climate change projections for the Mediterranean region. Global and Planetary Change 63:90–104.

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

Gorji, S. G., E. G. Gorji, and M. A. Mohammadifar. 2014. Characterisation of gum tragacanth (*Astragalus gossypinus*)/sodium caseinate complex coacervation as a function of pH in an aqueous medium. Food Hydrocolloids 34:161–168.

Graven, H. D., R. F. Keeling, S. C. Piper, P. K. Patra, B. B. Stephens, S. C. Wofsy, L. R. Welp, C. Sweeney, P. P. Tans, J. J. Kelley, B. C. Daube, E. A. Kort, G. W. Santoni, and J. D. Bent. 2013. Enhanced seasonal exchange of CO_2 by northern ecosystems since 1960. Science 341:1085–1089.

Gričar, J., P. Prislan, M. de Luis, V. Gryc, J. Hacurová, H. Vavrčík, and K. Čufar. 2015. Plasticity in variation of xylem and phloem cell characteristics of Norway spruce under different local conditions. Frontiers in Plant Science 6:730.

Griffiths, H., and J. Males. 2017. Succulent plants. Current Biology 27:R890–R896.

Guarino, R., G. Giusso del Galdo, and S. Pignatti. 2005. The Mediterranean dwarf shubs: origin and adaptive radiation. Annali di Botanica 5:39–58.

Guo, C., L. Ma, S. Yuan, and R. Wang. 2017. Morphological, physiological and anatomical traits of plant functional types in temperate grasslands along a large-scale aridity gradient in northeastern China. Scientific Reports 7:1–10.

Guo, J. S., K. R. Hultine, G. W. Koch, H. Kropp, and K. Ogle. 2020. Temporal shifts in iso/anisohydry revealed from daily observations of plant water potential in a dominant desert shrub. New Phytologist 225:713–726.

Hanewinkel, M., D. A. Cullmann, M.-J. Schelhaas, G.-J. Nabuurs, and N. E. Zimmermann. 2013. Climate change may cause severe loss in the economic value of European forest land. Nature Climate Change 3:203–207.

Heide, O. M. 1993. Dormancy release in beech buds (*Fagus sylvatica*) requires both chilling and long days. Physiologia Plantarum 89:187–191.

Herrero, J., and M. J. Polo. 2016. Evaposublimation from the snow in the Mediterranean mountains of Sierra Nevada (Spain). The Cryosphere 10:2981–2998.

IPCC. Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change.

Jiménez-Moreno, G., and R. S. Anderson. 2012. Holocene vegetation and climate change recorded in alpine bog sediments from the Borreguiles de la Virgen, Sierra Nevada, southern Spain. Quaternary Research 77:44–53.

Jones, H. G. 1998. Stomatal control of photosynthesis and transpiration. Journal of Experimental Botany 387–398.

Kaya, M., M. Odabasi, M. Mujtaba, M. Sen, E. Bulut, and B. Akyuz. 2016. Novel three-dimensional cellulose produced from trunk of *Astragalus gummifer* (Fabaceae) tested for protein adsorption performance. Materials Science and Engineering C 62:144–151.

Kidron, G. J. 1999. Altitude dependent dew and fog in the Negev Desert, Israel. Agricultural and Forest Meteorology 96:1–8.

Körner, C. 1998. A re-assessment of high elevation treeline positions and their explanation. Oecologia 115:445–459.

Körner, C. 2016. Plant adaptation to cold climates. F1000Research 5:1–5.

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

Körner, C. 2012. Treelines will be understood once the functional difference between a tree and a shrub is. Ambio 41:197–206.

Kozlowski, T. T., and S. G. Pallardy. 2002. Acclimation and adaptive responses of woody plants to environmental stresses. The Botanical Review 68:270–334.

Kucheryavskiy, S. 2020. mdatools – R package for chemometrics. Chemometrics and Intelligent Laboratory Systems 198:103937.

Larsen, K. S., A. Michelsen, S. Jonasson, C. Beier, and P. Grogan. 2012. Nitrogen uptake during fall, winter and spring differs among plant functional groups in a subarctic heath ecosystem. Ecosystems 15:927–939.

Lens, F., A. Tixier, H. Cochard, J. S. Sperry, S. Jansen, and S. Herbette. 2013. Embolism resistance as a key mechanism to understand adaptive plant strategies. Current Opinion in Plant Biology 16:287–292.

Lianopoulou, V., A. M. Bosabalidis, A. Patakas, D. Lazari, and E. Panteris. 2014. Effects of chilling stress on leaf morphology, anatomy, ultrastructure, gas exchange, and essential oils in the seasonally dimorphic plant *Teucrium polium* (Lamiaceae). Acta Physiologiae Plantarum 36:2271–2281.

Lindfors, L., J. Atherton, A. Riikonen, and T. Hölttä. 2019. A mechanistic model of winter stem diameter dynamics reveals the time constant of diameter changes and the elastic modulus across tissues and species. Agricultural and Forest Meteorology 272:20–29.

Lionello, P., F. Abrantes, M. Gacic, S. Planton, R. Trigo, and U. Ulbrich. 2014. The climate of the Mediterranean region: research progress and climate change impacts. Regional Environmental Change 14:1679–1684.

Liphschitz, N., and S. Lev-Yadun. 1986. Cambial activity of evergreen and seasonal dimorphics around the Mediterranean. IAWA Journal 7:145–153.

Löffler, J., and R. Pape. 2020. Thermal niche predictors of alpine plant species. Ecology 101:e02891.

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

Löffler, J., S. Dobbert, R. Pape and D. Wundram. 2021. Dendrometer measurements of arctic-alpine dwarf shrubs and micro-environmental drivers of plant growth - Dataset from long-term alpine ecosystem research in central Norway. Erdkunde 75:DP311201.

Lorite, J., M. Ruiz-Girela, and J. Castro. 2007. Patterns of seed germination in Mediterranean mountains: study on 37 endemic or rare species from Sierra Nevada, SE Spain. Candollea 62:5.

Magaña Ugarte, R., A. Escudero, and R. G. Gavilán. 2019. Metabolic and physiological responses of Mediterranean high-mountain and alpine plants to combined abiotic stresses. Physiologia plantarum 165:403–412.

Marcati, C. R., V. Angyalossy, and R. F. Evert. 2006. Seasonal variation in wood formation of Cedrela fissilis (Meliaceae). IAWA Journal 27:199–211.

Martens, H., and T. Næs. 1989. Multivariate calibration. John Wiley & Sons, Chichester, UK.

Mauseth, J. D. 2000. Theoretical aspects of surface-to-volume ratios and water-storage capacities of succulent shoots. American Journal of Botany 87:1107–1115.

Mehmood, T., K. H. Liland, L. Snipen, and S. Sæbø. 2012. A review of variable selection methods in Partial Least Squares Regression. Chemometrics and Intelligent Laboratory Systems 118:62–69.

Meinzer, F.C., J. R. Brooks, B. L. Gartner, J. M. Warren, D. R. Wodru, K. Bible, and D. C. Shaw. 2006. Dynamics of water transport and storage in conifers studied with deuterium and heat tracing techniques. Plant, Cell and Environment 29:105–114.

Melendo, M., E. Giménez, E. Cano, F. Gómez-Mercado, and F. Valle. 2003. The endemic flora in the south of the Iberian Peninsula: taxonomic composition, biological spectrum, pollination, reproduction mode and dispersal. Flora 198:260–276.

Mitrakos, K. 1980. A theory for Mediterranean plant life. Acta Oecologica, Oecologia Plantarum Montreuil 1:245–252.

Mohammadifar, M. A., S. M. Musavi, A. Kiumarsi, and P. A. Williams. 2006. Solution properties of targacanthin (water-soluble part of gum tragacanth exudate from *Astragalus gossypinus*). International Journal of Biological Macromolecules 38:31–39.

Molina, A., and J. Izco. 1986. Comportamiento ecológico y fitosociológico de *Astragalus granatensis* Lam. En la Provincia Castellano-Maestranzgo-Manchega. Trabajos del Departamiento de Botánica 13:83–97.

Mooney, H. A., S. L. Gulmon, J. Ehleringer, and P. W. Rundel. 1980. Atmospheric water uptake by an atacama dersert shrub. Science 209:693–694.

Morales, A. I. G. C., J. M. O. Mendoza, M. E. Gozalbo, and J. J. C. Martínez. 2012. Arboreal and prostrate conifers coexisting in Mediterranean high mountains differ in their climatic responses. Dendrochronologia 30:279–286.

Muffler L., C. Beierkuhnlein, G. Aas, A. Jentsch, A. H. Schweiger, C. Zohner, and J. Kreyling. 2016. Distribution ranges and spring phenology explain late frost sensitivity in 170 woody plants from the Northern Hemisphere. Gobal Ecology and Biogeography 25:1061–1071.

Myers-Smith, I. H., J. T. Kerby, G. K. Phoenix, J. W. Bjerke, H. E. Epstein, J. J. Assmann, C. John, L. Andreu-Hayles, S. Angers-Blondin, P. S. A. Beck, L. T. Berner, U. S. Bhatt, A. D. Bjorkman, D. Blok, A. Bryn, C. T. Christiansen, J. H. C. Cornelissen, A. M. Cunliffe, S. C. Elmendorf, B. C. Forbes, S. J. Goetz, R. D. Hollister, R, de Jong, M. M. Loranty, M. Macias-Fauria, K. Maseyk, S, Normand, J. Olofsson, T. C. Parker, F.-J. W. Parmentier, E. Post, G. Schaepman-Strub, F. Stordal, P. F. Sullivan, H. J. D. Thomas, H. Tømmervik, R. Treharne, C. E. Tweedie, D. A. Walker, M. Wilmking, and S. Wipf. 2020. Complexity revealed in the greening of the Arctic. Nature Climate Change 10:106–117.

Neuner, G. 2014. Frost resistance in alpine woody plants. Frontiers in Plant Science 5:654.

Niittynen, P., and M. Luoto. 2018. The importance of snow in species distribution models of arctic vegetation. Ecography 41:1024–1037.

Olano, J. M., I. Almería, M. Eugenio, and G. von Arx. 2013. Under pressure: how a Mediterranean high-mountain forb coordinates growth and hydraulic xylem anatomy in response to temperature and water constraints. Functional Ecology 27:1295–1303.

Oliva, M., A. G. Ortiz, F. Salvador, M. Salvà, P. Pereira, and M. Geraldes. 2014. Long-term soil temperature dynamics in the Sierra Nevada, Spain. Geoderma 235:170–181.

Oribe, Y., and T. Kubo. 1997. Effect of heat on cambial reactivation during winter dormancy in evergreen and deciduous conifers. Tree Physiology 17:81–87.

Pacheco, A., J. J. Camarero, M. Ribas, A. Gazol, E. Gutierrez, and M. Carrer. 2018. Disentangling the climate-driven bimodal growth pattern in coastal and continental Mediterranean pine stands. Science of the Total Environment 615:1518–1526.

Pan, Y., R. A. Birdsey, J. Fang, R. Houghton, R., P. E. Kauppi, W. A. Kurz, O. L. Phillips, A. Shvidenko, S. L. Lewis, J. G. Canadell, P. Ciais, R. B. Jackson, S. W. Pacala, A. D. McGuire, S. Piao, A. Rautiainen, S. Sitch, and D. Hayes. 2011. A large and persistent carbon sink in the World's Forests. Science 333:988–993.

Pasho, E., J. J. Camarero, and S. M. Vicente-Serrano. 2012. Climatic impacts and drought control of radial growth and seasonal wood formation in *Pinus halepensis*. Trees 26:1875–1886.

Pauli, J. N., B. Zuckerberg, J. P. Whiteman, and W. Porter. 2013. The subnivium: a deteriorating seasonal refugium. Frontiers in Ecology and the Environment 11:260–267.

Pellizzari, E., J. J. Camarero, A. Gazol, E. Granda, R. Shetti, M. Wilmking, P. Moiseev, M. Pividori, and M. Carrer. 2017. Diverging shrub and tree growth from the Polar to the Mediterranean biomes across the European continent. Global Change Biology 23:3169–3180.

Pescador, D. S., F. de Bello, F. Valladares, and A. Escudero. 2015. Plant trait variation along an altitudinal gradient in Mediterranean high mountain grasslands: controlling the species turnover effect. PLoS One 10(3):e0118876.

Podlech, D. 2008. The genus *Astragalus* L. (Fabaceae) in Europe with exclusion of the former Soviet Union. Feddes Repertorium 119:310–387.

Pop, E. W., S. F. Oberbauer, and G. Starr. 2000. Predicting vegetative bud break in two arctic deciduous shrub species, *Salix pulchra* and *Betula nana*. Oecologia 124:176–184.

Petty, S. K., B. Zuckerberg, and J. N. Pauli. 2015. Winter conditions and land cover structure the subnivium, a seasonal refuge beneath the snow. PLoS ONE 10:e0127613.

Puglielli, G. 2019. Beyond the concept of winter-summer leaves of mediterranean seasonal dimorphic species. Frontiers in Plant Science 10:696.

R Core Team. 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

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

Rammig, A., T. Jonas, N. E. Zimmermann, and E. Rixen. 2010. Changes in alpine plant growth under future climate conditions. Biogeosciences 7:2013–2024.

Ritonga F. N., and S. Chen. 2020. Physiological and molecular mechanism involved in cold stress tolerance in plants. Plants 9:560.

Roberts, N., D. Brayshaw, C. Kuzucuolu, R. Perez, and L. Sadori. 2011. The mid-Holocene climatic transition in the Mediterranean: causes and consequences. The Holocene 21:3–13.

Ropars, P., S. Angers-Blondin, M. Gagnon, I. H. Myers-Smith, E. Lévesque, and S. Boudreau. 2017. Different parts, different stories: climate sensitivity of growth is stronger in root collars vs. stems in tundra shrubs. Global Change Biology 23:3281–3291.

Rossi, S., A. Deslauriers, J. Gričar, J. W. Seo, C. B. K. Rathgeber, T. Anfodillo, H. Morin, T. Levanic, P. Oven, and R. Jalkanen. 2008. Critical temperatures for xylogenesis in conifers of cold climates. Global Ecology and Biogeography 17:696–707.

Schenk, H. J., S. Jansen, and T. Hölttä. 2021. Positive pressure in xylem and its role in hydraulic function. New Phytologist 230:27–45.

Sperling, O., L. C. R. Silva, A. Tixier, G. Théroux-Rancourt, and M. A. Zwieniecki. 2017. Temperature gradients assist carbohydrate allocation within trees. Nature Scientific Reports 7:3265.

Sperry, J. 1993. Winter xylem embolism and spring recovery in *Betula cordifolia*, *Fagus grandifolia*. Water transport in plants under climatic stress 86.

Sperry, J. S., and M. T. Tyree. 1988. Mechanism of water stress-induced xylem embolism. Plant Physiology 88:581–587.

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

Szymczak, S., M. Häusser, E. Garel, S. Santoni, F. Huneau, I. Knerr, K. Trachte, J. Bendix, and A. Bräuning, 2020. How do Mediterranean pine trees respond to drought and precipitation events along an elevation gradient? Forests 11:758.

Talavera, S., and P. Gibbs 1997. *Cytisus purgans* auct. (Leguminosae – Papilionoideae) comprises four distinct species. Botanical Journal of the Linnean Society 125:331–342.

Tardieu, F., and T. Simonneau. 1998. Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. Journal of Experimental Botany 419–432.

Treml, V., J. Kašpar, H. Kuželová, and V. Gryc. 2015. Differences in intra-annual wood formation in *Picea abies* across the treeline ecotone, Giant Mountains, Czech Republic. Trees 29:515–526.

Tumajer, J., V. V. Shishov, V. A. Ilyin, and J. J. Camarero. 2021. Intra-annual growth dynamics of Mediterranean pines and junipers determines their climatic adaptability. Agricultural and Forest Meteorology 311:108685.

Valle, F., editor. 2003. Mapa de Series de Vegetación de Andalucía. Editorial Rueda, S.I., Madrid.

Vinzi, E. V. 2010. Handbook of partial least squares. Concepts, methods and applications. Springer, Berlin, Germany.

Weijers, S., N. Beckers, and J. Löffler. 2018. Recent spring warming limits near-treeline deciduous and evergreen alpine dwarf shrub growth. Ecosphere 9(6):e02328.

Weiser C. J. 1970. Cold resistance and injury in woody plant. Science 169:1269–1278.

Westman, W. E. 1981. Seasonal dimorphism of foliage in Californian coastal sage scrub. Oecologia 51:385–388.

Wheeler, C. T., D. A. Perry, O. Helgerson, and J. C. Gordon. 1979. Winter fixation of nitrogen in Scotch broom (*Cytisus scoparius* L.). New Phytologist 82:697–701.

Wold, H. 1975. Soft modelling by latent variables: The Non-Linear Iterative Partial Least Squares (NIPALS) approach. Journal of Applied Probability 12:117–142.

Wold, H. 1980. Evaluation of econometric models. Academic Press, New York, USA.

Wold, S. 1978. Cross-validatory estimation of the number of components in factor and principal components models. Technometrics 20:397–405.

Wyka, T. P., and J. Oleksyn. 2014. Photosynthetic ecophysiology of evergreen leaves in the woody angiosperms – a review. Dendrobiology 72:3–27.

Zweifel, R., L. Zimmermann, and D. M. Newbery. 2005. Modeling tree water deficit from microclimate: an approach to quantifying drought stress. Tree Physiology 25:147–156.

Zweifel, R., M. Haeni, N. Buchmann, and W. Eugster. 2016. Are trees able to grow in periods of stem shrinkage? New Phytologist 211:839–849.

Zweifel, R. 2016. Radial stem variations - a source of tree physiological information not fully exploited yet. Plant, Cell and Environment 39:231–232.

Zweifel, R., and R. Häsler. 2001. Dynamics of water storage in mature subalpine *Picea abies*: temporal and spatial patterns of change in stem radius. Tree Physiology 21:561–569.

Zweifel, R., F. Sterck, S. Braun, N. Buchmann, W. Eugster, A. Gessler, M. Häni, R. L. Peters, L. Walthert, M. Wilhelm, K. Ziemińska, and S. Etzold. 2021. Why trees grow at night. New Phytologist 231:2174–2185.

Table S1. Micro-environmental conditions from 2015 to 2020 averaged over all studied sites (+/-SE), for the focal species A. granatensis *(A.) and* C. galianoi *(C.).*

Year	2015	2016	2017	2018	2019	2020
T_{RZ} A./C. (mean) [°C]	7,36 (0,07)/ 9,24 (0,32)	7,64 (0,05)/ 9,51 (0,33)	8,33 (0,08)/ 9,94 (0,27)	5,83 (0,05)/ 7,64 (0,31)	7,66 (0,05)/ 9,67 (0,38)	8,03 (0,06)/ 9,94 (0,33)
T_{RZ} A./C. (max) [°C]	20,84 (0,25)/ 23,25 (0,28)	20,04 (0,24)/ 22,73 (0,31)	21,07 (0,21)/ 23,20 (0,21)	20,38 (0,26)/ 22,71 (0,25)	20,29 (0,22)/ 23,07 (0,32)	20,05 (0,32)/ 23,23 (0,30)
T_{RZ} A./C. (min) [°C]	-5,42 (0,58)/ -4,53 (0,41)	-1,56 (0,29)/ -1,18 (0,38)	-2,17 (0,50)/ -1,75 (0,26)	-3,45 (0,22)/ -2,27 (0,39)	-2,69 (0,42)/ -2,04 (0,50)	-0,47 (0,21)/ -0,11 (0,35)
SM_{RZ} A./C. (mean) [m^3/m^3]	0,16 (0,01)/ 0,16 (0,00)	0,15 (0,01)/ 0,16 (0,01)	0,14 (0,01)/ 0,16 (0,01)	0,18 (0,01)/ 0,20 (0,01)	0,15 (0,01)/ 0,16 (0,00)	0,18 (0,01)/ 0,18 (0,00)
SM_{RZ} A./C. (max) [m^3/m^3]	0,27 (0,01)/ 0,28 (0,01)	0,27 (0,02)/ 0,31 (0,01)	0,27 (0,01)/ 0,31 (0,01)	0,28 (0,02)/ 0,32 (0,01)	0,28 (0,02)/ 0,30 (0,01)	0,29 (0,01)/ 0,31 (0,01)
SM_{RZ} A./C. (min) [m^3/m^3]	0,06 (0,00)/ 0,07 (0,00)	0,06 (0,00)/ 0,07 (0,00)	0,06 (0,00)/ 0,06 (0,00)	0,06 (0,00)/ 0,07 (0,00)	0,06 (0,00)/ 0,06 (0,00)	0,07 (0,01)/ 0,06 (0,00)
GR_{SZ} A./C. (mean) [W/m^3]	204,61 (0,00)	209,42 (0,00)	223,01 (0,00)	204,94 (0,00)	223,53 (0,00)	212,70 (0,00)
GR_{SZ} A./C. (max) [W/m^3]	373,47 (0,00)	377,31 (0,00)	374,94 (0,00)	358,98 (0,00)	378,30 (0,00)	380,22 (0,00)
GR_{SZ} A./C. (min) [W/m^3]	10,49 (0,00)	35,18 (0,00)	22,16 (0,00)	16,97 (0,00)	29,81 (0,00)	17,38 (0,00)

Table S2. Growth rate as well as growth onset, duration and cessation averaged over all studied sites (+/- SE), aggregates by previously defined growth phases, for the focal species A. granatensis *(A.) and* C. galianoi *(C.).*

Year	2015	2016	2017	2018	2019	2020
Growth A./C. First phase [µm]	40,35 (19,2)/ 29,66 (8,9)	30,21 (21,9)/ 61,38 (21,1)	24,23 (9,1)/ 68,31 (20,8)	25,69 (8,1)/ 77,82 (43,9)	11,83 (5,6)/ 21,80 (13,7)	22,24 (5,7)/ 28,26 (15,5)
Onset A./C. First phase [DOI]	125,4 (13,7)/ 42,9 (13,3)	50,0 (22,2)/ 43,8 (12,4)	79,4 (12,3)/ 50,5 (16,3)	97,8 (13,6)/ 55,4 (14,6)	81,0 (14,3)/ 104,6 (4,3)	65,3 (9,7)/ 43,3 (12,8)
Duration A./C. First phase [DOI]	21,4 (0,58)/ 115,9 (14,5)	55,4 (25,5)/ 103,4 (14,0)	30,7 (17,2)/ 99,4 (16,2)	31,0 (14,0)/ 91,4 (17,3)	26,4 (13,8)/ 23,0 (11,9)	59,0 (10,8)/ 90,5 (18,4)
Cessation First phase [DOI]	146,9 (13,9)/ 158,8 (10,6)	105,4 (30,1)/ 147,2 (4,1)	110,1 (18,7)/ 149,9 (1,6)	128,8 (1,6)/ 146,9 (12,9)	107,4 (3,5)/ 127,6 (10,8)	124,3 (10,8)/ 133,8 (8,1)
Growth A./C. Second phase [µm]	116,1 (40,1)/ 14,15 (4,8)	142,06 (31,0)/ 21,15 (7,5)	70,01 (27,3)/ 49,19 (17,9)	102,96 (29,0)/ 52,71 (27,6)	101,58 (34,8)/ 17,06 (8,1)	109,00 (28,6)/ 14,53 (6,9)
Onset A./C. Second phase [DOI]	219,0 (6,4)/ 246,0 (11,4)	224,0 (20,7)/ 281,0 (15,6)	226,0 (9,6)/ 270,6 (16,3)	219,3 (4,1)/ 221,6 (1,9)	242,9 (18,0)/ 278,6 (21,2)	231,4 (15,2)/ 259,8 (22,7)
Duration A./C. Second phase [DOI]	98,6 (8,5)/ 63,0 (12,0)	121,2 (21,3)/ 64,1 (13,1)	94,1 (17,1)/ 82,0 (18,1)	111,4 (8,1)/ 114,4 (6,1)	105,1 (19,9)/ 68,4 (18,7)	105,3 (17,6)/ 76,0 (25,6)
Cessation A./C. Second phase [DOI]	317,6 (6,1)/ 309,0 (3,4)	345,2 (2,0)/ 345,1 (4,6)	320,1 (13,4)/ 352,6 (5,1)	330,8 (5,9)/ 336,0 (5,5)	348,0 (3,4)/ 347,0 (5,4)	336,8 (7,3)/ 335,8 (71)

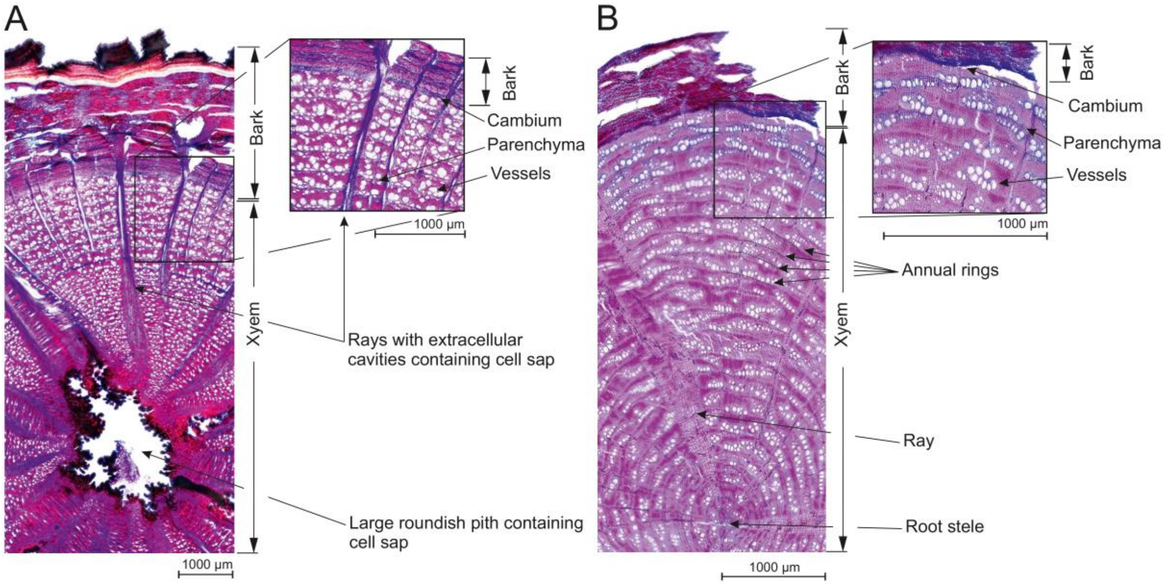

Fig. S1 Illustration of the species´ wood anatomy. (A) Cross section of A. granatensis *showing species ring-porous to semi-ring porous xylem anatomy. The extracellular cavities of the medullary rays and the pith contains gum, which we assume fulfils numerous storage functions, allowing species to partially decouple from environmental conditions by using stored water, nutrients and osmolytes for growth. (B) Cross section of* C. galianoi *showing species semi-ring porous xylem anatomy with clumps of vessels accompanied by parenchyma cells, which we assume allows species to repair air embolism likely occurring after severe dehydration during dry periods.*

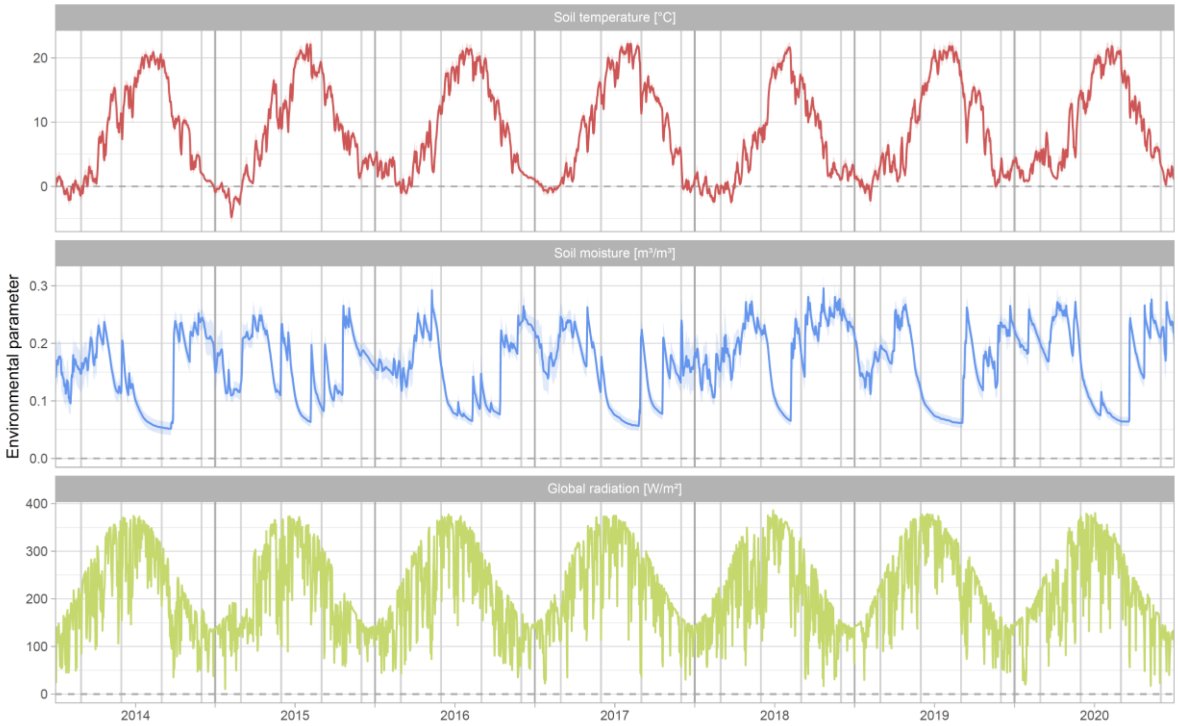

Fig. S2 Illustration of micro-environmental data. Root zone temperature (ST_{RZ}), root zone soil moisture (SM_{RZ}) and stem zone global radiation (GR_{SZ}) regimes (daily means, derived from hourly measurements) averaged over all study sites, with shaded areas indicating standard deviation. Daily means of global radiation wind speed and precipitation derived from hourly measurements at the climate station of the study area.

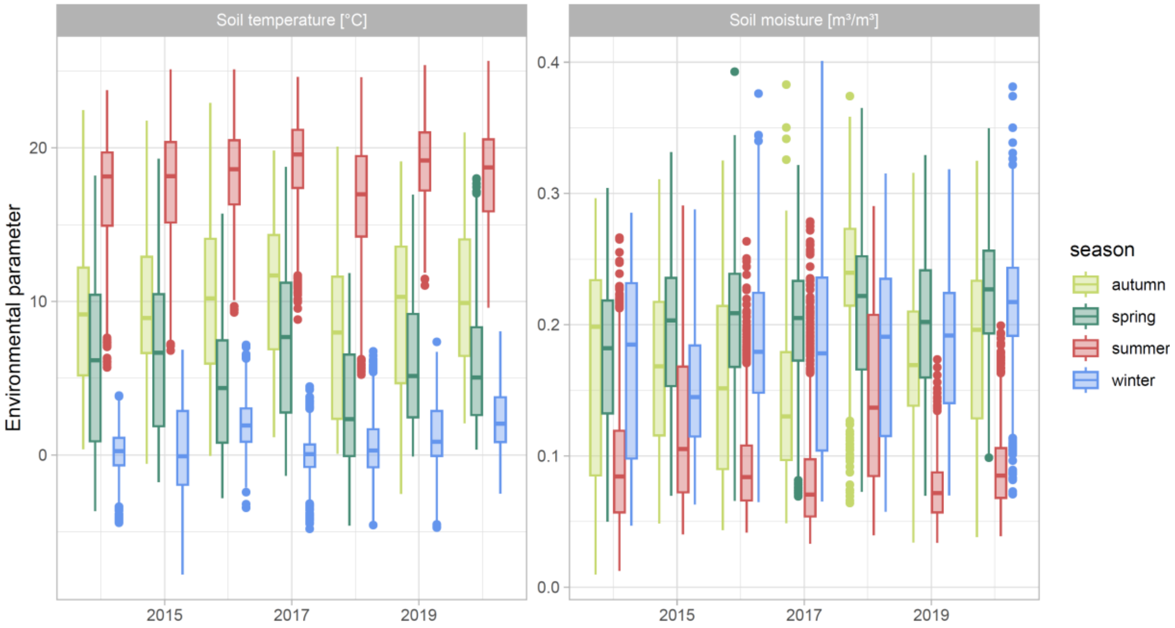

Fig. S3 Boxplot of environmental conditions showing the distribution of T_{RZ} and SM_{RZ} for the four seasons for all years under consideration.

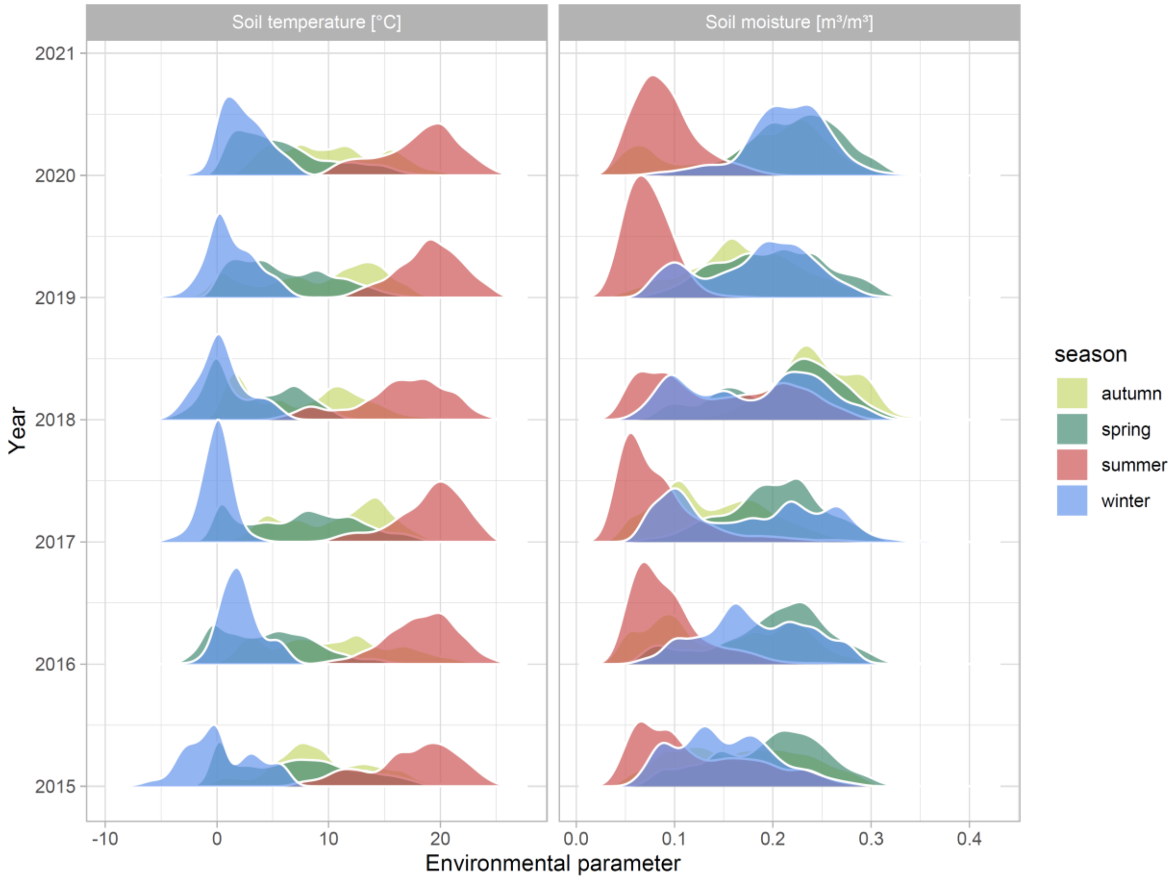

Fig. S4 Ridgeline plot of soil temperature (ST_{RZ}) and soil moisture (SM_{RZ}), showing the frequency of ST_{RZ} and SM_{RZ} values over all six monitored years at all studied sites.

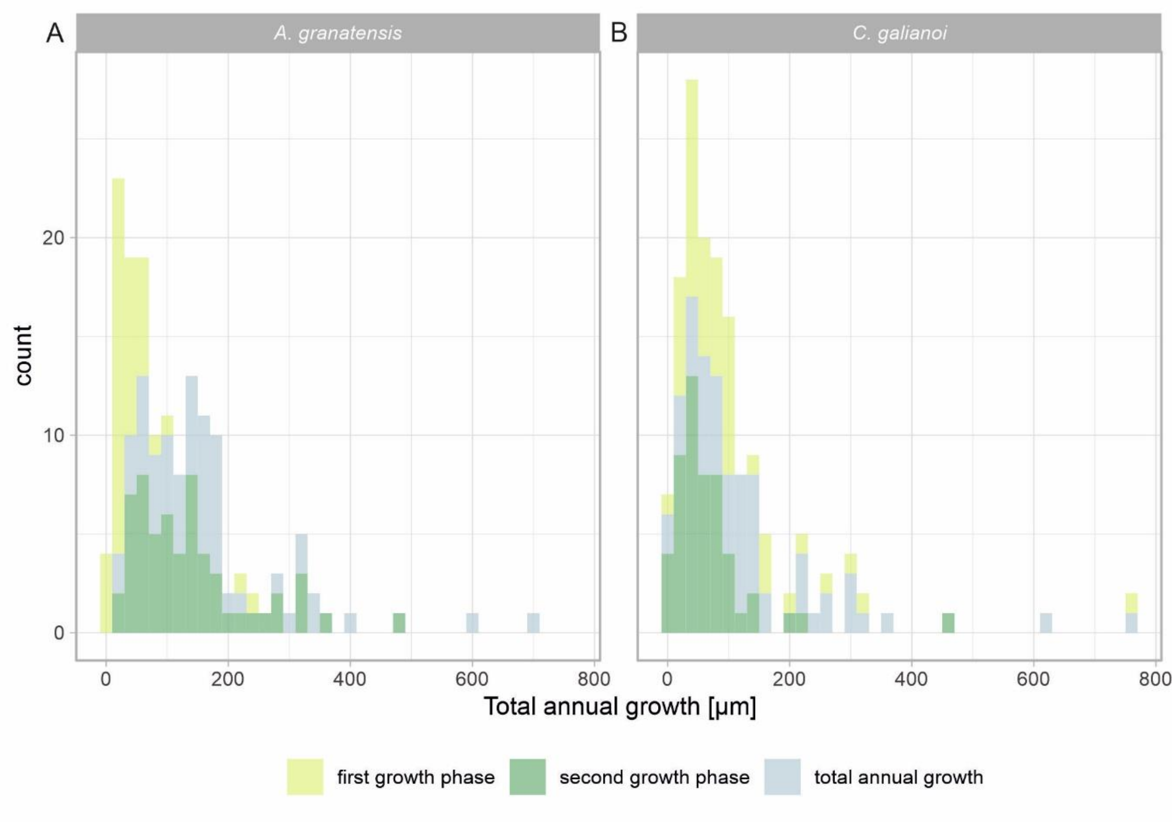

Fig. S5 Frequency distribution (histogram) for total annual growth as well as growth in the first and second growth phase in A. granatensis *and* C. galianoi*.*

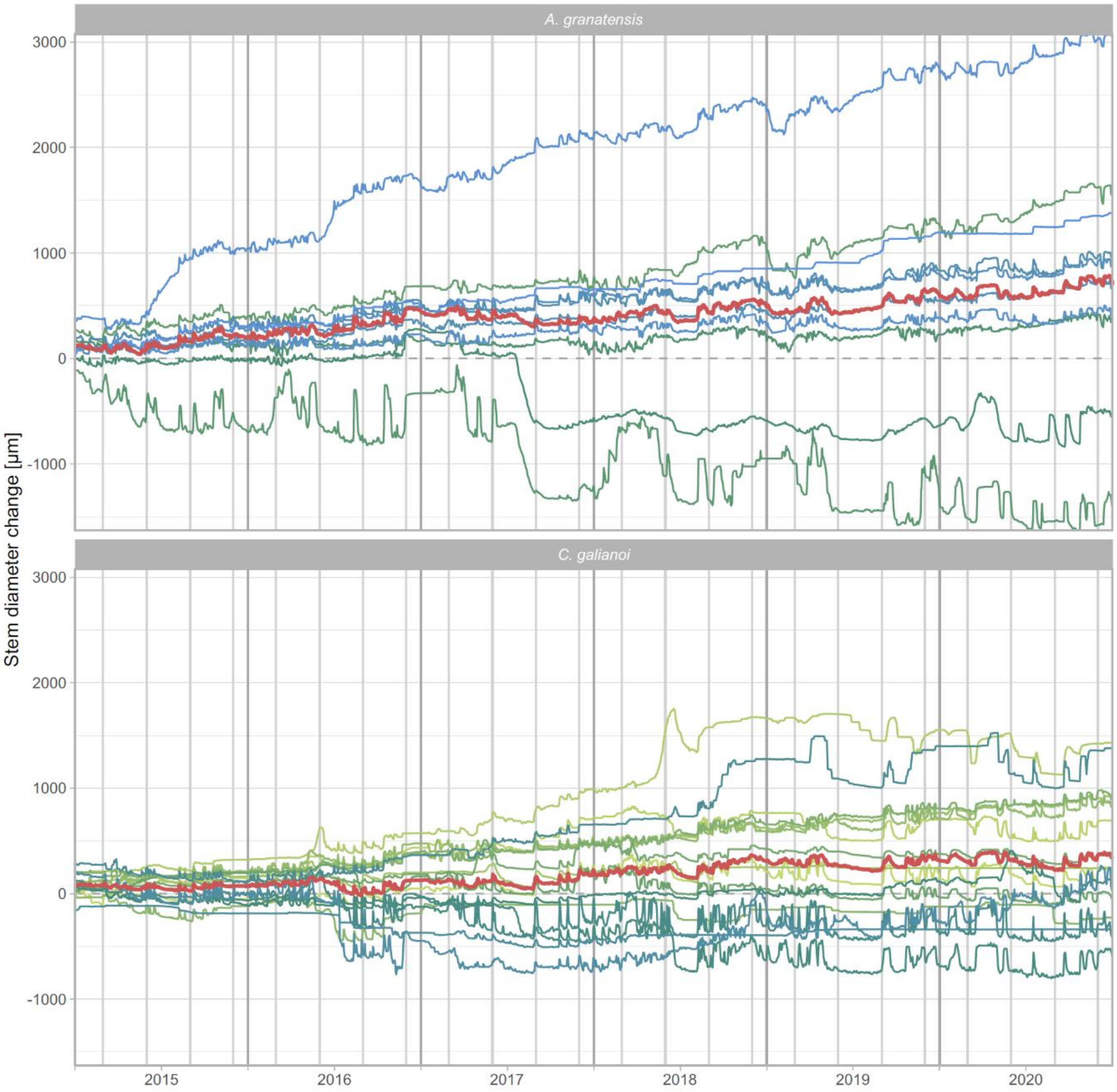

Fig. S6 Stem diameter change for all A. granatensis *and* C. galianoi *specimens as derived from dendrometer measurements with overall mean in red. In 2017, departed from the general pattern, when stem diameter of two specimens decreased, likely due to mechanical damage which resulted in the absence of the second growth phase.*

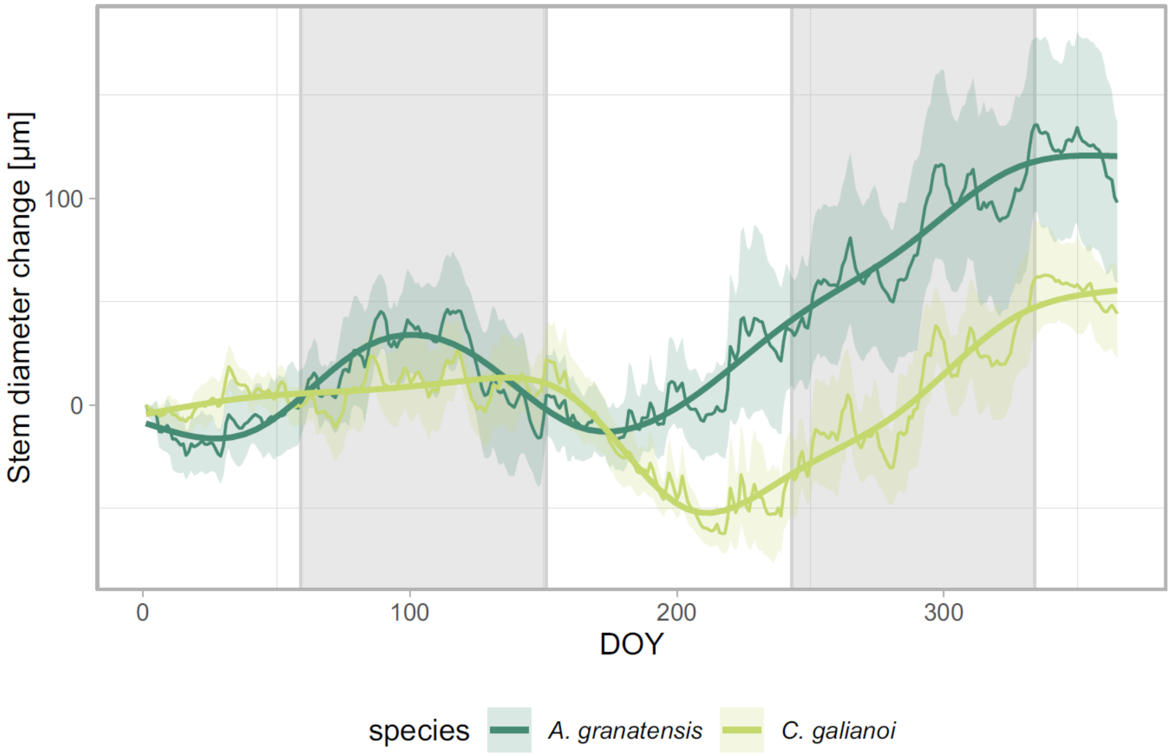

Fig. S7 *Seasonal pattern of stem diameter change during the curse of one year averaged over the studied period 2015 – 2020 and represented by generalized additive models (GAMs).*

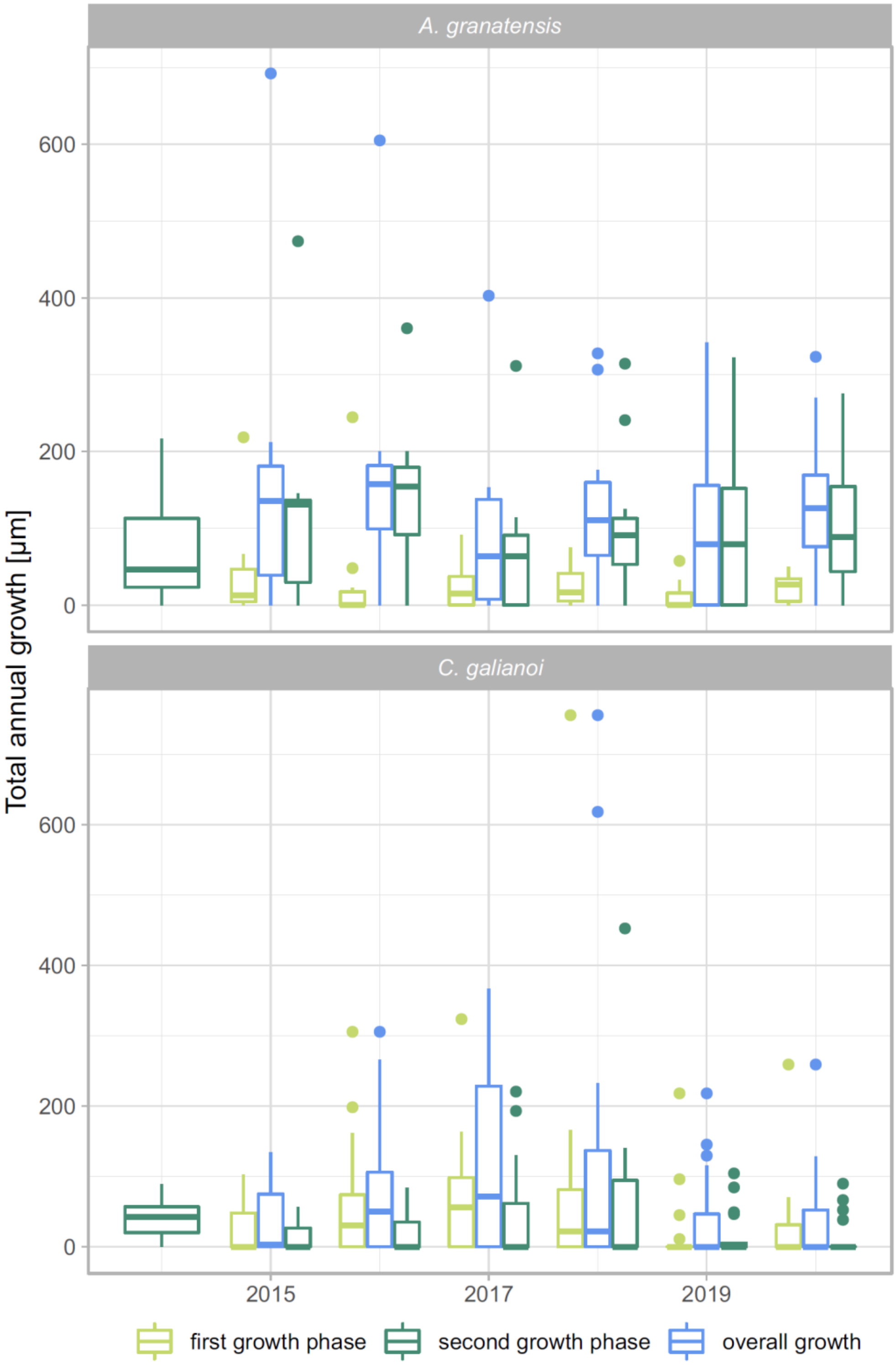

Fig. S8 Growth phases boxplot showing the distribution of total annual growth as well as growth in the first and second growth phase in A. granatensis *and* C. galianoi*.*

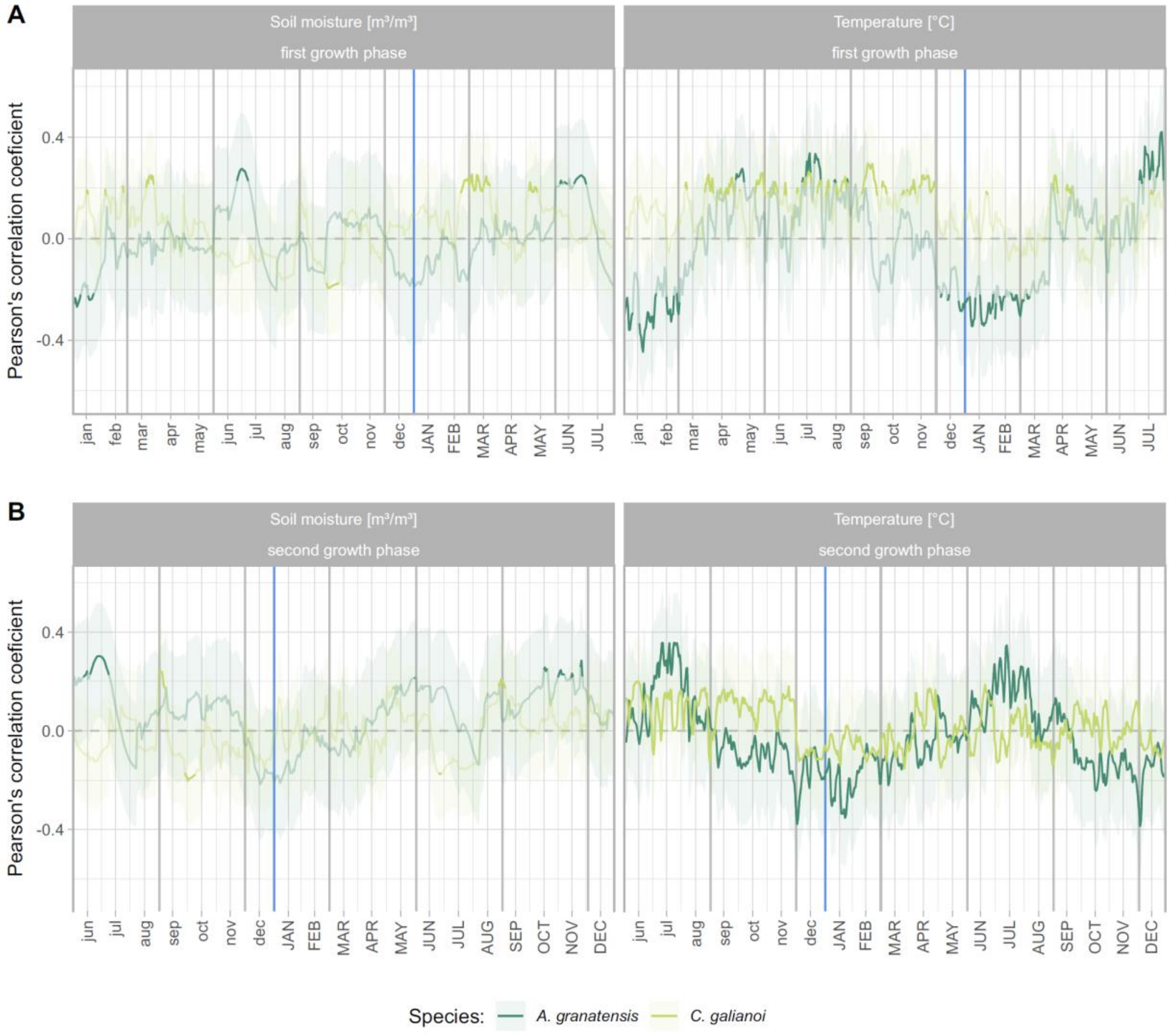

Fig. S9 Pearson's correlation coefficients calculated between first (A) and second (B) growth phase as derived from the dendrometer curves and daily soil moisture ($SM_{RZ)}$ and soil temperature ($T_{RZ)}$ data, measured at the individual sites. Transparency indicates non significance.

10 Patterns, timing, and environmental drivers of growth in two coexisting green-stemmed Mediterranean alpine shrubs species in the Sierra Nevada (Spain)

→ **Paper 3**

Albrecht, E. C., S. Dobbert, R. Pape, and J. Löffler. 2023c. Unpublished Manuscript.

Author contributions

J.L. had the idea, designed the research platform, and together with E.C.A. conducted the field work and ran the long-term LTAER-ES project. S.D. wrote the statistical codes and helped with data management and figures. E.C.A. led the writing of the manuscript, analysed the data, with contributions from S.D., R.P. and J.L. This manuscript is exclusively part of only this dissertation (E.C.A.).

Abstract

The Mediterranean alpine is one of the most vulnerable ecosystems under future global warming. Yet, patterns, timing and environmental controls of plant growth in these ecosystems are still poorly investigated. We aimed at a better understanding of growth processes within the Mediterranean alpine by closely examining two common, coexisting green-stemmed shrub species. Using dendrometers to measure daily stem diameter changes, we were able to separate 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, in combination with corresponding soil temperature and soil moisture data, we found species-specific growth patterns related to different drought-adaptive strategies. We show how the winter-cold adapted species *Cytisus galianoi* has a higher ecological plasticity using a drought tolerance strategy. Thus, this species might gain a competitive advantage under future climate warming. In contrast, the co-existing species *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. Contradicting the literature, we argue that pre-growth conditions are more relevant than conditions during growth, controlling the species resource availability and fitness.

Key words

Dwarf shrubs, secondary growth, climate-growth relations, dendrometer, growth physiology, *Cytisus galianoi*, *Genista versicolor*, alpine ecology, climate change, drought resistance.

Introduction

The Mediterranean alpine is discussed as one of the most vulnerable ecosystems under future global warming (Grabherr et al. 1994, Nogués-Bravo et al. 2008, Benito et al. 2011). However, little is known about the temporal, spatial, and interspecific differences in cambium dynamics, and the drivers of plant growth and plant productivity within these ecosystems are still poorly understood (Tumajer et al. 2021). Climatic variability has a direct effect on the rate and timing of xylem cell production in woody plants since cambial activity is generally understood as being controlled by temperature and humidity (Vaganov et al. 2006, Rossi et al. 2016, Huang et al.

2020). However, given the complexity and spatial heterogeneity of the observed environmental variability, overarching patterns and underlying physiological processes remain poorly understood (Gamm et al. 2018, Myers-Smith et al. 2020). Consequently, a better understanding of long-term patterns in cambial phenology of alpine shrubs is crucial (cf., Tumajer et al. 2021), especially for predicting their future performance (e.g., Cotto et al. 2017, Magaña Ugarte et al. 2019).

The Mediterranean climate with its warm, dry summers and cool, humid winters has been shown to influence cambium activity in Mediterranean woody plants. For these plants, growth is maximized during spring and autumn, but reduced during summer and winter (Cherubini et al. 2003, Gutiérrez et al. 2011, Touchan et al. 2012, Pacheco et al. 2018). Such a growth bimodality has been suggested as an adaptation enabling shrub species to withstand the dual climatic stressors of winter cold and summer drought by maximizing growth during the mild, moist seasons (Camarero et al. 2010, Mitrakos 1980).

Spring growth initiation has been subject of multiple studies across a variety of environments, which generally agree that spring growth is triggered by thermal thresholds (e.g., Deslauriers et al. 2008, Camarero et al. 2010, Vieira et al. 2014, Rossi et al. 2016, Zhang et al. 2018). However, increasing humidity from spring precipitation has been identified as an additional driver of spring growth in the Mediterranean (e.g., Camarero et al. 2010, de Luis et al. 2009, Vieira et al. 2014, Pellizzari et al. 2017). Furthermore, resumption of radial growth after the dry summer period has been linked to autumn rains (e.g., de Luis et al. 2007, 2009, Touchan 2012). Still, there has been little research into the influence of water availability on the onset of xylogenesis in cold semiarid climates (Ren et al. 2018).

In the Mediterranean, water availability is the most limiting abiotic factor for plant growth and productivity (Meinzer et al. 2006, Battipaglia et al. 2014, Szymczak et al. 2020). In the alpine areas of this biome water shortage during periods with frozen ground is crucial besides summer droughts (Dobbert et al. 2022a). Here, plants employ three common strategies to adapt to water scarcity: 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 levels (Chaves et al. 2003, Chen and Wang 2009). These strategies are not mutually exclusive, and plants can even use combined strategies (Guo et al. 2017). Little is known about the adaptive capacity necessary to use such strategies in specific alpine environments.

Here, we aimed at a better understanding of alpine shrub growth processes in the Mediterranean by observing growth patterns in two coexisting green-stemmed species, *Cytisus galianoi* and *Genista versicolor*. According to similarities in their traits, we expected to find a) similar intra- and inter-annual growth patterns, b) synchronicity of growth timing, and c) similar environmental drivers. By mounting dendrometers on the shrubs´ stems to monitor stem diameter changes, in combination with high-resolution environmental data, we were able to identify both water-related patterns of stem swelling and shrinking, as well as irreversible secondary growth.

Material and Methods

Shrub species

Here, we focused on the two coexisting green-stemmed dwarf shrubs *Cytisus galianoi* Talavera & Gibbs (hereafter *C. galianoi*) and *Genista versicolor* Boiss. (hereafter *G. versicolor*) (Fig.1), abundant in the Sierra Nevada mountains (Spain) and endemic to the south of the Iberian Peninsula (Kamari et al. 2010, Melendo et al. 2003, Giménez et al. 2004). Both are long-living, cushion-forming shrubs, with *C. galianoi* classified as chamaephyte and *G. versicolor* as nanophanerophyte (Melendo et al. 2003). They belong to the Fabaceae family and are both N-fixing species (Macek et al. 2016). Overall, they are of similar habit with slight distinctions. Both form dense cushions which literally merge into one another at many sites and produce only a few small leaves (up to 0.5 mm) during anthesis in May/June (Talavera and Gibbs 1997, Blanca et al. 2009a). But, both the elasticity of the above ground biomass and the greenness of their photosynthetic stems vary (cf. Bossard and Rejmanek 1992), with *C. galianoi* having more elastic and greener stems than *G. versicolor*, whose branches are comparatively rigid and unbending and appear rather greyish. In addition, *G. versicolor* forms one main taproot while *C. galianoi* has a more extensive, highly branched root system that extends less deeply into the soil and forms lateral ramets just below the soil surface (cf. Fernández-Santos et al. 2004). In contrast, their xylem anatomy and hydraulic architecture is again very similar, with both species showing semi-ring porous wood with clusters of vessels accompanied by small parenchyma cells (Fig. S1).

Density and surface cover of our species differ with elevation, aspect, slope and curvature. *C. galianoi* shows a relatively wide biogeographical and ecophysiological range, occurring at elevations up to 2700 m a.s.l. along the microtopographical gradient from exposed ridges with severe frosts during winter to early snowbeds. *G. versicolor* diminishes with elevation (cf. Lorite 2001) and is restricted to the more protected early snowbeds and slopes (Löffler et al. 2022). Like *C. galianoi*, *G. versicolor* presumably creates its own microhabitat (Pistón et al. 2016). In this study, nomenclature and taxonomy of the focal species followed Blanca et al. (2009b).

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 a.s.l. in the west, and from 2100 to 2600 m a.s.l. in the east, respectively (Fig. 1). Here, our focal species dominate the vegetation cover and coexist at the slopes in mid-alpine environments (Löffler et al. 2022). Located within the Mediterranean biome, 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, Anderson et al. 2011, Jiménez-Moreno and 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 and Polo 2016, Gómez-Ortiz 2019), with plants exposed to cold winters, high solar radiation, strong winds and snowfall, resulting in comparatively short growing seasons (Valle 2003).

Here, we studied slope positions that we stratified-randomly selected from the treeline upwards at ~100-m intervals following the framework of our long-term alpine ecosystem research project (LTAER; e.g., Löffler et al. 2021, Löffler et al. 2022). At these positions, our species experience periodic snow cover during longer winter periods as a result of wind drift and lee-side effects in the complex alpine topography, leading to a fine-scale mosaic of scattered shrub patches, grasses, open rock, and debris (Löffler et al. 2022).

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 DRO; Ecomatik, Dachau/Germany), using sensors with a temperature coefficient of <0.2 μm/K which recorded data at 1 minute intervals. The dendrometers were mounted on an aluminium bar, attached to the selected stems horizontally above the ground surface (approximately 1 cm above ground) (Fig. 1). To minimize the influence of hygroscopic swelling and shrinking of the bark (Zweifel and Häsler 2001), we removed the outermost layers of dead periderm (0.5 mm) at the contact point of the dendrometer sensors (cf., Dobbert et al. 2022b). In this monitoring setup, the dendrometers were placed on the main stem, as close as possible to the presumed root collar, which is believed to integrate the growth of all plant parts (Bär et al. 2006, 2007, Ropars et al. 2017). However, the variation within individual specimens and between multiple stems of the same specimen is not yet fully understood (Dobbert et al. 2021). To account for this variation, we monitored a large number of specimens, representative of the conditions observed at each site, avoiding positions near stones and small depressions. To obtain daily mean values from our raw data set, we averaged the dendrometer data following the "daily mean approach" (Deslauriers et al. 2007). Subsequently, we normalized the annual stem diameter curves by removing the initial stem diameter, which ranged from 3970.98 µm to 8779.10 µm for *C. galianoi* and from 4453.43 µm to 13307.36 µm for *G. versicolor,* from the annual curves. This was necessary because our dendrometers measured changes in stem diameter relative to the start of the measurement cycle and not the absolute stem diameter. Finally, we checked the data for outliers, defining the interquartile range (IQR) and the 25th (Q1) and 75th (Q3) percentile (Q1/Q3 -/+ 1.5*IQR) as cut-off ranges. Since we did not find any outliers, all daily measurements per curve were retained. Our measuring period comprised six full consecutive years (January 1, 2015, to December 31, 2020).

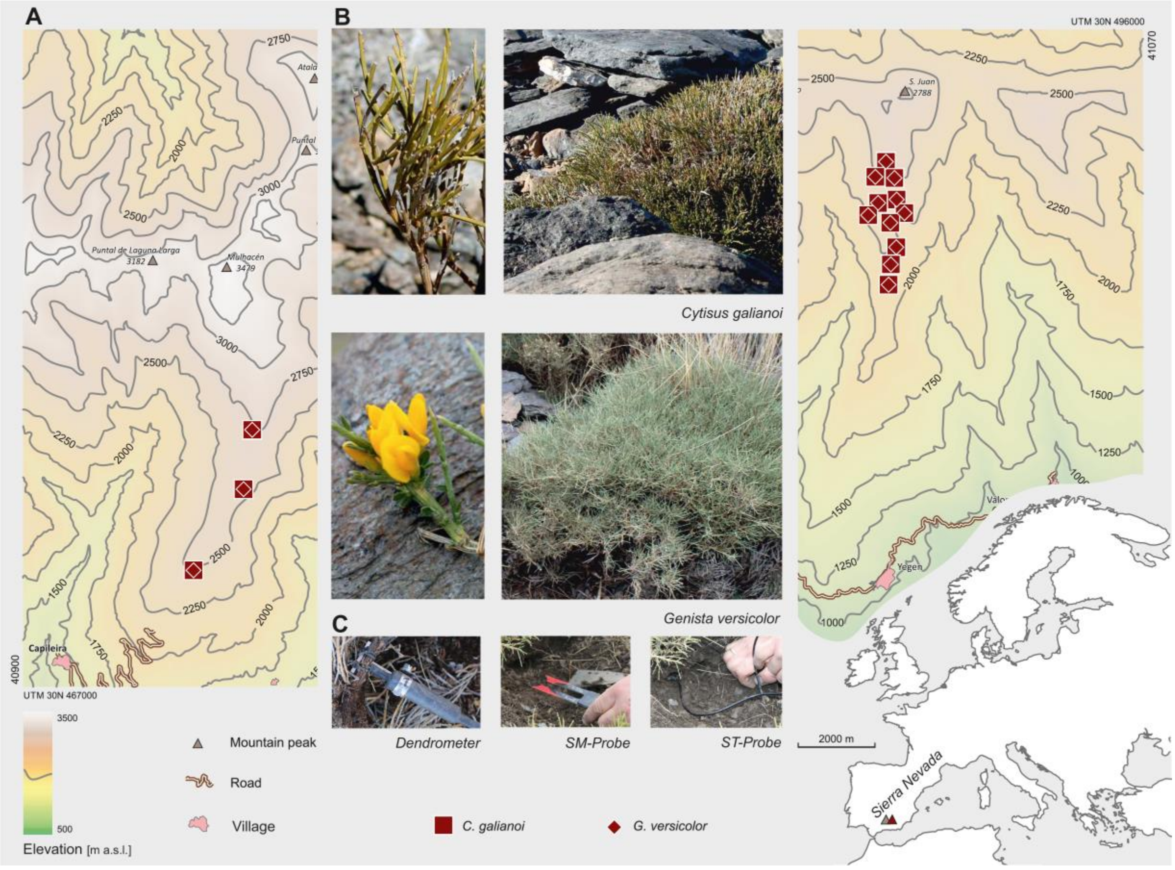

Fig. 1 Study regions in the Sierra Nevada (Spain) and location of the study sites (A). Photos show our two focal species C. galianoi *and* G. versicolor *(B) as well as our monitoring set up with a mounted dendrometer, soil moisture probe and soil temperatures probe (C).*

Micro-environmental conditions

To assess the environmental drivers of the monitored radial stem diameter variations, we measured micro-environmental parameters at each site and for each specimen separately, namely temperatures (°C, hereafter T_{RZ}) and volumetric soil water content (m^3/m^3, hereafter SM_{RZ}). Thermistors (type S-TMB-002, ±0.2°C accuracy) and soil moisture probes (type S-SMD-M005, ±3% accuracy) were installed at 10 cm soil depth within the root zone of each specimen (c.f. Löffler and Pape 2020, Dobbert et al 2021). Both environmental datasets were recorded at 1-min intervals and stored as daily averages using ONSET´s HOBO Loggers (type H21-002). Complementary, we recorded the global radiation (W/m^2) (hereafter GR_{SZ}) at 1 cm above the ground surface in the stem area of one specimen at a ridge site at 2692 m a.s.l. using a silicon pyranometer (type S-LIB-M003) with ±10 W/m^2 accuracy. All micro-environmental data were collected for the period January 1st, 2015 to December 31st, 2020, with additional data from 2014. There were no missing data at the selected sites.

The mean below-ground T_{RZ} and SM_{RZ} regimes for all monitored specimens as well as the near-ground GR_{SZ} regime measured at one site at 2692 m a.s.l. are shown in Figs. S2 and S3 and listed in Tab. S1 (see also Löffler et al. 2022). In accordance with the overarching Mediterranean climate (e.g. Mitrakos 1980, Camarero et al. 2012), the overall climatic conditions at our slope sites were characterized by mild and moist spring and autumn conditions, as well as warm and dry summers with high solar radiation and cold winters. These winters were characterized by periodic snow cover persisting over weeks, after long, cold winters especially at high elevations sometimes even into spring (Löffler et al. 2022). T_{RZ} began to rise in

March/April in most years, exceeding 10°C in May/June and reaching 20°C in July/August. Sub-zero T_{RZ} in winter did not occur. SM_{RZ} was usually high throughout winter, with the winters 2015/2016 and 2018/2019 forming exceptions. In these years SM_{RZ} increased in March/April and reached its spring peak in May, (> 0.20 m^3/m^3). Thereafter, SM_{RZ} decreased until August, when the first autumn rains replenished the soil. Yet, in most years SM_{RZ} decreased again and a soil moisture content of 0.20 m^3/m^3 was reached in November/December only. Overall, both, T_{RZ} and SM_{RZ}, were slightly higher for *C. galianoi*, with lowest annual mean T_{RZ}, than for *G. versicolor*. Highest SM_{RZ} was recorded in 2018, when an exceptionally short summer drought was followed by a comparatively long and moist autumn period. In contrast, the autumns in 2017 and 2019 were comparatively dry and were followed by humid winters.

Analysis of growth patterns

From the measured dendrometer curves, we defined two growth phases, one during the first half of the year (first growth phase) and one during the second half of the year (second growth phase), which are intermitted by a first phase of stem contraction during summer (drought period) and a second phase during winter (cold period). 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 species (e.g., Camarero et al. 2010) and potentially also in Mediterranean alpine species (Olano et al. 2013). Here, growth-induced irreversible stem expansion (hereafter 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 incremental increase in stem radius when the measured radius 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, but does not necessarily occur every year or every half year, i.e. 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).

Correlations analysis and linear mixed effects models

To uncover climate-growth relations for our two focal species, we examined the influence of microclimate on shrub growth using Pearson´s correlation coefficients, calculated in the statistical software R (R Core Team 2020). Correlations were calculated between semi-annual irreversible stem growth and daily mean values for our environmental parameters T_{RZ} and SM_{RZ} for the years 2015 to 2020. To account for possible lagged effects of previous-year conditions on current-year growth, we included environmental data from the respective previous year in our correlation, similar to analyses of growth chronologies derived from ring width series (e.g., Bär et al. 2008, Weijers et al. 2018). For this purpose, we included additional environmental measurements from before the start of our study period (2014) in our calculations. To include 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, we chose semi-annual irreversible stem growth as response variable, and monthly mean values for all environmental parameters as fixed effect. The individual specimens were included as random effect. Overall, for the comparison of our focal species, we performed all correlation analyses separately for each *C. galianoi* and *G. versicolor* specimen to avoid generalizations that might result from averaging the data measured at each site. Averages were calculated for visualization purposes only.

Partial least squares regression

In a final step, we applied partial least squares regression (PLSR; Wold 1975, Abdi 2010), to our dataset to complement the correlation analysis and identify crucial environmental thresholds promoting or impeding growth. We used variable selection methods to define a subset of relevant conditions and to assess their relative importance. PLSR, originally intended for the analysis of multidisciplinary problems (Wold 1980), has been implemented in ecological studies over the past decade (Carrascal et al. 2009, Frindte et al. 2019, Löffler and Pape 2020). Its main advantages include that it works without distributional assumptions (Wold 1980, Dijkstra 1983, Vinzi et al. 2010) and its applicability to data where the number of predictors exceeds the number of observations or the predictors are highly correlated. This distinguishes PLSR from classical methods such as multiple linear regression and principal component regression and makes it particularly suitable for our purposes

(Geladi and Kowalski 1986, Carrascal et al. 2009, Frindte et al. 2019). We aggregated our environmental data and rounded them to 0.5 °C for T_{RZ} and 0.01 m^3/m^3 for SM_{RZ} values. We then counted and summed the frequency of each value occurring within the rounded time series (Löffler and Pape 2020) for each meteorological season. This approach yielded sets of predictor variables that were then scaled and centered. The associated response values were the semi-annual growth values, which turned out to be almost normally distributed (Fig. S4). 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 (overview in Mehmood et al. 2012) using the the selectivity ratio (SR), which is 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. The variables with the highest values represent the most influential variables (Rajalahti 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 and Pape 2020). In this way, we were able to clearly identify the environmental conditions that are significantly related to annual growth.

Results

Our results reveal a) general growth patterns, b) timing of growth, and c) environmental drivers of growth, differing between the two focal species.

a) Patterns of stem diameter change and growth

Overall, annual stem diameter change in our two focus species was of bimodal character, yet we observed pronounced intra- and inter-annual variability, as well as species-specific patterns (Fig. 2). *C. galianoi* showed a larger amplitude in stem diameter (Fig. S5) and a more pronounced bimodality than *G. versicolor*, with *G. versicolor* showing a right-skewed pattern (Fig. S6). Differences in stem diameter change between the two species were most apparent during the meteorological summer months, when *C. galianoi* showed much stronger stem contraction than *G. versicolor* (Fig. 2). 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, although its stem diameter also reached its maximum in autumn (Figs. 2, S7, S8).

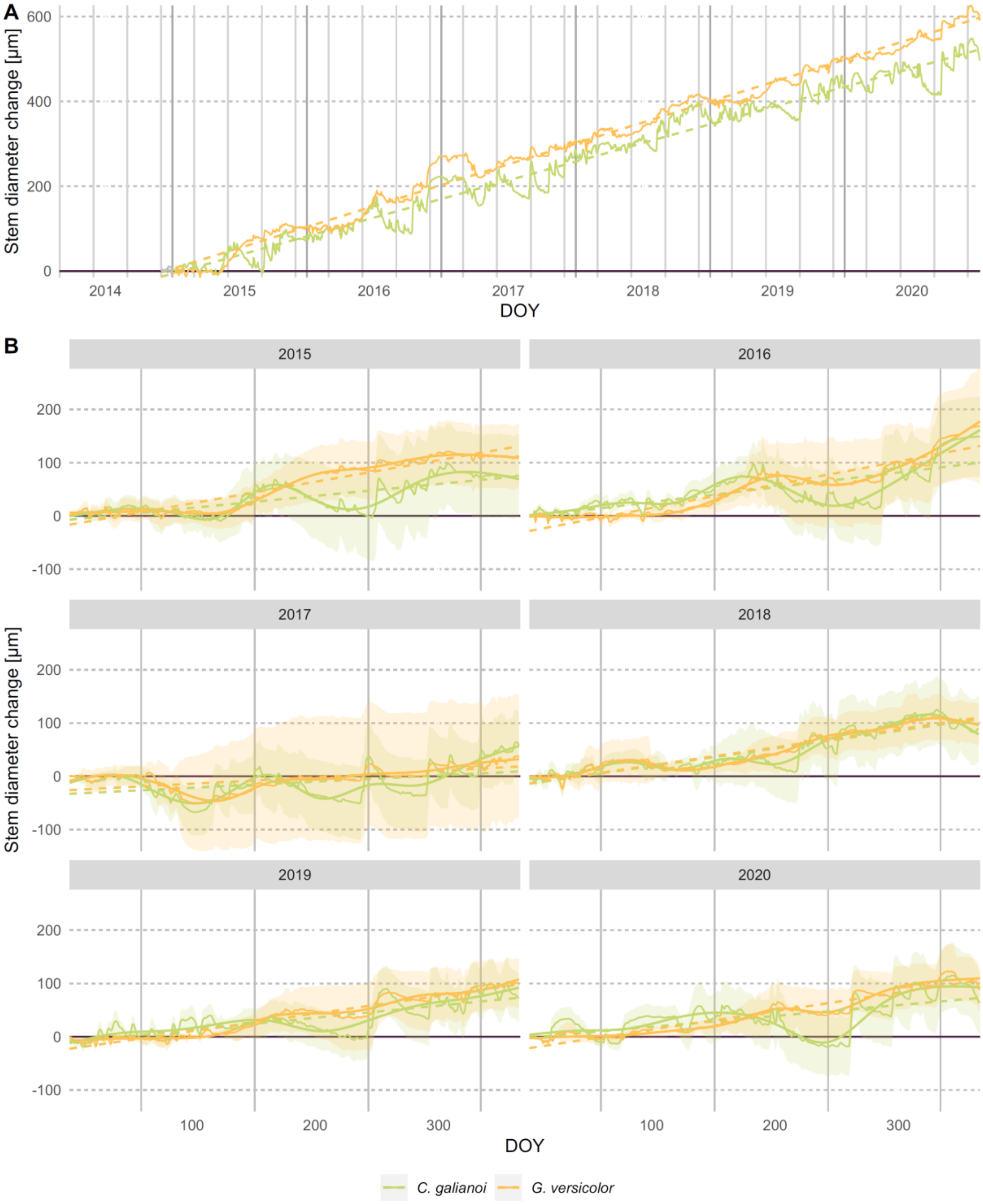

Fig. 2 Stem diameter change of our two focal species relative to the start of the measuring period (A) and averaged annual stem diameter change relative to the previous year's maximum represented by generalized additive splines (bold) and linear trends (dashed) (B). Transparency shows the standard deviation.

b) Timing of growth

The timing of growth (i.e., growth onset and growth cessation) in *C. galianoi* and *G. versicolor* is shown in Fig. 3 and Tab. S2. For both species, the onset of the first growth phase was usually in February/March, yet slightly earlier for *G. versicolor* compared to *C. galianoi*. Spring growth cessation usually occurred in May/June, and was usually slightly earlier in *G. versicolor* as well. In spring 2019, growth onset and cessation in *G. versicolor* were far delayed (by several weeks). Growth resumption after summer drought, i.e. the onset of the second growth phase, usually took place in August/September for *C. galianoi*, several weeks later than in *G. versicolor* (July/August). Growth cessation, however, was similar in both species (November/December). At the same time, the inter-annual variability of the duration of the two growth phases was high, and growth rates in both species were decoupled from this duration (Tab. S2, Fig. S8).

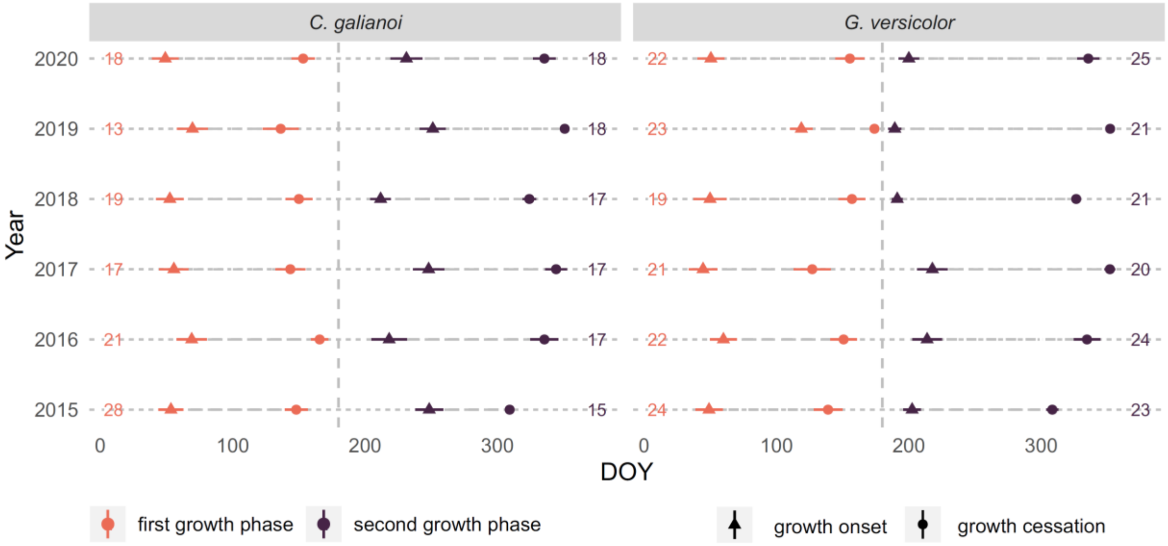

Fig. 3 Timing of growth (mean onset and cessation) derived from stem diameter curves averaged across all studied sites for the years 2015 – 2020. Numbers indicate the sample depth of the growing specimens. Short solid lines indicate the standard deviation of growth onset and cessation.

c) Environmental drivers of growth

Overall, we found complex, species-specific environmental controls of stem diameter change patterns. These controls strongly differed between the growth phases, with growth significantly linked to the environmental conditions prior to growth onset in both species (pre-growth conditions; Figs. 4, S9).

During the first growth phase *C. galianoi* performed best when the previous year (March to November) was characterized by high T_{RZ}, while there was no strong T_{RZ} control in *G. versicolor* during this period (Figs. 4, S9). On the other hand, previous year's SM_{RZ} conditions were not relevant for the first growth phase in both species, yet winter conditions prior to the growth onset showed contrasting relations to spring growth in both species. While winter T_{RZ} affected growth in *C. galianoi* slightly negatively (December to March) (Fig. 4), growth in *G. versicolor* was positively linked to winter T_{RZ} (December to February) (Figs. 4, S9). At the same time, both species benefitted from rather dry winter conditions (December to February), with *C. galianoi* benefitting explicitly from drought in February (Figs. 4, S9). 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. S2, Tab. S2). 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. S2, Tab. S2). We found negative correlations of spring growth in *C. galianoi* with April SM_{RZ} and positive correlations with June SM_{RZ} (Figs. 4, S9). Growth in *G. versicolor* positively correlated with April and June T_{RZ} (Figs. 4, S9).

During the second growth phase, growth in autumn was linked to pre-growth conditions, and both species performed best after a warm, dry winter, with winter T_{RZ} and SM_{RZ} signals being particularly significant in *G. versicolor* (Figs. 4, S9). Additionally, both species benefitted from low SM_{RZ} during early spring (especially March). *C. galianoi* performed best under high SM_{RZ} before the beginning of the dry period (May/June) but moisture supply during the dry period was detrimental (July), while *G. versicolor* was promoted by an earlier onset of the drought period (June) (Figs. 4, S9). 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. 4, S9). Furthermore, both species were promoted by high September T_{RZ} followed by cool and humid conditions during late autumn (October/November) (Figs. 4, S9). As such, low growth rates observed in autumn during the years 2017 and 2019 resulted from repeated drought spells in late autumn. In contrast, highest growth rates were achieved when the first autumn rains were followed by a warm, moderately humid autumn (Fig. S2, Tab. S2).

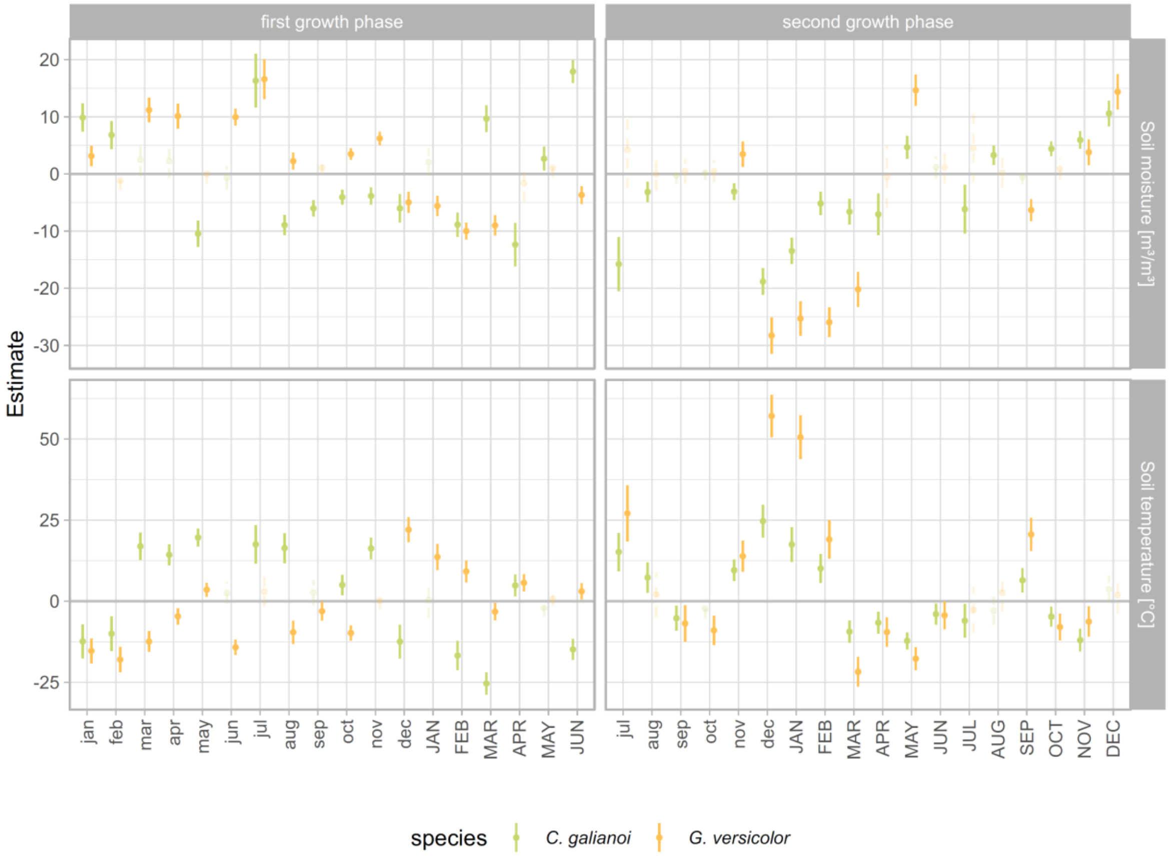

Fig. 4 Linear mixed effects analysis for growth during the first and second growth phase as derived from the dendrometer curves (dependent variable) and monthly environmental data (means) as fixed effects. The individual specimens entered as random effects. Short solid lines indicate the 95%-confidence interval. Abbreviations of months from the previous year are in lowercase letters and those of the current year are given in capitals.

The quantitative results from our PLSR analysis (Fig. 5) indicate that growth during the first growth phase in *C. galianoi* was promoted by T_{RZ} of 0.5°C during the pre-growth winter and during the current spring, whereas in *G. versicolor* was promoted by 5.0°C during the pre-growth winter. Inversely, spring growth of *C. galianoi* was impeded by T_{RZ} 3.5°C during the pre-growth winter, and in *G. versicolor* by 1.0°C during the pre-growth winter and the current spring. Growth in both species was co-driven by SM_{RZ} values indicating unfrozen ground (0.19 - 0.24 m^3/m^3), which in case of *C. galianoi* also occurred during the current spring.

During the second growth phase, growth of *G. versicolor* was promoted by pre-growth winter T_{RZ} of 5.0°C but impeded by pre-growth winter T_{RZ} 1.0°C, while *C. galianoi* had no pre-growth winter T_{RZ} driver, and both species did not have a strong pre-growth winter SM_{RZ} control. There was neither thermal nor hydric growth control from pre-growth spring conditions. However, autumn growth in *C. galianoi* was promoted when summer conditions were mild (10.0 – 16.5°C) and dry (~0.05 m^3/m^3) with T_{RZ} of 20.0°C having a negative influence on species performance, while again a significant signal was absent in *G. versicolor*. In autumn, *C. galianoi* was promoted by current 3.5°C T_{RZ}, while *G. versicolor* again was promoted by slightly higher T_{RZ} (5.0°), and T_{RZ} of 15.0°C were detrimental in both species.

All in all, the main findings on the environmental control of shrub growth in both species were that pre-growth conditions were far more decisive for growth than 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.

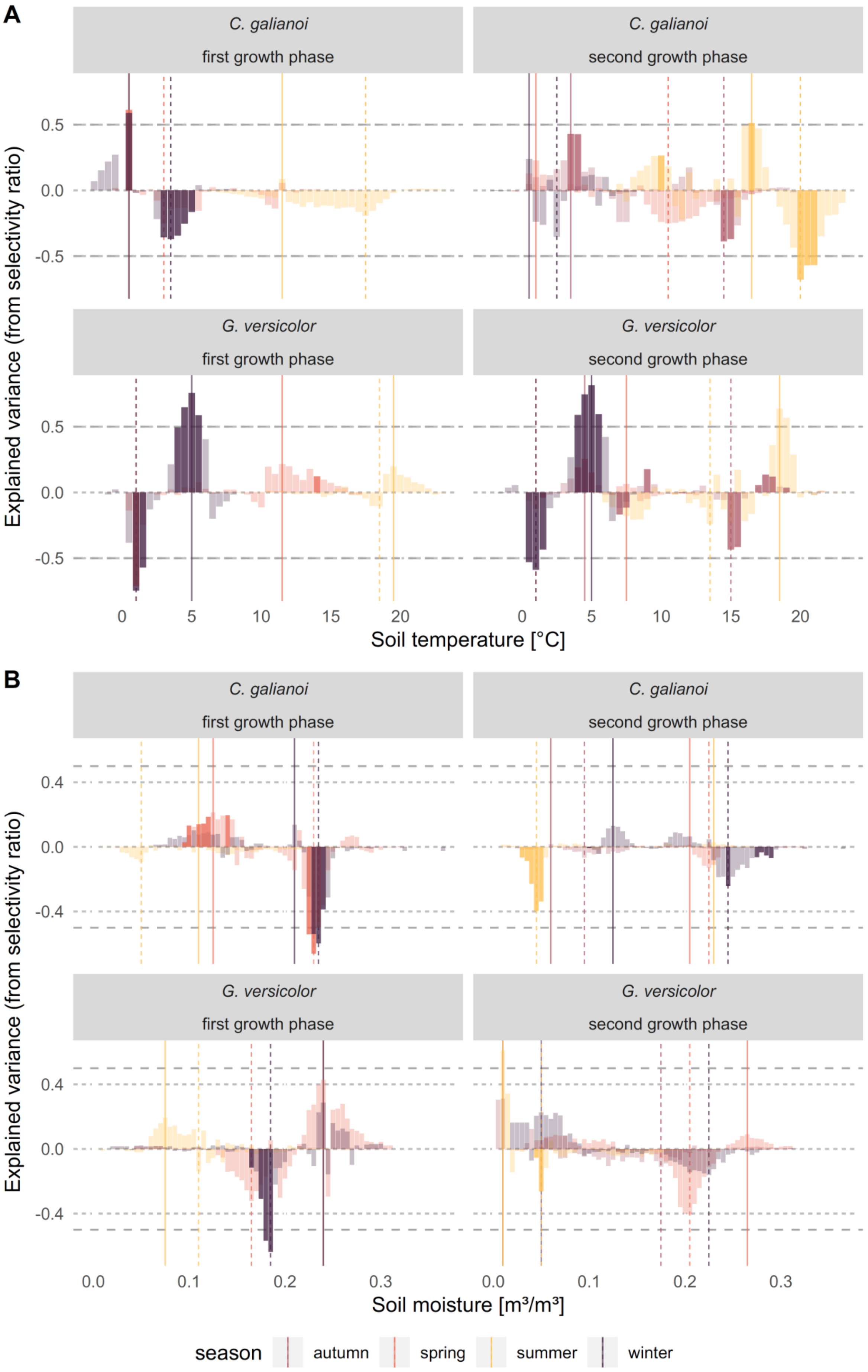
A
C. galianoi
first growth phase
C. galianoi
second growth phase
G. versicolor
first growth phase
G. versicolor
second growth phase
0.5
0.0
-0.5
Explained variance (from selectivity ratio)
0
5
10
15
20
Soil temperature [°C]
B
0.4
0.0
-0.4
0.0
0.1
0.2
0.3
Soil moisture [m³/m³]
season
autumn
spring
summer
winter

Fig. 5 Smoothed variance explained derived from selectivity ratio multiplied with the sign of its corresponding regression coefficient for soil temperature (ST_{RZ}, A) and soil moisture (SM_{RZ}, B) (independent variables) and total annual growth (dependent variable), derived from PLSR analysis. Shaded areas represent values rendered significance ($p<0.05$) and colors represent seasons. 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.

Discussion

a) Growth patterns

We observed bimodal annual patterns of stem diameter change in our two coexisting alpine shrub species and found from these overall stem diameter changes pronounced but contrasting bimodal growth patterns. However, while the patterns of stem diameter change showed strong similarities between the two species, they did not correspond to their growth patterns but rather reflect differences in rehydration patterns. As such, our results contradict general assumptions, suggesting that major growth processes in Mediterranean woody plants occur during spring, with a minor second growth phase in autumn (e.g., Pasho et al. 2012, Pellizzari et al. 2017, Alday et al. 2020, Camarero et al. 2021). For our focal species, contrasting growth patterns imply that the seasonality of xylogenesis is highly species-specific. Distinguishing between growth, defined as the irreversible radial stem expansion caused by dividing and enlarging wood and bark cells in the cambium, and reversible stem water deficit-induced shrinking and swelling of the stem caused by imbalances between transpiration and root water uptake (Zweifel et al. 2005, Zweifel 2016) helped us to deduce the species´ water use strategies from the overall stem diameter changes and to understand their contrasting growth patterns. Summer stem contractions and dehydration in *C. galianoi* suggest drought tolerance at the cost of reduced performance during autumn (cf. Bacelar et al. 2012), when rehydration is prioritized to increase the water potential prior to growth resumption, but with the advantage of benefiting from carbon fixation in winter and to maximize growth at high water potential in spring (cf., Bossard and Rejmanek 1992). The less pronounced summer stem contraction in *G. versicolor* suggests drought avoidance without compromising performance while maintaining physiological functionality for carbon fixation at high tissue water potential throughout summer (cf. Chaves et al. 2003, Bacelar et al. 2012), allowing the species to maximize growth with autumn rains.

b) *Timing of growth*

Our results confirm that the duration of rehydration processes depends on the species ability to withstand negative water potentials before cavitation occurs (Ennajeh et al. 2008), and on the duration and intensity of drought connected to the risk of embolism (Cochard and Delzon, 2013). Thus, the discrepancy in the timing of growth resumption between our two species is probably linked to differences in the species´ drought resistance. Their photosynthetically active stems might be key in achieving positive net photosynthetic rates in contrasting ways (cf., Bossard and Rejmanek 1992). 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 water deficit (stem contraction). As such, *C. galianoi* exhibits pronounced anisohydric behavior, and hence tolerates larger variation in plant water potential as a result of weak stem stomata regulation (cf., Jones 1998, Tardieu and Simonneau 1998). The species is thus able to still achieve high photosynthetic rates even under increasing water stress (Attia et al 2015). However, due to continued carbon uptake it will be more susceptible to damage from prolonged drought stress (Attia et al. 2015), which ultimately may reduce photosynthetic rates, and may lead to decelerated rehydration and consequently to delayed growth resumption. In contrast, *G. versicolor*, whose photosynthetically active stems are more greyish-green, retains higher water potential at the expense of lower net photosynthesis and exhibits less pronounced anisohydry (less severe stem contraction). Ultimately, the species will experience faster rehydration and consequently earlier growth resumption. Overall, we can conclude here that even slight variations in morphological traits in our alpine shrubs species result in distinct variations of species´ hydraulic behavior and thus in the timing of growth resumption.

The timing of spring and autumn growth in our species was variable and independent of the length of the growing season. This finding corresponds to several studies showing that plant performance under variable season lengths largely depends on the specific environmental drivers during and prior to the growth period (Hollesen et al. 2015, Weijers et al. 2018, Dobbert et al. 2021). The strong influence of pre-growth conditions on species performance has been linked to the critical time scale relevant to plant growth (cf., Löffler and Pape 2020), and is often still a missing dimension (Choler 2018, Niittynen and 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.

c) *Environmental drivers of growth*

Growth responses of our shrub species to their alpine environment are in line with earlier studies of Mediterranean tree growth, showing that late autumn to winter conditions prior to spring growth were crucial (e.g., Bogino and Bravo 2008, Camarero et al. 2013). We found that both of our species were promoted by dry winter conditions, while winter temperatures had contrasting growth responses, with *C. galianoi* showing a negative and *G. versicolor* a positive response. These contrasts in winter responses suggest that *C. galianoi* can cope with relatively low (but above zero) temperatures, possibly due its potential to tolerate dehydration by active stem contraction, similar to mechanisms shown in arctic-alpine shrubs (Dobbert et al. 2022b). Using its intensely green stems, *C. galianoi* may capitalize from additional photosynthetic opportunities (cf., Bossard and Rejmanek 1992, Wyka and Oleksyn 2014) which allow carbon fixation throughout winter, provided that snow cover does not hinder photosynthetic activity. Moreover, our finding that *C. galianoi* is promoted by winter temperatures of 0.5°C additionally confirms physiologically activity of winter-green species at low temperatures (cf., Oribe and Kubo 1997). As such, *C. galianoi* may benefit from increased synthesis of carbohydrates during the period of reduced respiration (cf., Gimeno et al. 2012, Camarero et al. 2013), when low soil temperatures promote the storage of carbohydrates in root parenchyma (cf., 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 (cf., Wheeler et al. 1979, Larsen et al. 2012). In contrast, our finding that *G. versicolor* is promoted by winter temperatures at 5°C indicates that it is sensitive to winter frosts and may therefore better perform under snow cover at lower alpine elevations. As such, our results underpin the biogeographical patterns of the species (Löffler et al. 2022). Since growth rates were highest in spring 2016 following a warm but snow-free winter, we assumed that *G. versicolor*, like *C. galianoi*, may capitalize from extra photosynthetic opportunities in snow-free winters, provided that temperatures are at 5°C.

C. galianoi's preference of humid and cool conditions at the beginning of the first growing season, when thin snow cover is still present, suggests that the species can capitalize from early defrost water and meltwater even during short windows of photosynthetic opportunities (cf., Starr and Oberbauer 2003). In contrast, *G. versicolor's* preference of warm and dry spring conditions suggests that precipitation, i.e. snow in the alpine, may hinder photosynthesis, possibly due to limited stomata conductance (cf., Starr 2001, Starr and Oberbauer 2003). Both of our species showed a positive correlation to April temperatures, which were previously identified as crucial in other Mediterranean alpine species, related to early cambium reactivation (Olano et al. 2013). However, since growth onset in our species was significantly earlier than April, April correlations here reflect the species' performance during the middle of our first growth phase. This is consistent with studies in arctic-alpine evergreen shrubs that have been shown to be promoted by mid-growing season temperatures (cf., Bär et al. 2008, Franklin 2012). At the end of the first growing season, *C. galianoi* preferred high soil moisture and low temperatures, while *G. versicolor* preferred continued drought and high temperatures. This suggests that *C. galianoi* benefits from early summer rains which provide sustained water supply well into the summer, being essential for the species´ tolerance to desiccate. In contrast, *G. versicolor* adjusts its hydraulic mode to drought by drought avoidance, and early summer rains might disrupt the species´ water-use efficiency.

Winter, spring and early summer drivers of growth during the first growth phase in our species, as described above, were still decisive for growth during the second growth phase, and only *C. galianoi* was additionally impeded by water supply in July. Such occasional summer rains may inforce the species´ stomata activity when they have adapted to drought, when summer rains might disrupt the species´ water-use efficiency in *C. galianoi* as well. 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. We argue that *C. galianoi´s* drought tolerance is based on elastic stems which may shrink upon water loss while maintaining high turgor (cf., Patakas and Noitsakis 1999). However, 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). Further water use efficiency is likely achieved by stomata control (cf., Chaves et al. 2003, Cherubini et al. 2003, de Micco et al. 2007). In contrast, in case of *G. versicolor*, we argue that its drought avoidance strategy is based on rigid stems which may increase water uptake from dry soil, while a decrease in soil moisture would reduce its water potential (Schulte 1993). Therefore, a conservative water use strategy (cf., Bacelar et al. 2009) presupposes access to sufficient water during drought, probably due to its long taproot that permits a sustainable water supply (cf., Passioura 1983, Bacelar et al. 2012).

At the end of the summer drought, only *C. galianoi* showed a positive moisture signal, while *G. versicolor* was promoted by high temperatures. In *C. galianoi,* we assume that a switch from anisohydry to partial isohydry is reasonable, since the latter has been shown to be effective after prolonged droughts when predictable seasonal rainfalls occur (Guo et al. 2020). Such a rapid switch is probably based on an extensive root system, which enables the species to benefit from pre-growing season water supply (cf., Bossard and Rejmanek 1992). In contrast, we assume that *G. versicolor* uses its taproot to absorb water from the deeper ground and as such maintains its isohydric mode until sufficient autumn rainfall has occurred (Reynolds et al. 1999, Ogle et al. 2004). Growth preference of sustained heat lasted until September, cool and moist conditions became promotive only in October and November and autumn droughts instead were growth limiting in both of our species. During this humid period, growth conditions in the Mediterranean alpine are overall favourable, and species-specific ecophysiological adaptation might not be necessary, which is in agreement with previous studies that showed strong precipitation drivers of growth across different species (de Luis et al. 2007, Valeriano et al. 2023).

Overall, the contrasting growth responses to winter temperature probably determine species´ distributional range, with *G. versicolor* being limited to the slopes where it is not at risk from low winter temperatures and soil freezing, while *C. galianoi* is able to occupy the most widespread ecological niche all over the Mediterranean alpine (cf., 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 tracheid 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 and

Lionello 2008), may affect our species less than expected, as we found that both were well adapted to severe summer-drought, with their cambial rhythm closely linked to seasonal water dynamics (cf. Dobbert et al. 2022a). However, differences in 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 the ultimate 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).

Conclusion

Here, we compare radial stem diameter changes of two co-occurring green-stemmed Mediterranean alpine shrub species and show clear differences in growth patterns, timing of growth, and the environmental drivers controlling growth processes, which we linked to contrasting winter freezing and summer drought adaptation strategies. We show that *C. galianoi* uses both 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 lose under severe summer droughts, and might be threatened by being exposed to winter cold, when its protective snow cover is missing/shortened. Both species were driven by pre-growth conditions, and this environmental control was more relevant than conditions during the actual growth phases. As a winter-cold adapted species *C. galianoi* has the higher ecological plasticity, and thus might be the winner under future climate warming.

Data Availability

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

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Literature Cited

Abdi, H. 2010. Partial least squares regression and projection on latent structure regression (PLSRegression). WIREs Computational Statistics 2:97–106.

Alday, J. G., J. J. Camarero, J. Revilla, and V. Resco de Dios. 2020. Similar diurnal, seasonal and annual rhythms in radial root expansion across two coexisting Mediterranean oak species. Tree Physiology 40:956–968.

Anderson, R. S., G. Jiménez-Moreno, J. S. Carrión, and C. Pérez-Martínez. 2011. Postglacial history of alpine vegetation, fire, and climate from Laguna de Río Seco, Sierra Navada, southern Spain. Quaternary Science Reviews 30:1615–1629.

Arndt, S. K. 2000. Mechanisms of drought resistance in the tropical fruit tree *Ziziphus*. Doctoral dissertation, University of Vienna, Austria.

Attia, Z., J. C. Domec, R. Oren, D. A. Way, and M. Moshelion. 2015. Growth and physiological responses of isohydric and anisohydric poplars to drought. Journal of Experimental Botany 66:4373–4381.

Bacelar, E. A., J. M. Moutinho-Pereira, B. C. Goncalves, J. L. Lopes, and C. M. Correia. 2009. Physiological responses of different olive genotypes to drought conditions. Acta Physiologiae Plantarum 31:611–621.

Bacelar, E. L., J. M. Moutinho-Pereira, B. M. Gonçalves, C. V. Brito, J. Gomes-Laranjo, H. M. Ferreira, and C. M. Correia. 2012. Water use strategies of plants under drought conditions. Pages 145–170 *in* R. Arcoca, editor. Plant responses to drought stress: from morphological to molecular features. Springer, Heidelberg, Germany.

Bär, A., A. Bräuning, and J. Löffler. 2006. Dendroecology of dwarf shrubs in the high mountains of Norway – A methodological approach. Dendrochronologia 24:17–27.

Bär, A., A. Bräuning, and J. Löffler. 2007. Ring-width chronologies of the alpine dwarf shrub *Empetrum hermaphroditum* from the Norwegian mountains. IAWA Journal 28:325–338.

Bär, A., R. Pape, A. Bräuning, and J. Löffler. 2008. Growth-ring variations of dwarf shrubs reflect regional climate signals in alpine environments rather than topoclimatic differences. Journal of Biogeography 35:625–636.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

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

Benito, B., J. Lorite, and J. Peñas. 2011. Simulating potential effects of climatic warming on altitudinal patterns of key species in Mediterranean-alpine ecosystems. Climatic Change 108:471–483.

Blanca, G., B. Cabezudo, M. Cueto, C. Fernández López, and C. Morales Torres. 2009a. Flora Vascular de Andalucía Oriental. Consejería de Medio Ambiente. Junta de Andalucía 1:306.

Blanca, G., B. Cabezudo, M. Cueto, C. Fernández López, and C. Morales Torres. 2009b. Flora Vascular de Andalucía Oriental. Consejería de Medio Ambiente. Junta de Andalucía 2:334.

Bogino, S. M., and F. Bravo. 2008. Growth response of *Pinus pinaster* Ait. to climatic variables in central Spanish forests. Annals of Forest Science 65:1–13.

Bossard, C. C., and M. Rejmanek. 1992. Why have green stems? Functional Ecology 197–205.

Camarero, J. J., J. M. Olano, and A. Parras. 2010. Plastic bimodal xylogenesis in conifers from continental Mediterranean climates. New Phytologist 185:471–480.

Camarero, J. J., J. M. Olano, S. J. A. Alfaro, B. Fernández-Marín, J. M. Becerril, and J. I. García-Plazaola. 2012. Photoprotection mechanisms in *Quercus ilex* under contrasting climatic conditions. Flora-Morphology, Distribution, Functional Ecology of Plants 207:557–564.

Camarero, J. J., S. Palacio, and G. Montserrat-Martí. 2013. Contrasting seasonal overlaps between primary and secondary growth are linked to wood anatomy in Mediterranean sub-shrubs. Plant Biology 15:798–807.

Camarero, J. J., C. Valeriano, A. Gazol, M. Colangelo, and R. Sánchez-Salguero. 2021. Climate differently impacts the growth of coexisting trees and shrubs under semi-arid mediterranean conditions. Forests 12:381.

Carrascal, L. M., I. Galván, and O. Gordo. 2009. Partial least squares regression as an alternative to current regression methods used in ecology. Oikos 118:681–690.

Chaves, M. M., J. P. Maroco, and J. S. Pereira. 2003. Understanding plant responses to drought—from genes to the whole plant. Functional Plant Biology 30:239–264.

Chen, L., and R. Z. Wang. 2009. Anatomical and physiological divergences and compensatory effects in two *Leymus chinensis* (Poaceae) ecotypes in Northeast China. Agriculture, Ecosystems and Environment 134:46–52.

Cherubini, P., B. L. Gartner, R. Tognetti, O. U. Bräker, W. Schoch, and J. L. Innes. 2003. Identification, measurement and interpretation of tree rings in woody species from Mediterranean climates. Biological Reviews 78:119–148.

Choler, P. 2018. Winter soil temperature dependence of alpine plant distribution: Implications for anticipating vegetation changes under a warming climate. Perspectives in Plant Ecology, Evolution and Systematics 30:6–15.

Cochard, H., and S. Delzon. 2013. Hydraulic failure and repair are not routine in trees. Annals of Forest Science 70:659–661.

Connor, D. J. 2005. Adaptation of olive (*Olea europaea* L.) to water-limited environments. Australian Journal of Agricultural Research 56:1181–1189.

Cotto, O., J. Wessely, D. Georges, G. Klonner, M. Schmid, S. Dullinger, W. Thuiller and F. Guillaume. 2017. A dynamic eco-evolutionary model predicts slow response of alpine plants to climate warming. Nature Communications 8:15399.

de Jong, S. 1993. SIMPLS: an alternative approach to partial least squares regression. Chemometrics and Intelligent Laboratory Systems 18:251–263.

de Luis, M., J. Gričar, K. Čufar, and J. Raventós. 2007. Seasonal dynamics of wood formation in *Pinus halepensis* from dry and semi-arid ecosystems in Spain. IAWA Journal 28:389–404.

de Luis, M., K. Novak, K. Čufar, and J. Raventós. 2009. Size mediated climate–growth relationships in *Pinus halepensis* and *Pinus pinea*. Trees 23:1065–1073.

de Micco, V., M. Saurer, G. Aronne, R. Tognetti and P. Cherubini. 2007. Variations of wood anatomy and δ13C within tree rings of coastal *Pinus pinaster* Ait. showing intra-annual density fluctuations. IAWA Journal 28:61–74.

Deslauriers, A., S. Rossi, and T. Anfodillo. 2007. Dendrometer and intra-annual tree growth: what kind of information can be inferred? Dendrochronologia 25:113–124.

Deslauriers, A., S. Rossi, T. Anfodillo, and A. Saracino. 2008. Cambial phenology, wood formation and temperature thresholds in two contrasting years at high altitude in southern Italy. Tree Physiology 28:863–871.

Dijkstra, T. 1983. Some comments on maximum likelihood and partial least squares methods. Journal of Econometrics 22:67–90.

Dobbert, S., E. C. Albrecht, R. Pape, and J. Löffler. 2022a. Alpine shrub growth follows bimodal seasonal patterns across biomes–unexpected environmental controls. Communications Biology 5:1–12.

Dobbert, S., R. Pape, and J. Löffler. 2021. Contrasting growth response of evergreen and deciduous arctic-alpine shrub species to climate variability. Ecosphere 12(8):e03688.

Dobbert, S., R. Pape, and J. Löffler. 2022b. The application of dendrometers to alpine dwarf shrubs–a case study to investigate stem growth responses to environmental conditions. Biogeosciences 19:1933–1958.

Ennajeh, M., T. Tounekti, A. M. Vadel, H. Khemira, and H. Cochard. 2008. Water relations and drought-induced embolism in olive (*Olea europaea*) varieties ‘Meski’ and ‘Chemlali’ during severe drought. Tree Physiology 28:971–976.

Farrés, M., S. Platikanov, S. Tsakovski, and R. Tauler. 2015. Comparison of the variable importance in projection (VIP) and of the selectivity ratio (SR) methods for variable selection and interpretation. Journal of Chemometrics 29:528–536.

Fernández-Santos, B., C. Martínez, J. A. García, and A. Puerto. 2004. Postfire regeneration in *Cytisus oromediterraneus*: sources of variation and morphology of the below-ground parts. Acta Oecologica 26:149–156.

Franklin, R. S. 2012. Growth response of the alpine shrub, *Linanthus pungens*, to snowpack and temperature at a rock glacier site in the eastern Sierra Nevada of California, USA. Quaternary International 30:1e14.

Frindte, K., R. Pape, K. Werner, J. Löffler, and C. Knief. 2019. Temperature and soil moisture control microbial community composition in an arctic-alpine ecosystem along elevational and micro-topographic gradients. ISME Journal 13:2031–2043.

Gamm, C. M., P. F. Sullivan, A. Buchwal, R. J. Dial, A. B. Young, D. A. Watts, S. M. P. Cahoon, J. M. Welker, and E. Post. 2018. Declining growth of deciduous shrubs in the warming climate of continental western Greenland. Journal of Ecology 106:640–654.

Geladi, P., and B. R. Kowalski. 1986. Partial least-squares regression: a tutorial. Analytica Chimica Acta 185:1–17.

Giménez, E., M. Melendo, F. Valle, F. Gómez-Mercado, and E. Cano. 2004. Endemic flora biodiversity in the south of the Iberian Peninsula: altitudinal distribution, life forms and dispersal modes. Biodiversity and Conservation 13:2641–2660.

Gimeno, T. E., J. J. Camarero, E. Granda, B. Pías, and F. Valladares. 2012. Enhanced growth of *Juniperus thurifera* under a warmer climate is explained by a positive carbon gain under cold and drought. Tree Physiology 32:326–336.

Giorgi, F., and P. Lionello. 2008. Climate change projections for the Mediterranean region. Global and Planetary Change 63:90–104.

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

Grabherr, G., M. Gottfried, and H. Pauli.1994. Climate effects on mountain plants. Nature 369:448.

Guo, C., L. Ma, S. Yuan, and R. Wang. 2017. Morphological, physiological and anatomical traits of plant functional types in temperate grasslands along a large-scale aridity gradient in northeastern China. Scientific Reports 7:1–10.

Guo, J. S., K. R. Hultine, G. W. Koch, H. Kropp, and K. Ogle. 2020. Temporal shifts in iso/anisohydry revealed from daily observations of plant water potential in a dominant desert shrub. New Phytologist 225:713–726.

Gutiérrez, E., F. Campelo, J. J. Camarero, M. Ribas, E. Muntán, C. Nabais, and H. Freitas. 2011. Climate controls act at different scales on the seasonal pattern of *Quercus ilex* L. stem radial increments in NE Spain. Trees 25:637–646.

Herrero, J., and M. J. Polo. 2016. Evaposublimation from the snow in the Mediterranean mountains of Sierra Nevada (Spain). The Cryosphere 10:2981–2998.

Hollesen, J., A. Buchwal, G. Rachlewicz, B. U. Hansen, M. O. Hansen, O. Stecher, and B. Elberling. 2015. Winter warming as an important co-driver for *Betula nana* growth in western Greenland during the past century. Global Change Biology 21:2410–2423.

Huang, J.-G., Q. Ma, S. Rossi, F. Biondi, A. Deslauriers, P. Fonti, E. Liang, H. Makinen, W. Oberhuber, C. B. Rathgeber, R. Tognetti, V. Treml, B. Yang, J.-L .Zhang, S. Antonucci, Y. Bergeron, J.J. Camarero, F. Campelo, K. Čufar, H. Cuny, M. de Luis, A. Giovannelli, J. Gričar, A. Gruber, V. Gryc,, A. Güney, X. Guo, W. Huang, T. Jyske, J. Kaspar, G. King, C. Krause, A. Lemay, F. Liu, F. Lombardi, E. Martinez, H. Morin, C. Nabais, P. Nöjd, R. L. Peters, P. Prislan, A. Saracino, I. Swidrak, H. Vavrčík,, J. Vieira, B. Yu, S. Zhang, Q. Zeng, Y. Zhang, and E. Ziaco. 2020. Photoperiod and temperature as dominant environmental drivers triggering secondary growth resumption in Northern Hemisphere conifers. Proceedings of the National Academy of Sciences 117:20645–20652.

Jackson, R. B., J. S. Sperry, and T. E. Dawson. 2000. Root water uptake and transport: using physiological processes in global predictions. Trends in Plant Science 5:482–488.

Jiménez-Moreno, G., and R. S. Anderson. 2012. Holocene vegetation and climate change recorded in alpine bog sediments from the Borreguiles de la Virgen, Sierra Nevada, southern Spain. Quaternary Research 77:44–53.

Jones, H. G. 1998. Stomatal control of photosynthesis and transpiration. Journal of Experimental Botany 387–398.

Kamari, G., C. Blanché, and S. Siljak-Yakovlev. 2010. Mediterranean chromosome number reports-20.

Kucheryavskiy, S. 2020. mdatools – R package for chemometrics. Chemometrics and Intelligent Laboratory Systems 198:103937.

Larsen, K. S., A. Michelsen, S. Jonasson, C. Beier, and P. Grogan. 2012. Nitrogen uptake during fall, winter and spring differs among plant functional groups in a subarctic heath ecosystem. Ecosystems 15:927–939.

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

Löffler, J., S. Dobbert, R. Pape, and D. Wundram. 2021. Dendrometer measurements of arctic-alpine dwarf shrubs and micro-environmental drivers of plant growth—Dataset from long-term alpine ecosystem research in central Norway. Erdkunde 75:DP311201.

Löffler, J., and R. Pape. 2020. Thermal niche predictors of alpine plant species. Ecology 101:e02891.

Lorite, J. 2001. La vegetación de Sierra Nevada. Pages 23–45 *in* G. Blanca, M. R. López Onieva, J. Lorite, M. J. Martínez Lirola, J. Molero Mesa, and S. Vidal, editors. Flora amenazada y endémica de Sierra Nevada. Editorial Universidad de Granada, Granada, Spain.

Ludlow, M. M. 1980. Adaptive significance of stomatal responses to water stress. Pages 123–138 in N. C. Turner, and P. J. Kramer, editors. Adaptation of plants to water and high temperature stress. Wiley Interscience, New York, USA.

Macek, P., I. Prieto, J. Macková, N. Pistón, and F. I. Pugnaire. 2016. Functional plant types drive plant interactions in a Mediterranean mountain range. Frontiers in Plant Science 7:662.

Magaña Ugarte, R., A. Escudero, and R. G. Gavilán. 2019. Metabolic and physiological responses of Mediterranean high-mountain and alpine plants to combined abiotic stresses. Physiologia plantarum 165:403–412.

Martens, H., and T. Næs. 1989. Multivariate calibration. John Wiley & Sons, Chichester, UK.

Mehmood, T., K. H. Liland, L. Snipen, and S. Sæbø. 2012. A review of variable selection methods in Partial Least Squares Regression. Chemometrics and Intelligent Laboratory Systems 118:62–69.

Meinzer, F. C., J. R. Brooks, J. C. Domec, B. L. Gartner, J. M. Warren, D. R. Woodruff, K. Bible, and D. C. Shaw. 2006. Dynamics of water transport and storage in conifers studied with deuterium and heat tracing techniques. Plant, Cell and Environment 29:105–114.

Melendo, M., E. Giménez, E. Cano, F. G. Mercado, and F. Valle. 2003. The endemic flora in the south of the Iberian Peninsula: taxonomic composition, biological spectrum, pollination, reproductive mode and dispersal. Flora-Morphology, Distribution, Functional Ecology of Plants 198:260–276.

Mitrakos, K. 1980. A theory for Mediterranean plant life. Acta Oecologica-Oecologia Plantarum Montreuil 1:245–252.

Myers-Smith, I. H., J. T. Kerby, G. K. Phoenix, J. W. Bjerke, H. E. Epstein, J. J. Assmann, C. John, L. Andreu-Hayles, S. Angers-Blondin, P. S. A. Beck, L. T. Berner, U. S. Bhatt, A. D. Bjorkman, D. Blok, A. Bryn, C. T. Christiansen, J. H. C. Cornelissen, A. M. Cunliffe, S. C. Elmendorf, B. C. Forbes, S. J. Goetz, R. D. Hollister, R, de Jong, M. M. Loranty, M. Macias-Fauria, K. Maseyk, S, Normand, J. Olofsson, T. C. Parker, F.-J. W. Parmentier, E. Post, G. Schaepman-Strub, F. Stordal, P. F. Sullivan, H. J. D. Thomas, H. Tømmervik, R. Treharne, C. E. Tweedie, D. A. Walker, M. Wilmking, and S. Wipf. 2020. Complexity revealed in the greening of the Arctic. Nature Climate Change 10:106–117.

Niittynen, P., and M. Luoto. 2018. The importance of snow in species distribution models of arctic vegetation. Ecography 41:1024–1037.

Nogués-Bravo, D., M. B. Araújo, T. Lasanta, and J. I. López Moreno. 2008. Climate change in Mediterranean mountains during the 21st century. Ambio 37:280–285.

Ogle, K., and J. F. Reynolds. 2004. Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays. Oecologia 141:282–294.

Olano, J. M., I. Almería, M. Eugenio, and G. von Arx. 2013. Under pressure: how a Mediterranean high-mountain forb coordinates growth and hydraulic xylem anatomy in response to temperature and water constraints. Functional Ecology 27:1295–1303.

Oribe, Y., and T. Kubo. 1997. Effect of heat on cambial reactivation during winter dormancy in evergreen and deciduous conifers. Tree Physiology 17:81–87.

Pacheco, A., J. J. Camarero, M. Ribas, A. Gazol, E. Gutierrez, and M. Carrer. 2018. Disentangling the climate-driven bimodal growth pattern in coastal and continental Mediterranean pine stands. Science of the Total Environment 615:1518–1526.

Pasho, E., J. J. Camarero, and S. M. Vicente-Serrano. 2012. Climatic impacts and drought control of radial growth and seasonal wood formation in *Pinus halepensis*. Trees 26:1875–1886.

Passioura, J. B. 1983. Roots and drought resistance. Developments in Agricultural and Managed Forest Ecology 12:265–280.

Patakas, A., and B. Nortsakis. 1999. Mechanisms involved in diurnal changes of osmotic potential in grapevines under drought conditions. Journal of Plant Physiology 154:767–774.

Pellizzari, E., J. J. Camarero, A. Gazol, E. Granda, R. Shetti, M. Wilmking, P. Moiseev, M. Pividori, and M. Carrer. 2017. Diverging shrub and tree growth from the Polar to the Mediterranean biomes across the European continent. Global Change Biology 23:3169–3180.

Pistón, N., C. Schöp, C. Armas, I. Prieto and F. I. Pugnaire. 2016. Contribution of co-occurring shrub species to community richness and phylogenetic diversity along an environmental gradient. Perspectives in Plant Ecology, Evolution and Systematics 19:30–39.

R Core Team. 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

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

Ren, P., S. Rossi, J. J. Camarero, A. M. Ellison, E. Liang, and J. Peñuelas. 2018. Critical temperature and precipitation thresholds for the onset of xylogenesis of *Juniperus przewalskii* in a semi-arid area of the north-eastern Tibetan Plateau. Annals of Botany 121:617–624.

Reynolds, J. F., R. A. Virginia, P. R. Kemp, A. G. de Soyza, and D. C. Tremmel. 1999. Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. Ecological Monographs 69:69–106.

Roberts, N., D. Brayshaw, C. Kuzucuolu, R. Perez and L. Sadori. 2011. The mid-Holocene climatic transition in the Mediterranean: causes and consequences. Holocene 21:3–13.

Ropars, P., S. Angers-Blondin, M. Gagnon, I. H. Myers-Smith, E. Lévesque, and S. Boudreau. 2017. Different parts, different stories: climate sensitivity of growth is stronger in root collars vs. stems in tundra shrubs. Global Change Biology 23:3281–3291.

Rossi, S., T. Anfodillo, K. Čufar, H. E. Cuny, A. Deslauriers, P. Fonti, D. Frank, J. Gričar, A. Gruber, J.-G. Huang, T. Jyske, J. Kašpar, G. King, C. Krause, E. Liang, H. Mäkinen, H. Morin, P. Nöjd, W. Oberhuber, P. Prislan, C. B. K. Rathgeber, A. Saracino, I. Swidrak and V. Treml. 2016. Pattern of xylem phenology in conifers of cold ecosystems at the Northern Hemisphere. Global Change Biology 22:3804–3813.

Schulte, P. J. 1993. Tissue hydraulic properties and the water relations of desert shrubs. Pages 171–191 in J. A. C. Smith, and H. Griffiths, editors. Water Deficits: Plant Responses from Cell to Community. BIOS Scientific Publishers, Oxford, UK.

Sperling, O., L. C. R. Silva, A. Tixier, G. Théroux-Rancourt, and M. A. Zwieniecki. 2017. Temperature gradients assist carbohydrate allocation within trees. Nature Scientific Reports 7:3265.

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

Starr, G., and S. F. Oberbauer. 2003. Photosynthesis of arctic evergreens under snow: implications for tundra ecosystem carbon balance. Ecology 84:1415–1420.

Szymczak, S., M. Häusser, E. Garel, S. Santoni, F. Huneau, I. Knerr, K. Trachte, J. Bendix, and A. Bräuning, 2020. How do Mediterranean pine trees respond to drought and precipitation events along an elevation gradient? Forests 11:758.

Talavera, S., and P. Gibbs. 1997. *Cytisus purgans* auct. (Leguminosae-Papilionoideae) comprises four distinct species. Botanical Journal of the Linnean Society 125:331–342.

Tardieu, F., and T. Simonneau. 1998. Variability among species of stomatal control under fluctuating soil water status and evaporative demand: modelling isohydric and anisohydric behaviours. Journal of Experimental Botany 419–432.

Tumajer, J., V. V. Shishov, V. A. Ilyin, and J. J. Camarero. 2021. Intra-annual growth dynamics of Mediterranean pines and junipers determines their climatic adaptability. Agricultural and Forest Meteorology 311:108685.

Touchan, R., V. V. Shishov, D. M. Meko, I. Nouiri and A. Grachev. 2012. Process based model sheds light on climate sensitivity of Mediterranean tree-ring width. Biogeosciences 9:965–972.

Vaganov, E.A., M.K. Hughes, and A.V. Shashkin. 2006. Growth dynamics of conifer tree rings: Images of Past and Future Environments, Ecological Studies 183. Springer, Berlin, Germany.

Valeriano, C., E. Gutiérrez, M. Colangelo, A. Gazol, R. Sánchez-Salguero, J. Tumajer, V. Shishov, J. A. Bonet, J. Martínez de Aragón, R. Ibáñez, M. Valerio, and J. J. Camarero. 2023. Seasonal precipitation and continentality drive bimodal growth in Mediterranean forests. Dendrochronologia 78:126057

Valle, F., editor. 2003. Mapa de Series de Vegetación de Andalucía. Editorial Rueda, S.I., Madrid.

Vieira, J., S. Rossi, F. Campelo, H. Freitas, and C. Nabais. 2014. Xylogenesis of *Pinus pinaster* under a Mediterranean climate. Annals of Forest Science 71:71–80.

Vinzi, E. V. 2010. Handbook of partial least squares. Concepts, methods and applications. Springer, Berlin, Germany.

Weijers, S., N. Beckers, J. Löffler. 2018. Recent spring warming limits near-treeline deciduous and evergreen alpine dwarf shrub growth. Ecosphere 9 (6):e02328.

Wheeler, C. T., D. A. Perry, O. Helgerson, and J. C. Gordon. 1979. Winter fixation of nitrogen in Scotch broom (*Cytisus scoparius* L.). New Phytologist 82:697–701.

Wold, H. 1975. Soft modelling by latent variables: The Non-Linear Iterative Partial Least Squares (NIPALS) approach. Journal of Applied Probability 12:117–142.

Wold, S. 1978. Cross-validatory estimation of the number of components in factor and principal components models. Technometrics 20:397–405.

Wold, H. 1980. Evaluation of econometric models. Academic Press, New York, USA.

Wyka, T. P. and J. Oleksyn. 2014. Photosynthetic ecophysiology of evergreen leaves in the woody angiosperms – a review. Dendrobiology 72:3–27.

Zweifel, R., L. Zimmermann, and D. M. Newbery. 2005. Modeling tree water deficit from microclimate: an approach to quantifying drought stress. Tree Physiology 25:147–156.

Zweifel, R. 2016. Radial stem variations - a source of tree physiological information not fully exploited yet. Plant, Cell and Environment 39:231–232.

Zweifel, R., and R. Häsler. 2001. Dynamics of water storage in mature subalpine *Picea abies*: temporal and spatial patterns of change in stem radius. Tree Physiology 21:561–569.

Zweifel, R., F. Sterck, S. Braun, N. Buchmann, W. Eugster, A. Gessler, M. Häni, R. L. Peters, L. Walthert, M. Wilhelm, K. Ziemińska, and S. Etzold. 2021. Why trees grow at night. New Phytologist 231:2174–2185.

Zhang, W., P. A. Miller, C. Jansson, P. Samuelsson, J. Mao, and B. Smith. 2018. Self-amplifying feedbacks accelerate greening and warming of the Arctic. Geophysical Research Letters 45:7102–7111.

Table S1. Micro-environmental conditions from 2015 to 2020 averaged over all studied sites (+/-SE), for the focus species C. galianoi *(C.) and* G. versicolor *(G.).*

Year	2015	2016	2017	2018	2019	2020
T_{RZ} C./G. (mean) [°C]	9,04 (0,14)/ 9,04 (0,17)	9,18 (0,14)/ 9,17 (0,17)	9,54 (0,13)/ 9,55 (0,16)	7,40 (0,15)/ 7,41 (0,17)	9,27 (0,14)/ 9,23 (0,16)	9,37 (0,15)/ 9,38 (0,16)
T_{RZ} C./G. (max) [°C]	20,77 (0,27)/ 20,61 (0,33)	20,24 (0,25)/ 20,05 (0,27)	20,73 (0,25)/ 20,59 (0,28)	19,59 (0,26)/ 19,28 (0,30)	20,67 (0,28)/ 20,39 (0,33)	20,06 (0,27)/ 19,73 (0,29)
T_{RZ} C./G. (min) [°C]	-0,18 (0,13)/ -0,12 (0,10)	0,39 (0,06)/ 0,38 (0,06)	0,32 (0,10)/ 0,35 (0,08)	0,02 (0,09)/ 0,01 (0,09)	0,38 (0,06)/ 0,41 (0,06)	0,89 (0,03)/ 0,90 (0,03)
SM_{RZ} C./G. (mean) $[m^3/m^3]$	0,15 (0,00)/ 0,14 (0,00)	0,14 (0,00)/ 0,13 (0,00)	0,15 (0,00)/ 0,14 (0,00)	0,19 (0,00)/ 0,18 (0,00)	0,15 (0,01)/ 0,14 (0,00)	0,17 (0,00)/ 0,15 (0,00)
SM_{RZ} C./G. (max) $[m^3/m^3]$	0,26 (0,00)/ 0,24 (0,00)	0,26 (0,00)/ 0,24 (0,00)	0,26 (0,00)/ 0,25 (0,00)	0,27 (0,00)/ 0,26 (0,00)	0,27 (0,00)/ 0,25 (0,00)	0,27 (0,00)/ 0,24 (0,00)
SM_{RZ} C./G. (min) $[m^3/m^3]$	0,05 (0,00)/ 0,04 (0,00)	0,05 (0,00)/ 0,04 (0,00)	0,05 (0,00)/ 0,05 (0,00)	0,06 (0,00)/ 0,06 (0,00)	0,05 (0,00)/ 0,05 (0,00)	0,05 (0,00)/ 0,05 (0,00)
GR_{SZ} C./G. (mean) $[W/m^3]$	204,61 (0,00)	209,41 (0,00)	223,00 (0,00)	204,94 (0,00)	223,53 (0,00)	212,70 (0,00)
GR_{SZ} C./G. (max) $[W/m^3]$	373,46 (0,00)	377,31 (0,00)	374,93 (0,00)	385,97 (0,00)	378,29 (0,00)	380,22 (0,00)
GR_{SZ} C./G. (min) $[W/m^3]$	10,49 (0,00)	35,18 (0,00)	22,16 (0,00)	16,97 (0,00)	29,80 (0,00)	17,37 (0,00)

Table S2. Onset, cessation, duration [DOY], and growth [µm] averaged over all studied sites (+/- SE), aggregated by previously defined growth phases, for the focus species C. galianoi *(C.) and* G. versicolor *(G.).*

Year	2015	2016	2017	2018	2019	2020
Onset C./G. First phase [DOI]	53,37 (9,4)/ 49,08 (10,2)	69,04 (11,3)/ 59,95 (10,1)	55,61 (11,0)/ 44,59 (10,7)	52,55 (10,3)/ 49,85 (12,5)	69,64 (11,6)/ 118,83 (8,5)	49,10 (9,9)/ 50,47 (10,1)
Cessation First phase [DOI]	148,03 (8,6)/ 139 (10,8)	165,72 (6,5)/ 150,73 (10,0)	143,55 (11,2)/ 127,04 (13,9)	150,05 (10,2)/ 157,05 (10,2)	136,28 (13,5)/ 174,04 (1,7)	153,26 (8,6)/ 155,47 (11,0)
Duration C./G. First phase [DOI]	94,65 (10,6)/ 89,92 (12,2)	96,68 (13,0)/ 90,78 (11,8)	87,94 (12,4)/ 82,45 (13,6)	97,5 (13,0)/ 107,2 (14,0)	66,64 (15,5)/ 55,20 (8,9)	104,15 (11,6)/ 105 (13,0)
Growth C./G. First phase [µm]	83,93 (11,8) 55,04 (10,6)	69,94 (15,4)/ 68,12 (15,9)	24,23 (11,7)/ 44,25 (11,7)	56,64 (16,0)/ 32,95 (6,7)	24,71 (7,6)/ 21,80 (10,4)	49,60 (15,7)/ 45,70 (8,8)
Onset C./G. Second phase [DOI]	248,5 (10,5)/ 202,5 (6,6)	218,22 (13,5)/ 213,84 (11,1)	248,05 (11,6)/ 217,80 (11,6)	211,77 (7,6)/ 191,27 (4,0)	251,21 (9,7)/ 189,40 (5,0)	231,26 (12,0)/ 200,03 (7,8)
Cessation C./G. Second phase [DOI]	309,25 (1,7)/ 308,41 (4,6)	335,5 (10,4)/ 334,6 (10,0)	344,33 (8,3)/ 351,90 (4,0)	324,11 (5,1)/ 326,45 (3,4)	350,84 (3,5)/ 352,09 (1,8)	335,47 (8,5)/ 335,57 (8,3)
Duration C./G. Second phase [DOI]	60,75 (9,9)/ 105,91 (7,6)	117,27 (15,9)/ 120,76 (13,1)	96,27 (12,9)/ 134,09 (12,3)	112,33 (8,6)/ 135,18 (6,4)	99,63 (8,9)/ 162,68 (6,1)	104,21 (13,5)/ 135,53 (11,2)
Growth C./G. Second phase [µm]	35,62 (12,2)/ 53,66 (9,1)	57,70 (18,7)/ 98,61 (28,2)	27,67 (6,2)/ 29,81 (5,4)	50,69 (11,8)/ 56,99 (9,2)	39,49 (8,2)/ 46,95 (6,3)	41,26 (10,2)/ 60,41 (8,8)

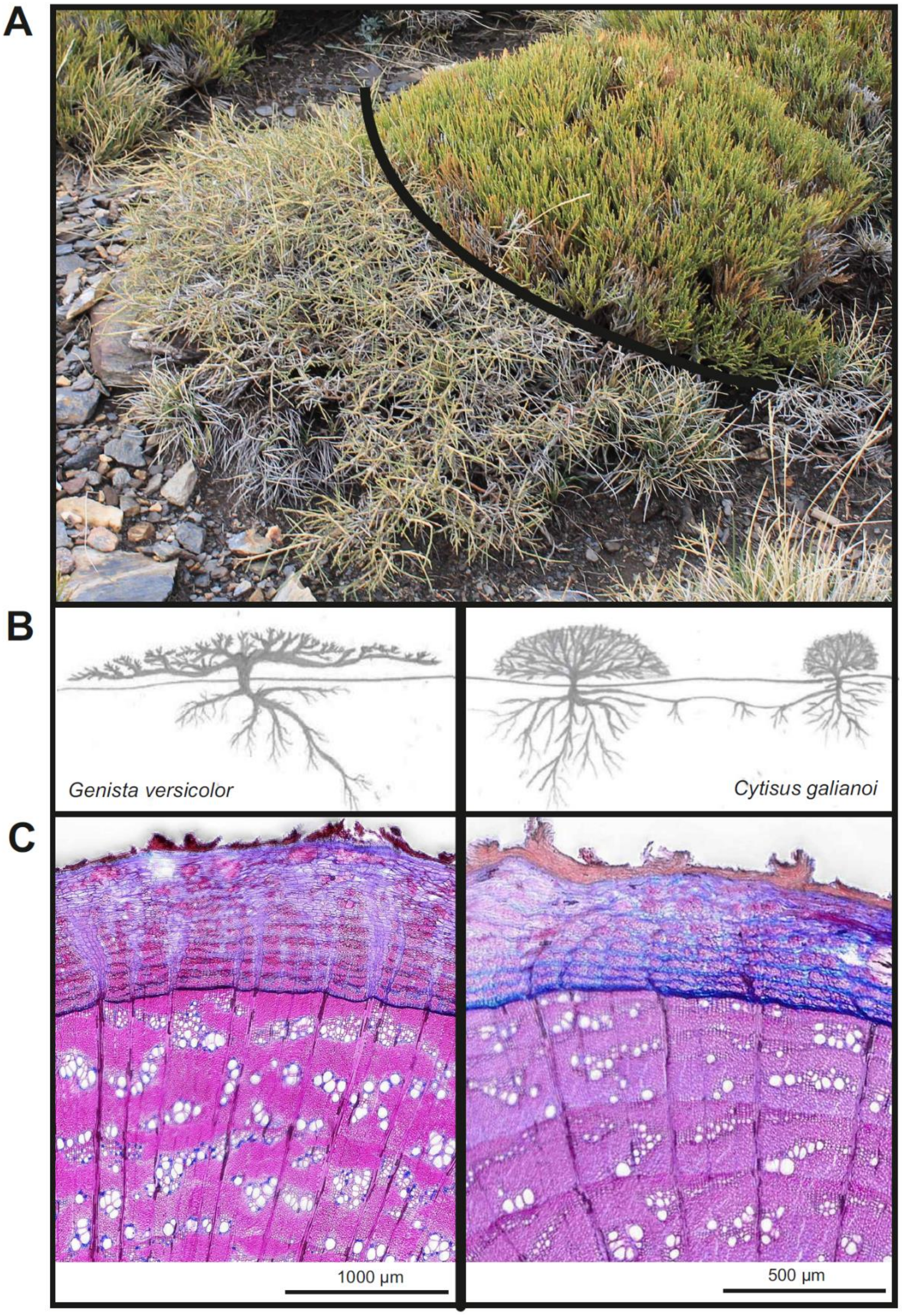

Fig. S1 (A) Picture showing the coexistence of our two focus species (B), illustration of the species´ habitus including their distinct root systems, with G. versicolor *having one main sparsely branched root and* C. galianoi *having an intensively branched root system. (C) Cross section of G. versicolor and* C. galianoi *showing the species´ semi-ring porous xylem anatomy with clumps of vessels accompanied by parenchyma cells.*

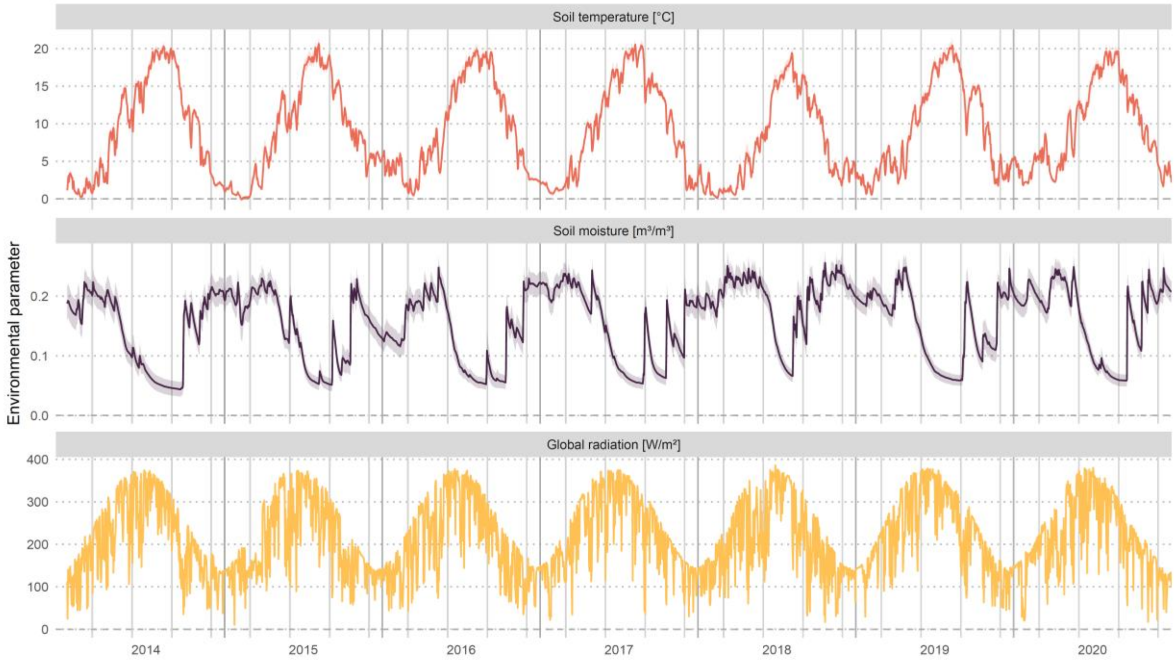

Fig. S2 Illustration of micro-environmental data. Root zone temperature (ST_{RZ}), root zone soil moisture (SM_{RZ}) and stem zone global radiation (GR_{SZ}) regimes (daily means, derived from hourly measurements) averaged over all study sites, with shaded areas indicating standard deviation. Daily means of global radiation were derived from hourly measurements at the climate station of the study area.

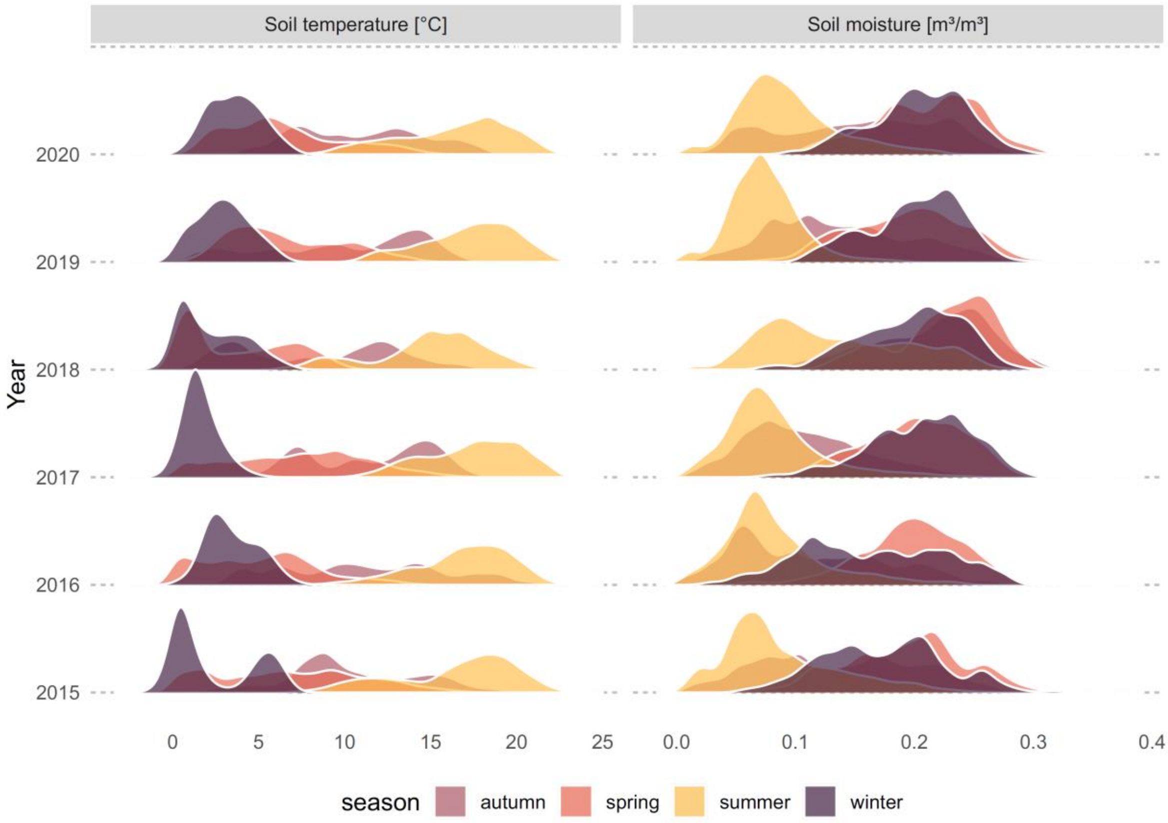

Fig. S3 Ridgeline plot of soil temperature (ST$_{RZ}$) and soil moisture (SM$_{RZ}$), showing the frequency of ST$_{RZ}$ and SM$_{RZ}$ values over all six monitored years at all studied sites.

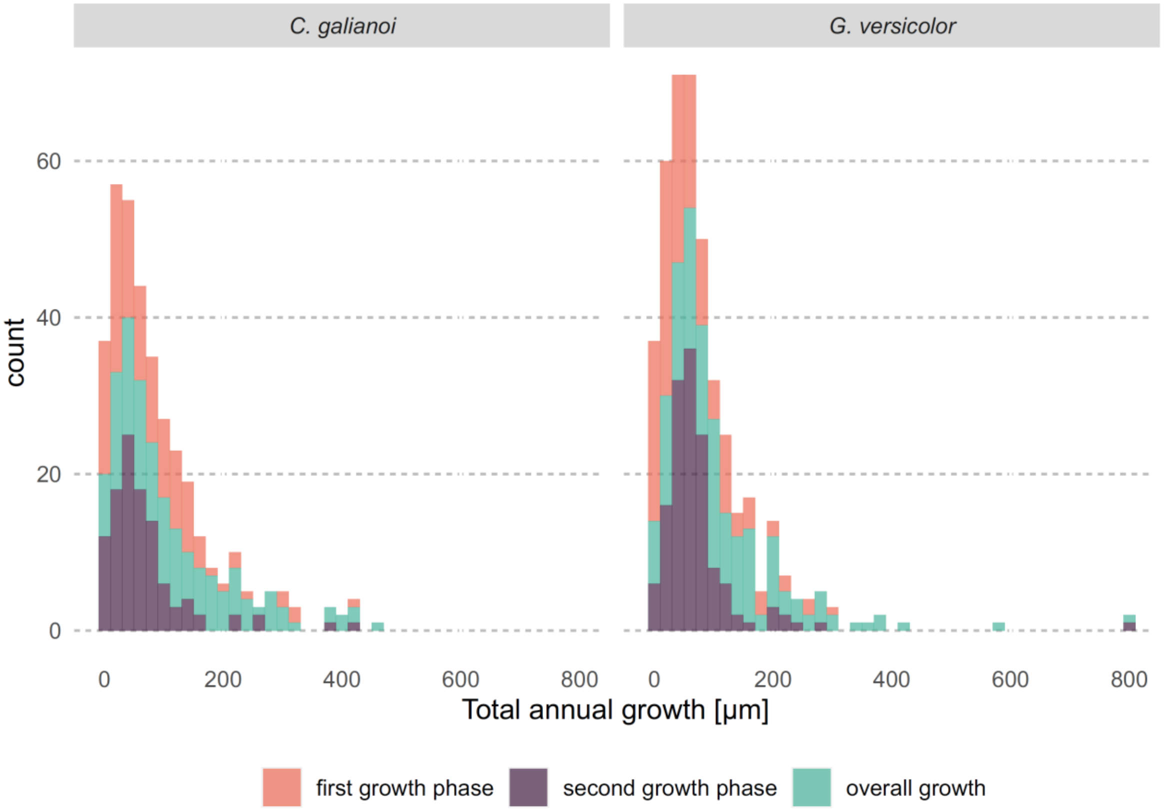

Fig. S4 Histogram for total annual growth as well as growth for the first and second growth phase in C. galianoi *and* G. versicolor*.*

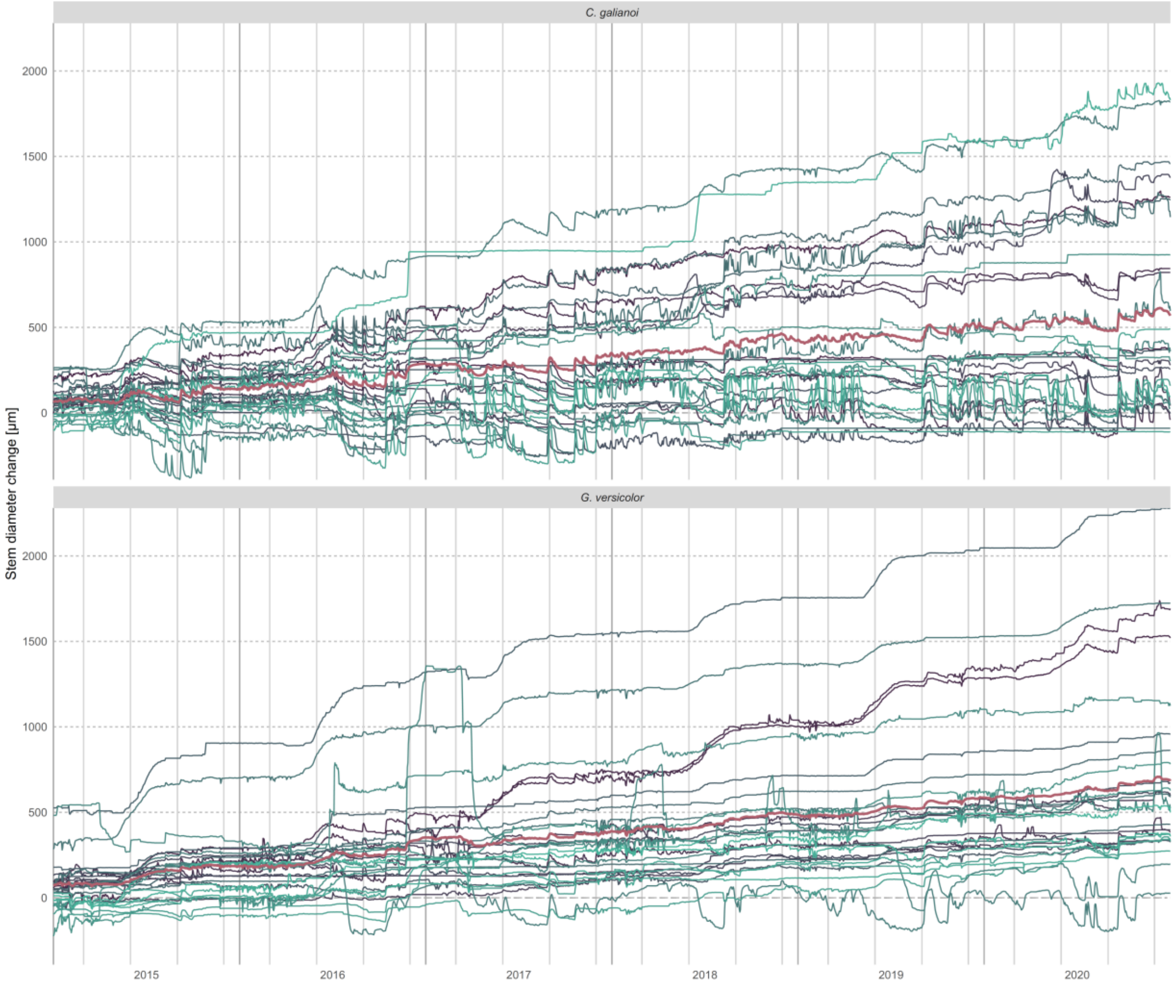

Fig. S5 Stem diameter change for individual specimens, as derived from dendrometer measurements for C. galianoi *and* G. versicolor *with overall mean in red.*

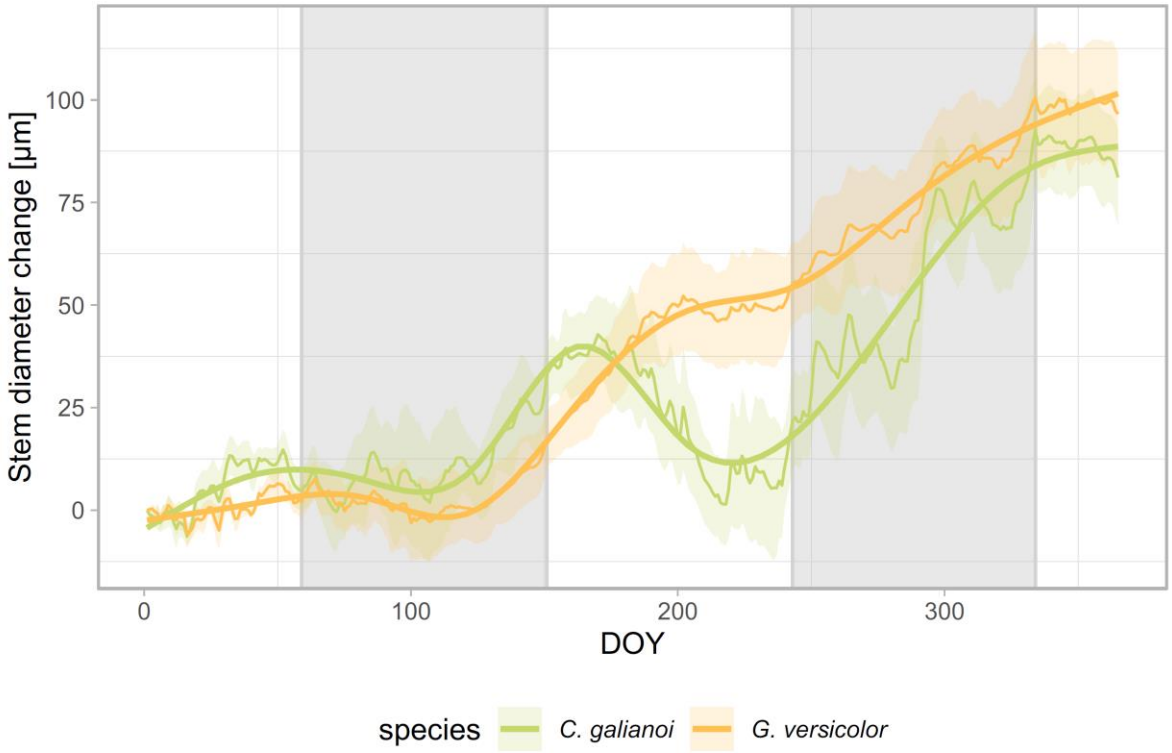

Fig. S6 Seasonal pattern of stem diameter change during the curse of one year averaged over the studied period 2015 – 2020 and represented by generalized additive models (GAMs).

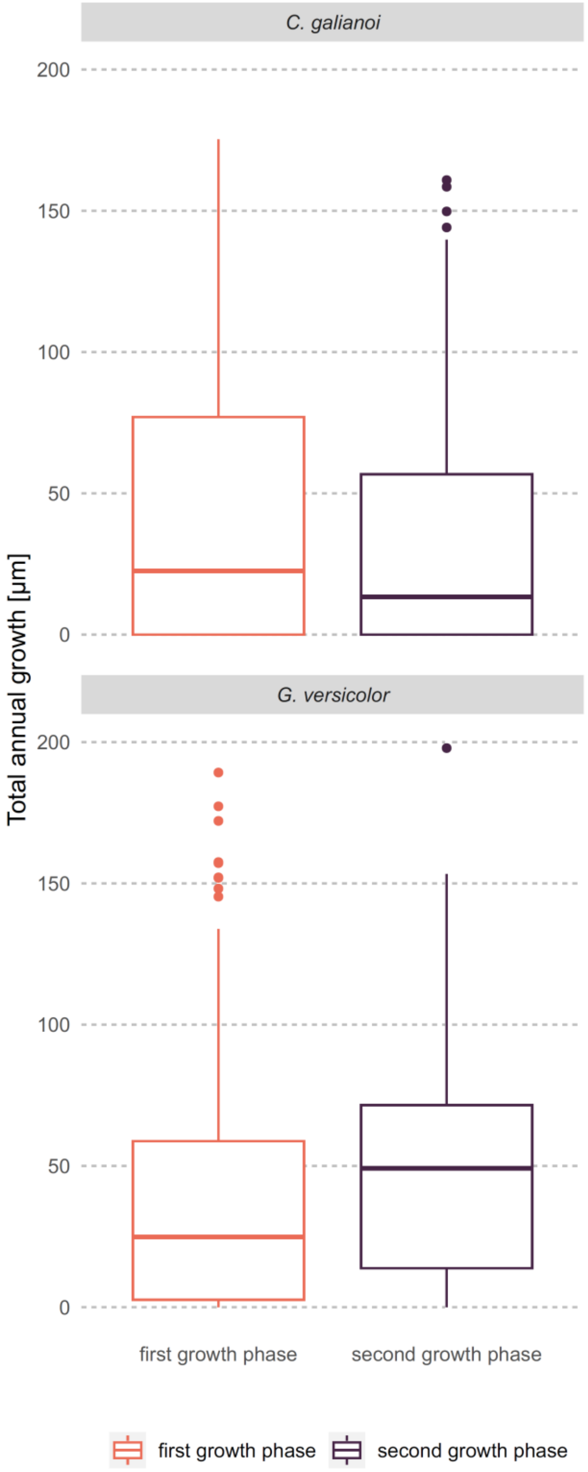

Fig. S7 Boxplot showing the distribution of growth in the first and second growth phase in C. galianoi *and* G. versicolor *over the studied period 2015 – 2020.*

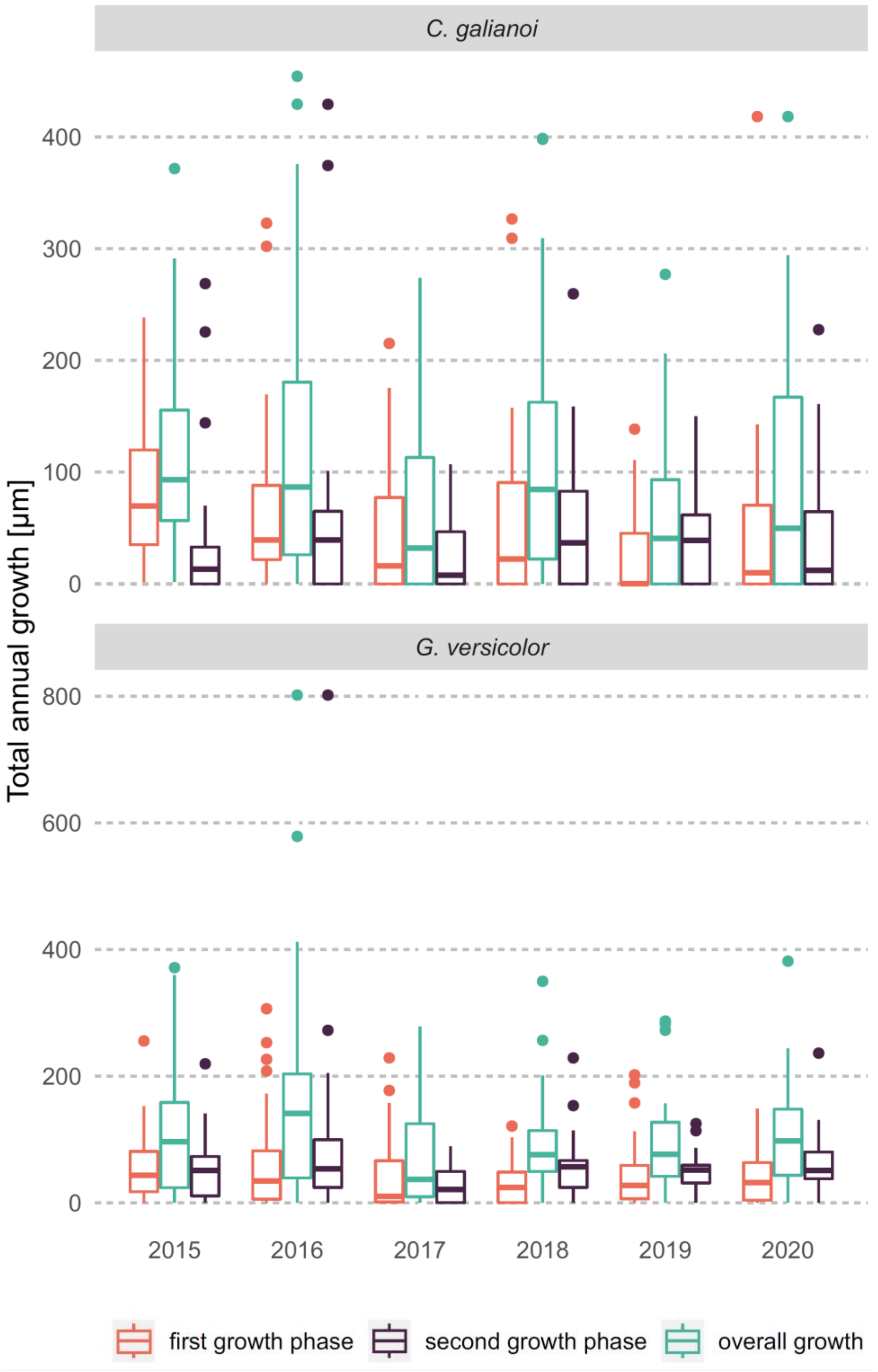

Fig. S8 Boxplot showing the distribution of total annual growth as well as growth in the first and second growth phase in C. galianoi *and* G. versicolor.

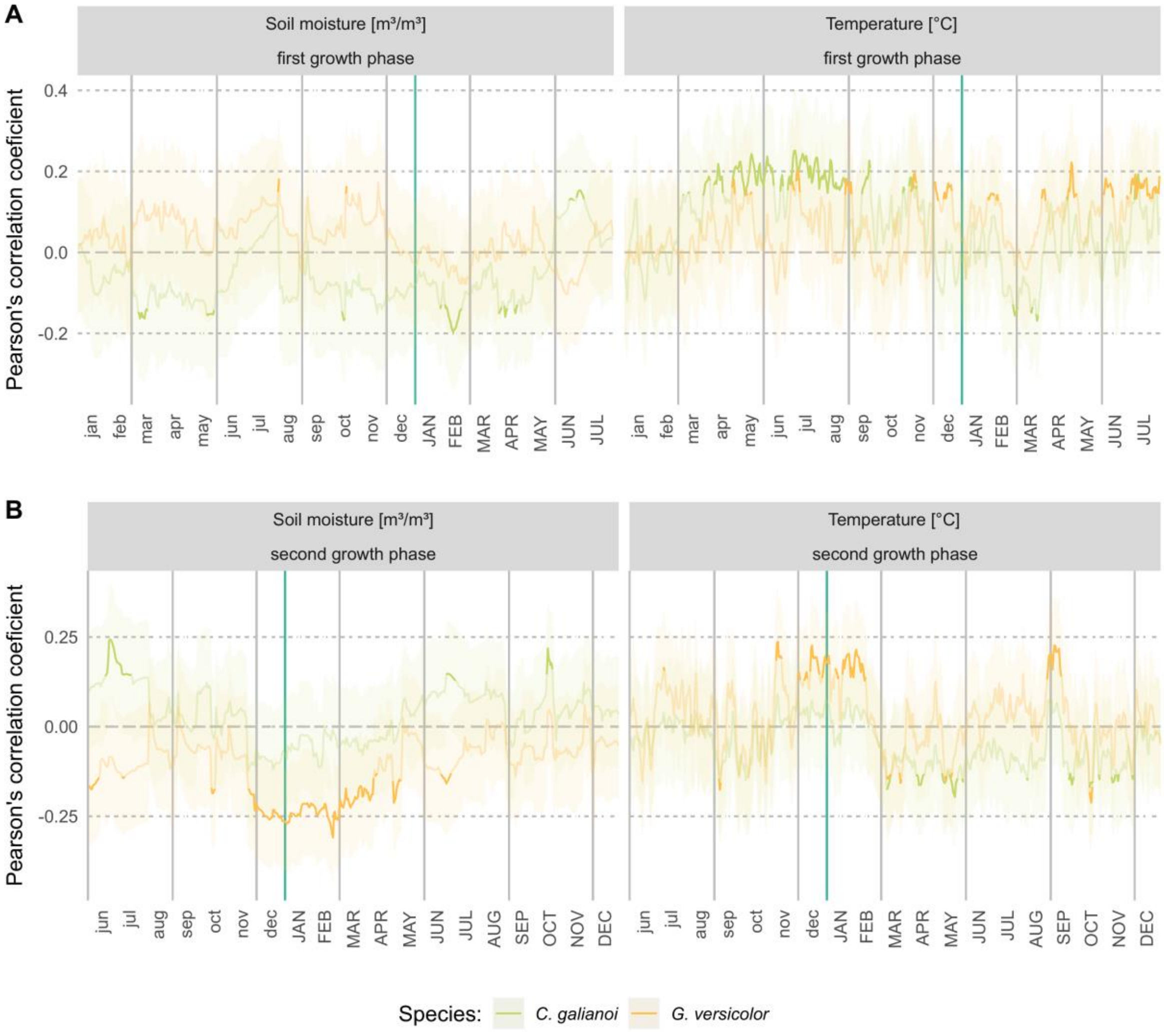

Fig. S9 Pearson's correlation coefficients calculated between on-site measured daily soil moisture (SM_{RZ}) and soil temperature (T_{RZ}) data and first (A) and second (B) growth phase as derived from the dendrometer curves, with shaded area indicating standard deviation (+/- SE) and transparency non significance.

11 Synthesis

We studied the growth and its environmental controls of three Mediterranean alpine shrubs species in the Sierra Nevada, Spain, along an elevational and microtopographical gradient. *Cytisus galianoi* was abundant at all sites (A, B, C; Figs. 11, 12) and co-occurred with *Astragalus granatensis* at the exposed alpine ridge positions and with *Genista versicolor* at the snow-covered alpine slopes. As such, our focal species *C. galianoi* had a wide ecological range along multiple biogeographical gradients, whereas the two other shrubs species had narrower ecological niches. Therefore, in the **Papers 2** and **3**, we focussed on ridges and slopes, where *C. galianoi* co-occurred with one of the other species, and as such, snowbeds (C) are not shown separately, here. Our dendrometer measurements revealed species-specific patterns of stem diameter change (Fig. 13), from which we derived growth, defined as irreversible stem increment. Growth differed strongly between species and topographical positions and was represented by pronounced cumulative growth curves (Fig. 14). The timing of growth varied both, between species and sites, and a pronounced bimodal growth pattern emerged showing two distinct growth phases (Fig. 15). However, growth rates during the different phases did not correspond with the length of the growth phases (Fig. 16).

Our study showed that stem diameter changes, which we directly derived from the raw dendrometer data, were contrasting between sites and showed pronounced differences in the bimodality, the latter of which was driven by differences of the species' response to summer droughts (Fig. 13). While *C. galianoi* showed strongest stem contraction during late summer, stem contraction already peaked during early summer in *A. granatensis*, while *G. versicolor* showed least summer stem contraction. As such, the results on water-related stem diameter changes highlighted species-specific responses to seasonal water dynamics, associated with differences in stem water deficit and plant water potential.

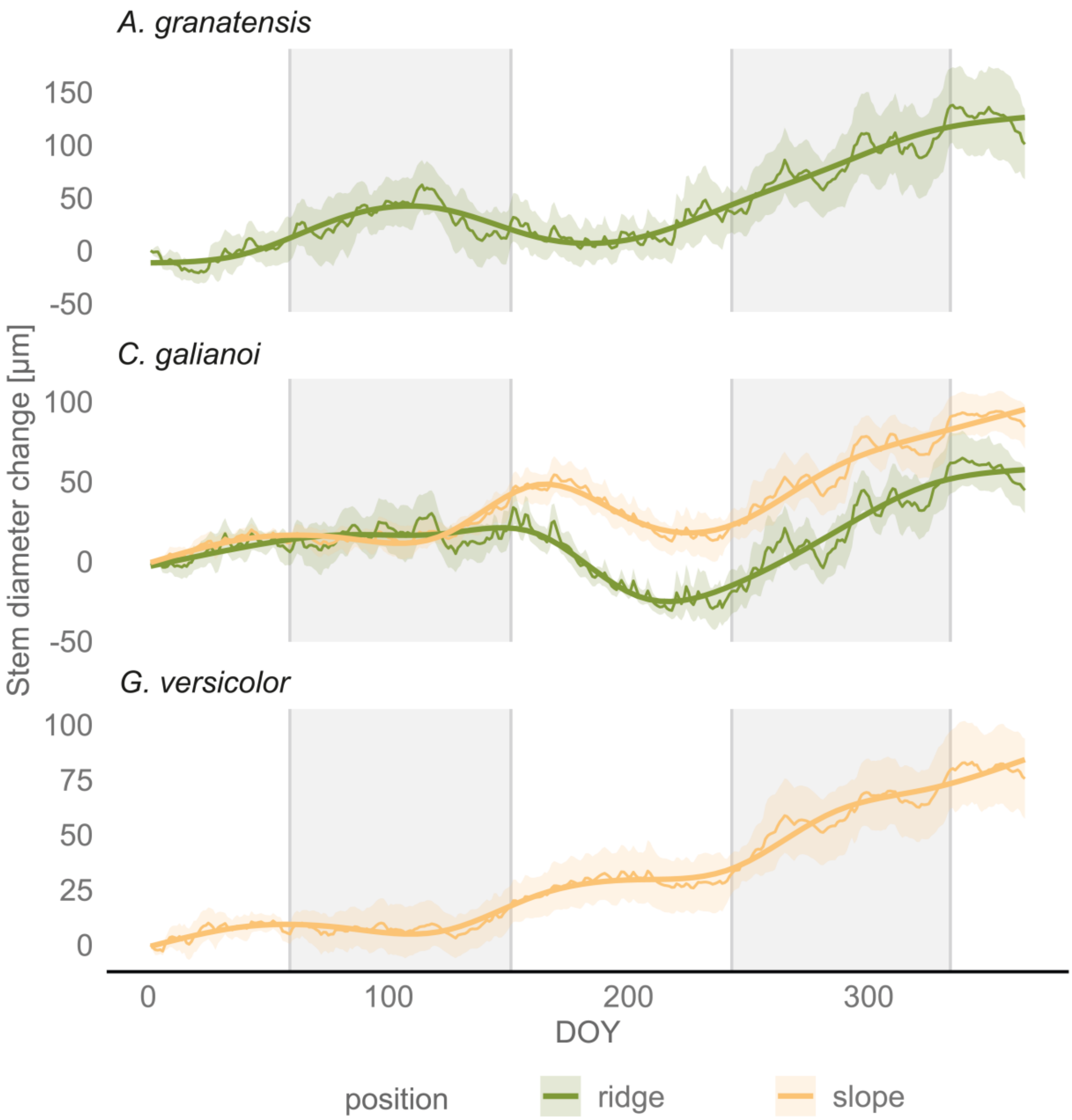

Fig. 13 Seasonal patterns of stem diameter change in A. granatensis, C. galianoi, *and* G. versicolor *at different topographical positions (ridges and slopes, see A and B in Figs. 11, 12) during the course of one year averaged over the studied period 2015 – 2020 and represented by generalized additive models (GAMs).*

Contrasting the patterns of stem diameter changes, our cumulative growth curves in *C. galianoi* showed highest growth rates during spring, particularly at the slopes, whereas *A. granatensis*, and to a lesser extent, *G. versicolor* showed higher growth rates in autumn (Fig. 14). By separating growth from water-related stem diameter changes, we derived irreversible stem diameter increments (growth) from cell division and expansion, only (**Papers 1**, **2**, and **3**). These cumulative growth curves, apart from the magnitude of growth, also uncover its timing.

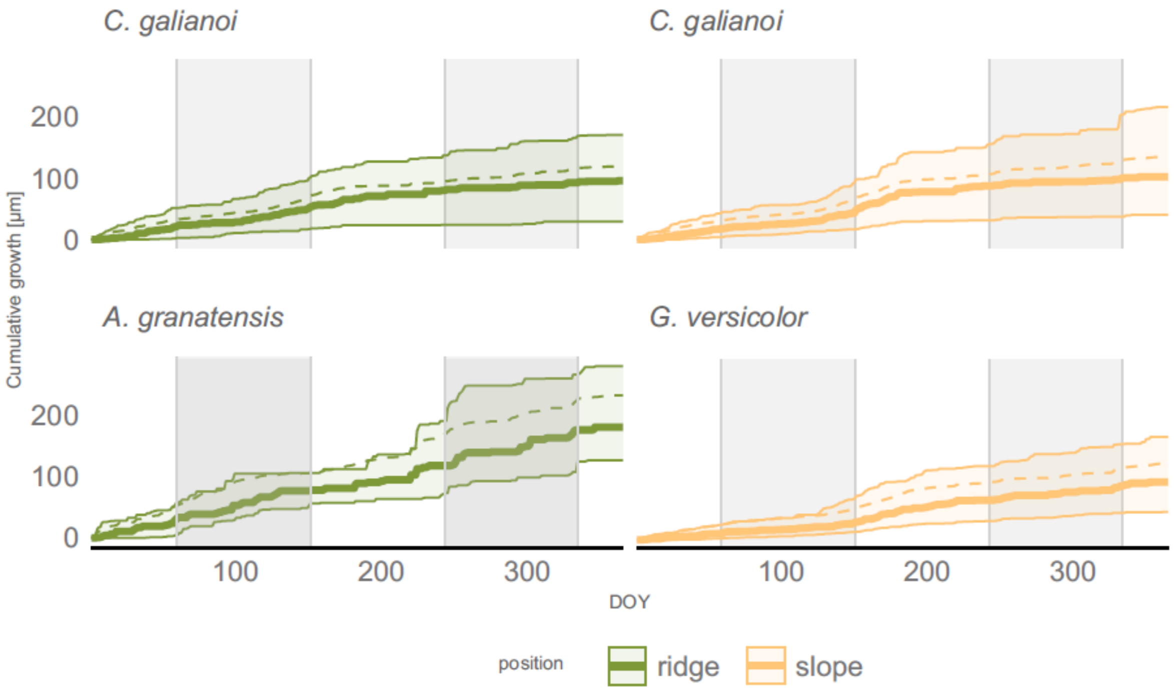

Fig. 14 Cumulative growth in C. galianoi*,* A. granatensis *and* G. versicolor *at different topographical positions (ridges and slopes, see A and B in Figs. 11, 12) shown as median (solid line), average (dashed line) and the 25% and 75% quartiles (shaded), over the day of the year using growth data of consecutive six years (2015 – 2020).*

We observed high inter-annual variability in the timing of growth, which was reflected by the different species with the most striking differences at the ridges during the first growth phase (Fig. 15). As a consequence, this variability of growth onset and cessation reflected a complex environmental control of growth, dependent on the alpine environment, site-specific conditions, and the species' trait-based coping strategies.

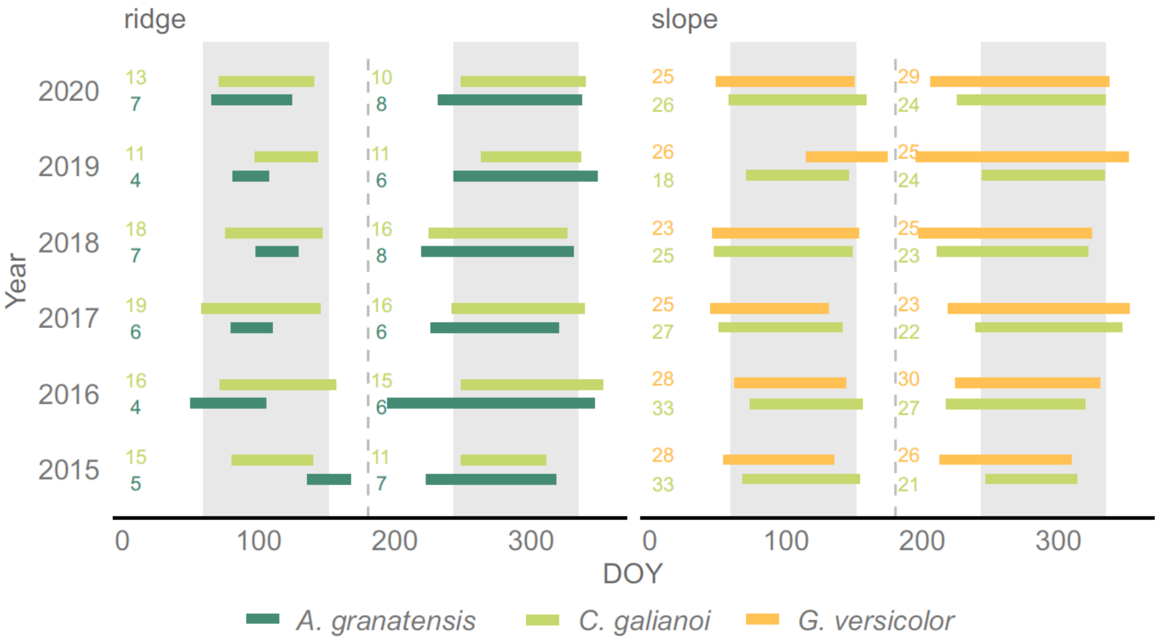

Fig. 15 Average growth onset and cessation in A. granatensis, C. galianoi*, and* G. versicolor *at different topographical positions for the first and second growth phases in 2015 – 2020, derived from stem diameter curves. Numbers indicate the number of growing specimens.*

The growth rates in our three alpine species show a high inter- and antra-annual variability, with higher spring growth rates in *C. galianoi*, and higher autumn growth rates in *G. versicolor* (Fig. 16). As such, our results revealed that the co-occurrence of alpine shrub species, which are generally competitors for the same resources, is not critical as long as the timing of resource acquisition and growth are maximally decoupled.

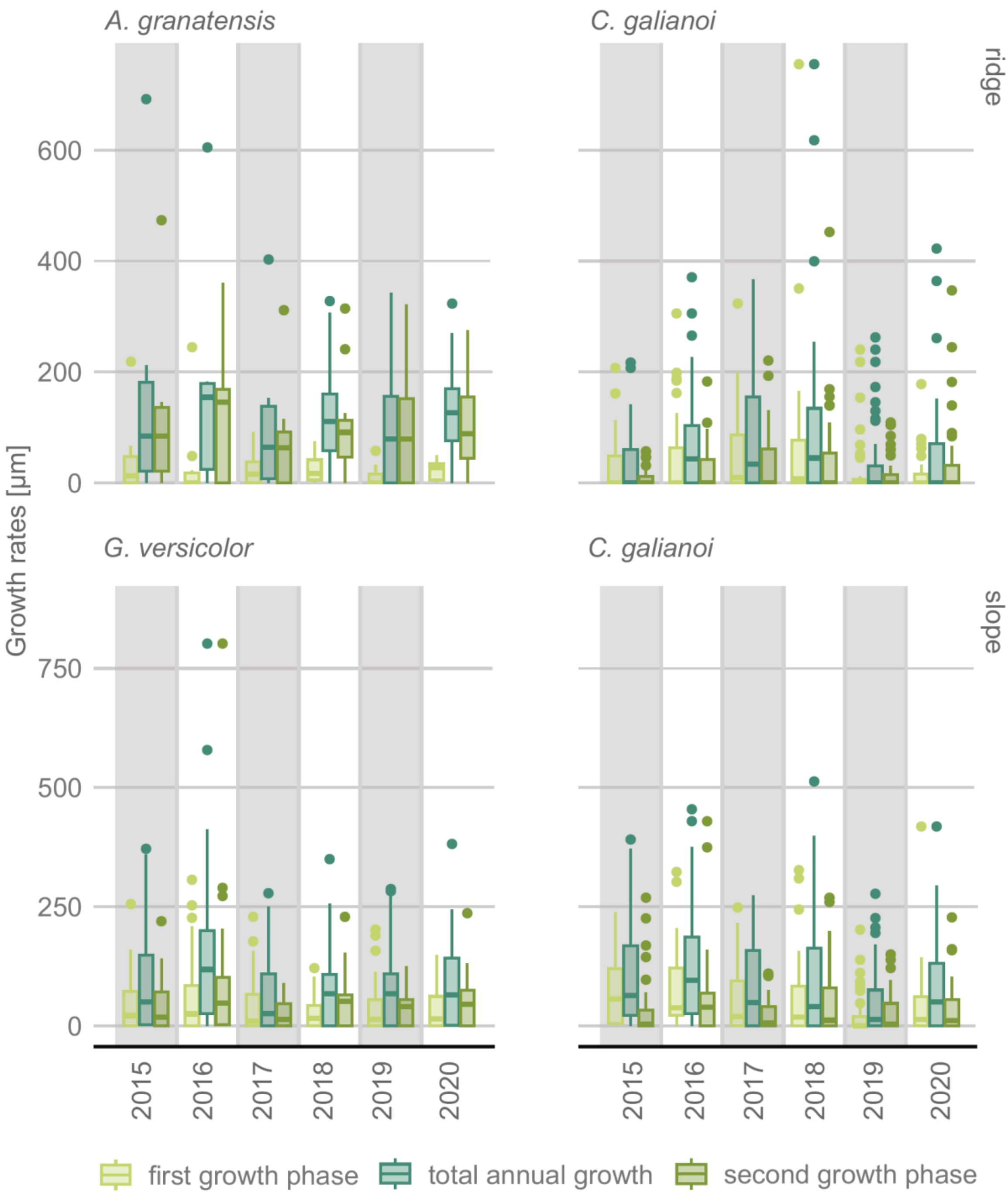

Fig. 16 Boxplot of growth phases showing the distribution of total annual growth as well as growth in the first and second growth phase in A. granatensis*,* C. galianoi *and* G. versicolor at different topographical positions.

From our overall findings on the detailed growth patterns in each species, we were able to deduce the species´ strategies to cope with the growth constraints of winter cold and summer drought. Using soil temperature and soil moisture data from the specific growth sites of each specimen, we found the species-specific environmental controls of growth. Using different statistical approaches, robust and significant driver constellations were revealed, allowing to argue for pronounced carry-over effects for both growth phases. Such effects were clearly visible for *C. galianoi*, which as a green-stemmed, frost-tolerant species was found to profit from cold and snow-free winters, mobilizing assimilates from winter photosynthesis for major spring growth (**Papers 1**, **2**, and **3**). As a drought tolerating species, *C. galianoi* showed severe summer stem contractions, and had strong water-related stem diameter increase in autumn caused by rehydration rather than growth. Using these combined winter-cold and summer-drought adapted growth strategies, *C. galianoi* was shown to perform best at all alpine sites, with high growth plasticity.

Compared to the two co-occurring shrub species, the combined cold and drought tolerance growth strategies in *C. galianoi* led to high competitive advantages. We synthesized the different growth strategies in Table 1 and used the single papers to address a), the overall growth performance of the species *C. galianoi* over its distributional range in the Sierra Nevada (**Paper 1**), b), the advantages and disadvantages of the strategies in green-stemmed *C. galianoi* vs. seasonal dimorphic *A. granatensis* (**Paper 2**), and c), the differences in growth across two co-existing green-stemmed species *C. galianoi* and *G. versicolor* (**Paper 3**).

Table 1 Synthesis of identified growth strategies in the Mediterranean alpine shrub species A. granatensis, C. galianoi, *and* G. versicolor.

	Winter cold resistance	Summer drought resistance
Astragalus granatensis	**avoidance**	**avoidance**
Cytisus galianoi	**tolerance**	**tolerance**
Genista versicolor	**escape**	**avoidance**

In **Paper 1**, we highlighted that growth in *C. galianoi* was maximized during spring, as was usually observed in other Mediterranean woody plants (Pellizzari et al. 2017, Alday et al. 2020, Camarero et al. 2021). Autumn radial increment is caused by both, growth and water-related swelling (Mäkinen et al. 2008, Zweifel et al. 2016). Our results further underpin the importance of pre-growth environmental conditions with carry-over effects, helping the plant to decouple growth from carbon uptake (cf., Iwasa and Kubo 1997, Wyka 1999, Meloche and Diggle 2003). As such, **Paper 1** suggests that for our alpine species, the spatio-temporal environmental drivers of bimodality should be scrutinized, and common assumptions on the actuality of driver – growth relations should be viewed with caution. The high year-to-year variability of climatic constraints for growth in *C. galianoi* led to adjusted growth responses revealing overall high temporal plasticity, which is a prerequisite in the Mediterranean, where secondary growth must be adjusted to a broad array of climatic conditions (Camarero et al. 2010). The adaptation to the heterogeneity of the alpine landscape could be attributed as spatial plasticity to environmental variance (Pacheco et al. 2018, Tumajer et al. 2021, Valeriano et al. 2023), which is of general importance in alpine ecosystems particularly under future climate change (Löffler et al.

2011), to which *C. galianoi* is probably well adapted by taking advantage from warmer winters, and tolerating even longer summer droughts (Albrecht et al. 2023a).

In **Paper 2**, we highlighted contrasting bimodal growth patterns in our physiologically different species. Patterns of stem contraction in *C. galianoi* suggested drought tolerance at the cost of reduced performance during autumn (cf. Bacelar et al. 2012) and frost tolerance paired with the advantage of benefiting from carbon fixation during winter and maximizing growth in spring (cf., Bossard and Rejmanek 1992, Wyka and Oleksyn 2014). Patterns of stem contraction in *A. granatensis* suggested drought avoidance without compromising performance (cf. Chaves et al. 2003, Bacelar et al. 2012), allowing to maximize growth during autumn precipitation, and frost avoidance by osmoregulation (cf., Essiamah and Eschrich 1985, Boughalleb et al. 2016, Schenk et al. 2021). In both co-existing species, pre-growth environmental drivers proved to be highly relevant for species performance, however with contrasting mechanisms. The temporal decoupling of growth from photosynthetic opportunities was, to our knowledge, not yet shown in the literature.

In **Paper 3**, we highlighted contrasting bimodal growth patterns in two coexisting green-stemmed alpine shrub species. In comparison to frost and drought tolerance in *C. galianoi* (Albrecht et al. 2023b), patterns of stem contraction in *G. versicolor* suggested drought avoidance without compromising performance during summer (cf. Chaves et al. 2003, Bacelar et al. 2012), and a frost escape strategy during winter, forcing the species into the snow-protected sites. Despite common traits, our species showed contrasting responses to winter soil temperatures, likely explaining the species´ distributional range, limiting *G. versicolor* to the slopes and allowing *C.*

galianoi a widespread ecological niche all over the Mediterranean alpine (cf., Dobbert et al. 2022a, Löffler et al 2022). As such, we argued that *G. versicolor* might profit from warmer winters, being constrained under severe summer droughts and threatened under winter cold when its protective snow cover is shortened, whereas the winter-cold adapted species *C. galianoi* has the higher ecological plasticity, and thus might be the winner under future climate warming (Albrecht et al. 2023c).

By using a novel approach to alpine shrub growth, this cumulative dissertation succeeded in deriving seasonal growth patterns and understanding the species´ growth strategies in the Mediterranean alpine. Our results help explain the biogeographical patterns of three of the most abundant alpine shrub species and support predicting their potential future range shifts in the Sierra Nevada, Spain. Provided relative stability under a continuous moderate grazing regime within the National Park and a low fire regime in the Sierra Nevada, our results suggest that shrub performance, particularly of *C. galianoi*, will be promoted under a future Mediterranean alpine climate, characterized by longer summer droughts and milder winters. Counterintuitively, such future near-natural vegetation succession might end up in backcoupling effects with an increase in above-ground biomass, i.e. fuel density, and thus with the unintended serious consequence of an increased fire risk.

Data availability

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

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Literature cited

Alados, C. L., A. El Aich, V. P. Papanastasis, H. Ozbekd, T. Navarro, H. Freitas, M. Vrahnakis, D. Larrosi, and B. Cabezudo. 2004. Change in plant spatial patterns and diversity along the successional gradient of Mediterranean grazing ecosystems. Ecological Modelling 180:523–535.

Altesor, A., M. Oesterheld, E. Leoni, F. Lezama, and C. Rodríguez. 2005. Effect of grazing on community structure and productivity of a Uruguayan grassland. Plant Ecology 179:83–91.

Anderson, R. S., G. Jiménez-Moreno, J. S. Carrión, and C. Pérez-Martínez. 2011. Postglacial history of alpine vegetation, fire, and climate from Laguna de Río Seco, Sierra Navada, southern Spain. Quaternary Science Reviews 30:1615–1629.

Arndt, S. K. 2000. Mechanisms of drought resistance in the tropical fruit tree Ziziphus. Doctoral dissertation, University of Vienna, Austria.

Bachelet, D., J. M. Lenihan, C. Daly, and R. P. Neilson. 2000. Interactions between fire, grazing and climate change at Wind Cave National Park, SD. Ecological Modelling 134:229–244.

Bacelar, E. L., J. M. Moutinho-Pereira, B. M. Gonçalves, C. V. Brito, J. Gomes-Laranjo, H. M. Ferreira, and C. M. Correia. 2012. Water use strategies of plants under drought conditions. Pages 145–170 *in* R. Arcoca, editor. Plant responses to drought stress: from morphological to molecular features. Springer, Heidelberg, Germany.

Bär, A., A. Bräuning, and J. Löffler. 2007. Ring-width chronology derived from ring widths of the alpine dwarf shrub *Empetrum nigrum* ssp. *hermaphroditum* in the Norwegian mountains. IAWA Journal 28:325–338.

Bär, A., R. Pape, A. Bräuning, and J. Löffler. 2008. Growth-ring variations of dwarf shrubs reflect regional climate signals in alpine environments rather than topoclimatic differences. Journal of Biogeography 35:625–636.

Barthlott, W., A. Hostert, G. Kier, W. Küper, H. Kreft, J. Mutke, M. D. Rafiqpoor, and J. H. Sommer. 2007. Geographic patterns of vascular plant diversity at continental to global scale. Erdkunde 61:305–316.

Blackman, V. H. 1991. Osmotic pressure, root pressure, and exudation. New Phytologist 20:106–115.

Blanca, G. 1996. Protección de la flora de Sierra Nevada (Granada y Almería). Conservación Vegetal 1:6.

Blanca, G., B. Cabezudo, M. Cueto, C. Fernández López, C. Morales Torres. 2009a. Flora Vascular de Andalucía Oriental. Consejería de Medio Ambiente. Junta de Andalucía 2:334.

Blanca, G., B. Cabezudo, M. Cueto, C. Fernández López and C. Morales Torres. 2009b. Flora Vascular de Andalucía Oriental. Consejería de Medio Ambiente. Junta de Andalucía 1:306.

Bossard, C. C., and M. Rejmanek. 1992. Why have green stems? Functional Ecology 6:197–205.

Boughalleb, F., R. Abdellaoui, N. Ben Brahim, and M. Neffati. 2016. Growth, photosynthesis, water use efficiency, and osmoregulation of the wild species *Astragalus gombiformis* Pomel. Under water deficit. Brazilian Journal of Botany 39:147–156.

Braun, H. J. 1984. The significance of the accessory tissues of the hydrosystem for osmotic water shifting as the second principle of water ascent, with some thoughts concerning the evolution of trees. IAWA Journal 5:275–294.

Briske, D. D. 1996. Strategies of plant survival in grazed systems: a functional interpretation. Pages 37–67 *in* J. Hodgson, and A. W. Illius, editors. The ecology and management of grazing systems. CAB International, Wallingford, UK

Buhk, C., A. Meyn, and A. Jentsch. 2007. The challenge of plant regeneration after fire in the Mediterranean Basin: scientific gaps in our knowledge on plant strategies and evolution of traits. Plant Ecology 192:1–19.

Calatrava, J., and S. Sayadi. 2019. Evolution of farming systems in the Mediterranean high mountain: The case of the Alpujarra Alta (Spain). Sustainability 11:704.

Calvo, L., R. Tárrega, and E. Luis. 2002. Regeneration patterns in a *Calluna vulgaris* heathland in the Cantabrian mountains (NW Spain): Effects of burning, cutting and ploughing. Acta Oecologica 23:81–90.

Cámara, A. D. 2009. Long-term trends in height in rural eastern Andalusia (1750–1950). Historia Agraria 47:45–67.

Camarero, J. J., J. M. Olano, S. J. A. Alfaro, B. Fernández-Marín, J. M. Becerril, and J. I. García-Plazaola. 2012. Photoprotection mechanisms in *Quercus ilex* under contrasting climatic conditions. Flora-Morphology, Distribution, Functional Ecology of Plants 207:557–564.

Camarero, J. J., J. M. Olano, and A. Alfonso Parras. 2010. Plastic bimodal xylogenesis in conifers from continental Mediterranean climates. New Phytologist 185:471–480.

Camarero, J. J., C. Valeriano, A. Gazol, M. Colangelo, and R. Sánchez-Salguero. 2021. Climate differently impacts the growth of coexisting trees and shrubs under semi-arid mediterranean conditions. Forests 12:381.

Cañadas, E. M., G. Fenu, J. Peñas, J. Lorite, E. Mattana, and G. Bacchetta. 2014. Hotspots within hot-spots: Endemic plant richness, environmental drivers, and implications for conservation. Biological Conservation 170:282–291.

Carrión, J. S., N. Fuentesa, P. González-Sampériz, L. Sánchez Quirante, J. C. Finlayson, S. Fernández, and A. Andrade. 2007. Holocene environmental change in a montane region of southern Europe with a long history of human settlement. Quaternary Science Reviews 26:1455–1475.

Chaves, M. M., J. P. Maroco, and J. S. Pereira. 2003. Understanding plant responses to drought-from genes to the whole plant. Functional Plant Biology 30:239–264.

Christopoulou, A., P. Z. Fulé, P. Andriopoulos, D. Sarris, and M. Arianoutsou. 2013. Dendrochronology-based fire history of *Pinus nigra* forests in Mount Taygetos, Southern Greece. Forest Ecology and Management 293:132–139.

Copenheaver, C. A., H. Gärtner, I. Schäfer, F. P. Vaccari, and P. Cherubini. 2010. Drought-triggered false ring formation in a Mediterranean shrub. Botany 88:545–555.

Cotto, O., J. Wessely, D. Georges, G. Klonner, M. Schmid, S. Dullinger, W. Thuiller, and F. Guillaume. 2017. A dynamic eco-evolutionary model predicts slow response of alpine plants to climate warming. Nature Communications 8:15399.

Crisp, M. D., S. Laffan, H. P. Linder, and A. Monro. 2001. Endemism in the Australian flora. Journal of Biogeography 28:183–198.

Crivellaro, A., and F. H. Schweingruber. 2013. Atlas of wood, bark and pith anatomy of Eastern Mediterranean trees and shrubs: with a special focus on *Cyprus*. Springer, Heidelberg, Germany.

de Micco, V., F. Campelo, M. de Luis, A. Bräuning, M. Grabner, G. Battipaglia, and P. Cherubini. 2016. Intra-annual density fluctuations in Tree rings. How, when, where and why? IAWA Journal 37:232–259.

Devecioğlu, A. G., and Y. Biçer. 2016. The effects of tragacanth addition on the thermal and mechanical properties of lightweight concretes mixed with expanded clay. Periodica Polytechnica Civil Engineering 60:45–50.

Díaz, S., S. Lavorel, S. McIntyre, V. Falczuk, F. E. Casanoves, D. G. Milchunas, C. Skappe, G. Rusch, M. Sternberg, I. Noy-Meir, J. Lansberg, W. Zhang, H. Clark, and B. D. Campbell. 2007. Plant trait responses to grazing – a global synthesis. Global Change Biology 13:313–341.

Dobbert, S., E. C. Albrecht, R. Pape, and J. Löffler. 2022a. Alpine shrub growth follows bimodal seasonal patterns across biomes–unexpected environmental controls. Communications Biology 5:793.

Dobbert, S., R. Pape, and J. Löffler. 2021a. Contrasting growth response of evergreen and deciduous arctic-alpine shrub species to climate variability. Ecosphere 12:e03688.

Dobbert, S., R. Pape, and J. Löffler. 2021b. How does spatial heterogeneity affect inter- and intraspecific growth patterns in tundra shrubs? Journal of Ecology 109:4115–4131.

Dobbert, S., R. Pape, and J. Löffler. 2022b. The application of dendrometers to alpine dwarf shrubs—a case study to investigate stem growth responses to environmental conditions. Biogeosciences 19:1933–1958.

Douglas, T. D., S. J. Kirkby, R. W. Critchely, and G. J. Park. 1994. Agricultural Terrace abandonment in the Alpujarrra, Andalusia, Spain. Land Degradation and Rehabilitation 5:281–291.

Eibes, P. M., D. Kienle, and C. Beierkuhnlein. 2017. Endemic vascular plants in the high mountains of the Sierra Nevada National Park (Spain). 6th Symposium for Research in Protected Areas 2 to 3 November 2017, Salzburg Conference Volume 133–136.

Essiamah, S., and W. Eschrich. 1985. Changes of starch content in the storage tissues of deciduous trees during winter and spring. IAWA Journal 6:97–106.

Fernández Calzado, M. R., and J. Molero Mesa. 2013. Changes in the summit flora of a Mediterranean mountain (Sierra Nevada, Spain) as a possible effect of climate change. LAZAROA 34:65–75.

Fernández-Santos, B., C. Martínez, J. A. García, and A. Puerto. 2004. Postfire regeneration in *Cytisus oromediterraneus*: sources of variation and morphology of the below-ground parts. Acta Oecologica 26:149–156.

Friedlander, J. D. 1980. The status of rare and endangered plant species in Mesa Verde National Park, Colorado. M. Sc. thesis, Colorado State University, Fort Collins, USA.

Frindte, K., R. Pape, K. Werner, J. Löffler, and C. Knief. 2019. Temperature and soil moisture control microbial community composition in an arctic-alpine ecosystem along elevational and micro-topographic gradients. ISME Journal 13:2031–2043.

Fulé, P. Z., M. Ribas, E. Gutiérrez, R. Vallejo, and M. W. Kaye. 2008. Forest structure and fire history in an old *Pinus nigra* forest, eastern Spain. Forest Ecology and Management 255:1234–1242.

García, A. V. 1994. Un fuego causado por las botellas de una acampada calcina 1.500 hectáreas en las Alpujarras. El Pais, Granada 9 AGO 1994.

Gazol, A., and J. J. Camarero. 2012. Mediterranean dwarf shrubs and coexisting trees present different radial-growth synchronies and responses to climate. Plant Ecology 213:1687–1698.

Giménez, E., M. Melendo, F. Valle, F. Gómez-Mercado, and E. Cano. 2004. Endemic flora biodiversity in the south of the Iberian Peninsula: altitudinal distribution, life forms and dispersal modes. Biodiversity and Conservation 13:2641–2660.

Golodets, C., J. Kigel, and M. Sternberg. 2010. Recovery of plant species composition and ecosystem function after cessation of grazing in a Mediterranean grassland. Plant Soil 329:365–378.

Gómez-Ortiz, A., M. Olivia, M. Salvá-Catarineu, and F. Salvador-Franch. 2013. The environmental protection of landscapes in the high semiarid Mediterranean mountain of Sierra Nevada National Park (Spain): Historical evolution and future perspectives. Applied Geography 42:227–239.

Gorji, S. G., E. G. Gorji, and M. A. Mohammadifar. 2014. Characterisation of gum tragacanth (*Astragalus gossypinus*)/sodium caseinate complex coacervation as a function of pH in an aqueous medium. Food Hydrocolloids 34:161–168.

Guarino, R., G. Giusso del Galdo, and S. Pignatti. 2005. The Mediterranean dwarf shubs: origin and adaptive radiation. Annali di Botanica 5:39–58.

Hessl, A., and S. Spackman. 1995. Effects of fire on threatened and endangered plants: An annotated bibliography. Information and Technology Report 2. U.S. Department of the Interior National Biological Service, Washington, DC, USA.

Huntly, N. 1991. Herbivores and the Dynamics of Communities and Ecosystems Annual Review of Ecology and Systematics 22:477–503.

INE (Instituto Nacional de Estatisticas). 2019a. Total Population for Alpujarra de la Sierra and Andalusia for the period from 1787 to 1986. (https://www.ine.es/dyngs/INEbase/es/operacion.htm?c=Estadistica_C&cid=1254736176998&&menu=resultados&idp=1254735572981) (Last Access: 01.09.2019)

INE (Instituto Nacional de Estatisticas). 2019b. Total Population for Alpujarra de la Sierra and Andalusia for the period from 1996 to 2018.

(https://www.ine.es/nomen2/inicio_r.do) (Last Access: 01.09.2019)

IUCN (World Conservation Union). 1998. United Nations list of protected areas. Prepared by WCMC and WCPA. IUCN Publications Services Unit, Gland, Switzerland.

Iwasa, Y., and T. Kubo.1997. Optimal size of storage for recovery after unpredictable disturbances. Evolutionary Ecology 11:41–65.

Jiménez-Moreno, G. and R. S. Anderson. 2012. Holocene vegetation and climate change recorded in alpine bog sediments from the Borreguiles de la Virgen, Sierra Nevada, southern Spain. Quaternary Research 77:44–53.

Jiménez-Moreno, G., A. García-Alix, M. D. Hernández-Corbalán, R. S. Anderson, and A. Delgado-Huertas. 2013. Vegetation, fire, climate and human disturbance history in the southwestern area during the late Holocene. Quaternary Research 79:110–122.

Junta de Andalucía. 2019a. Consejería de agricultura, ganaderia, pesca y desarollo sostenible. Animal numbers for Granada province from 2001 to 2015. (https://www.juntadeandalucia.es/organismos/agriculturaganaderiapescaydesarrollo-sostenible/servicios/estadistica-cartografia/estadisticas-ganaderas/paginas/censos-ganaderos.html) (Last Access: 01.09.2019)

Junta de Andalucía. 2019b. Red de Informacíon Ambiental de Andalucía (REDIAM). (http://www.juntadeandalucia.es/medioambiente/site/rediam/menu-item.04dc44281e5d53cf8ca78ca731525ea0/?vgnextoid=0a380c29bd9bc310VgnVCM2000000624e50aRCRD&vgnextchannel=50aedb27eb364410VgnVCM1000001325e50aRCRD&vgnextfmt=rediam&lr=lang_es#subapartadod9380c29bd9bc310VgnVCM2000000624e50a____%20) (Last Access: 01.09.2019)

Kaya, M., M. Odabasi, M. Mujtaba, M. Sen, E. Bulut, and B. Akyuz. 2016. Novel three-dimensional cellulose produced from trunk of *Astragalus gummifer* (Fabaceae) tested for protein adsorption performance. Materials Science and Engineering C 62:144–151.

Keeley, J. E. 1986. Resilience of Mediterranean shrub communities to fires. Pages 95–112 *in* B. Dell, A. J. M. Hopkins, and B. B. Lamont, editor. Resilience in Mediterranean-type ecosystems. Springer, Dordrecht, Germany.

Köhler, B., J. Löffler, and D.Wundram. 1994. Probleme der kleinräumigen Geoökovarianz im mittelnorwegischen Gebirge. Norwegian Journal of Geography 48:99–111.

Körner, C. 2021. Alpine plant life: functional plant ecology of high mountain ecosystems. Springer Nature, Cham, Switzerland.

Körner, C., and E. Hiltbrunner. 2018. The 90 ways to describe plant temperature. Perspectives in Plant Ecology, Evolution and Systematics 30:16–21.

Kropf, M., H. P. Comes, and J. W. Kadereit. 2006. Long-distance dispersal vs vicariance: the origin and genetic diversity of alpine plants in the Spanish Sierra Nevada. New Phytologist 172:169–184.

Lavorel, S. 1999. Ecological diversity and resilience of Mediterranean vegetation to disturbance. Diversity and Distributions 5:3–13.

Li, L., A. Bozec, S. Somot, K. Beranger, P. Bouruet-Aubertot, F. Sevault, and M. Crepon. 2006. Regional atmospheric, marine processes and climate modeling. Pages 373–397 *in* P. Lionello, P. Malanotte-Rizzoli, and R. Boscolo, editors. Mediterranean climate variability. Developments in Earth and Environmental Sciences 4. Elsevier Science, Amsterdam, Netherlands.

Lianopoulou, V., A. M. Bosabalidis, A. Patakas, D. Lazari, and E. Panteris. 2014. Effects of chilling stress on leaf morphology, anatomy, ultrastructure, gas exchange, and essential oils in the seasonally dimorphic plant *Teucrium polium* (Lamiaceae). Acta Physiologiae Plantarum 36:2271–2281.

Linares, J, C., A. J. García-Cervigón, M., L. Dugo-Díaz, D. Garcilaso, V. Lechuga, M. del Carmen Blanes, and B. Viñeglas. 2014. Sierra Nevada, the biodiversity legacy of the southernmost European glaciated mountain. Pages 43–64 *in* A. J. B. Gonçalves, and A. A. B. Vieira. Mountains. Nova Science Publishers, New York, USA.

Liphschitz, N., and S. Lev-Yadun. 1986. Cambial activity of evergreen and seasonal dimorphics around the Mediterranean. IAWA Journal 7:145–153.

Löffler, J. 2002: Altitudinal changes of ecosystem dynamics in the central Norwegian high mountains. Die Erde 133:227–258.

Löffler, J., and R. Pape. 2020. Thermal niche predictors of alpine plant species. Ecology 101:e02891.

Löffler, J., K. Anschlag, B. Baker, O.-D. Finch, B. Diekkrüger, D. Wundram, B. Schröder, R. Pape, and A. Lundberg. 2011. Mountain ecosystem response to global change. Erdkunde 65:189–213.

Löffler, J., S. Dobbert, R. Pape, and D. Wundram. 2021: Dendrometer measurements of arctic-alpine dwarf shrubs and micro-environmental drivers of plant growth—Dataset from long-term alpine ecosystem research in central Norway. Erdkunde 75:DP311201.

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

López-Merino, L., J. A. López-Sáez, F. Alba-Sánchez, S. Pérez-Díaz, J. S. Carrión. 2009. 2000 years of pastoralism and fire shaping high-altitude vegetation of Sierra de Gredos in central Spain. Review of Palaeobotany and Palynology 158:42–51.

Lorite, J. 2001. La vegetación de Sierra Nevada. Pages 23–45 *in* G. Blanca, M. R. López Onieva, J. Lorite, M. J. Martínez Lirola, J. Molero Mesa, and S. Vidal, editors. Flora amenazada y endémica de Sierra Nevada. Editorial Universidad de Granada, Granada, Spain.

Lorite, J. 2016. An updated checklist of the vascular flora of Sierra Nevada (SE Spain). Phytotaxa 261:1–57.

Lorite, J., M. Ruiz-Girela, and J. Castro. 2007. Patterns of seed germination in Mediterranean mountains: study on 37 endemic or rare species from Sierra Nevada, SE Spain. Candollea 62:5.

Mäkinen, H., J. W. Seo, P. Nöjd, U. Schmitt, and R. Jalkanen. 2008. Seasonal dynamics of wood formation: a comparison between pinning, microcoring and dendrometer measurements. European Journal of Forest Research 127:235–245.

Marlon, J. R., P. J. Bartlein, C. Carcaillet, D. G. Gavin, S. P. Harrison, P. E. Higuera, F. Joos, M. J. Power, and C. Prentice. 2008. Climate and human influences on global biomass burning over the past two millennia. Nature Geoscience 1:697–702.

Marriott, C., M. Fothergill, B. Jeangros, M. Scotton, and F. Louault. 2004. Long-term impacts of extensification of grassland management on biodiversity and productivity in upland areas. A review. Agronomie 24:447–462.

Martín-Vide, J., and J. A. López-Bustins. 2006. The Western Mediterranean Oscillation and rainfall in the Iberian Peninsula. International Journal of Climatology 26:1455–1475.

Médail, F., and P. Quézel. 1999. Biodiversity Hotspots in the Mediterranean Basin: Setting Global Conservation Priorities. Conservation Biology 13:1510–1513.

Melendo, M., E. Giménez, E. Cano, F. Gómez-Mercado, and F. Valle. 2003. The endemic flora in the south of the Iberian Peninsula: taxonomic composition, biological spectrum, pollination, reproduction mode and dispersal. Flora 198:260–276.

Meloche, C. G., and P. K. Diggle. 2003. The pattern of carbon allocation supporting growth of preformed shoot primordia in *Acomastylis rossi*i (Rosaceae). American Journal of Botany 90:1313–1320.

Mesa Garrido, M. A. 2019. Reforestación, silvicultura e incendios forestales en la dinámica del paisaje del Espacio Natural de Sierra Nevada (1881–2018). Investigaciones Geográficas 71:209–234.

Mohammadifar, M. A., S. M. Musavi, A. Kiumarsi, and P. A. Williams. 2006. Solution properties of targacanthin (water-soluble part of gum tragacanth exudate from Astragalus gossypinus). International Journal of Biological Macromolecules 38:31–39.

Molina, A., and J. Izco. 1986. Comportamiento ecológico y fitosociológico de Astragalus granatensis Lam. En la Provincia Castellano-Maestranzgo-Manchega. Trabajos del Departamiento de Botánica 13:83–97.

Molina-Venegas, R., A. Aparicio, S. Lavergne, and J. Arroyo. 2017. Climatic and topographical correlates of plant palaeo- and neoendemism in a Mediterranean biodiversity hotspot. Annals of Botany 119:229–238.

Moreno, J. M., and W. C. Oechel. 1991. Fire intensity and herbivory effects on postfire resprouting of Adenostoma fasciculatum in southern California chaparral. Oecologia 85:429–433.

Moreno, M. V., M. Conedera, E. Chuvieco, and G. B. Pezzatti. 2014. Fire regime changes and major driving forces in Spain from 1968 to 2010. Environmental Science and Policy 37:11–22.

Nassl, M., and J. Löffler. 2015. Ecosystem services in coupled social-ecological systems—Closing the cycle of service provision and societal feedback. Ambio 44:737–749.

Navarro, T., C. L. Alados, and B. Cabezudo. 2006. Changes of plant functional types in response to grazing in two semiarid shrub-lands of SE coast Spain. Journal of Arid Environments 64:298–322.

Nuñez, M. R., F. Bravo, and L. Calvo. 2003. Predicting the probability of seed germination in *Pinus sylvestris* L. and four competitor shrub species after fire. Annals of Forest Science 60:75–81.

Olano, J. M., I. Almería, M. Eugenio, and G. von Arx 2013. Under Pressure: how a Mediterranean high-mountain forb coordinates growth and hydraulic xylem anatomy in response to temperature and water constraints. Functional Ecology 27:1295–1303.

Pacheco, A., J. J. Camarero, M. Ribas, A. Gazol, E. Gutierrez, and M. Carrer. 2018. Disentangling the climate-driven bimodal growth pattern in coastal and continental Mediterranean pine stands. Science of the Total Environment 615:1518–1526.

Pape, R. and J. Löffler. 2017. Determinants of arctic-alpine pasture resources: The need for a spatially and functionally fine-scaled perspective. Geografiska Annaler: Series A, Physical Geography 99:353–370.

Pape, R., D. Wundram, and J. Löffler. 2009. Modelling near-surface temperature conditions in high mountain environments—an appraisal. Climate Research 39:99–109.

Pauli, H., M. Gottfried, S. Dullinger, O. Abdaladze, M. Akhalkatsi, J. L. B. Alonso, G. Coldea, J. Dick, B. Erschbamer, R. Fernández Calzado, D. Ghosn, J. I. Holten, R. Kanka, G. Kazakis, J. Kollár, P. Larsson, P. Moiseev, D. Moiseev, U. Molau, J. Molero Mesa, L. Nagy, G. Pelino, M. Puşcaş, G. Rossi, A. Stanisci, A. O. Syverhuset, J.-P. Theurillat, M. Tomaselli, P. Unterluggauer, L. Villar, P. Vittoz, and G. Grabherr. 2012. Recent plant diversity changes on Europe’s mountain summits. Science 336:353–355.

Pausas, J. G., and S. Fernández-Muñoz. 2012. Fire regime changes in the Western Mediterranean Basin: from fuel-limited to drought-driven fire regime. Climatic Change 110:215–226.

Pausas, J. G., J. Llovet, A. Rodrigo, and R. Vallejo. 2008. Are wildfires a disaster in the Mediterranean basin? –A review. International Journal of Wildland Fire 17:713–723.

Pausas, J. G., and R. Vallejo. 1999. The role of fire in European Mediterranean Ecosystems. Pages 3–16 *in* E. Chuvieco, editor. Remote sensing of large wildfires in the European Mediterranean basin. Springer, Berlin, Germany.

Patakas, A., and B. Nortsakis. 1999. Mechanisms involved in diurnal changes of osmotic potential in grapevines under drought conditions. Journal of Plant Physiology 154:767–774.

Pellizzari, E., J. J. Camarero, A. Gazol, E. Granda, R. Shetti, M. Wilmking, P. Moiseev, M. Pividori, and M. Carrer. 2017. Diverging shrub and tree growth from the Polar to the Mediterranean biomes across the European continent. Global Change Biology 23:3169–3180.

Piper, F. I., B. Viñegla, J. C. Linares, J. J. Camarero, L. A. Cavieres, and A. Fajardo. 2016. Mediterranean and temperate treelines are controlled by different environmental drivers. Journal of Ecology 104:691–702.

Pistón, N., C. Schöp, C. Armas, I. Prieto, and F. I. Pugnaire. 2016. Contribution of co-occurring shrub species to community richness and phylogenetic diversity along an environmental gradient. Perspectives in Plant Ecology, Evolution and Systematics 19:30–39.

Podlech, D. 2008. The genus *Astragalus* L. (Fabaceae) in Europe with exclusion of the former Soviet Union. Feddes Repertorium 119:310–387.

Prados de la Escosura, L., and J. R. Rosés. 2010: Human capital and economic growth in Spain, 1850-2000. Explorations in Economic History 47:520–532.

Prados, M. J. 2005. Territorial recognition and control of changes in dynamic rural areas: analysis of the naturbanization process in Andalusia, Spain. Journal of Environmental Planning and Management 48:65–83.

Puglielli, G. 2019. Beyond the concept of winter-summer leaves of Mediterranean seasonal dimorphic species. Frontiers in Plant Science 10:696.

Redolat, D., R. Monjo, J. A. Lopez-Bustins, and J. Martín-Vide. 2019. Upper-level Mediterranean Oscillation index and seasonal variability of rainfall and temperature. Theoretical and Applied Climatology 135:1059–1077.

Rivas-Martínez, S. 1981. Les étages bioclimatiques de la végétation de la Péninsula Ibérique. Actas del III Congreso Optima 1980. Anales Jardin Botanico de Madrid 37:251–268.

Rivas-Martínez, S. 1996. Clasificación bioclimática de la tierra. Folia Botanica Matritensis 16:1–33.

Rivas-Martínez S., and J. Loidi. 1999. Bioclimatology of the Iberian Peninsula. Itinera Geobotanica 13:41–47.

Roberts, N., D. Brayshaw, C. Kuzucuolu, R. Perez and L. Sadori. 2011. The mid-Holocene climatic transition in the Mediterranean: causes and consequences. Holocene 21:3–13.

Robles, A. B., J. Ruiz-Mirazo, M. E. Ramos, and J. L. González-Rebollar. 2009. Role of livestock grazing in sustainable use, naturalness promotion in naturalization of marginal ecosystems of southeastern Spain (Andalusia). Pages 211–231 *in* A. Rigueiro-Rodríuez, J. McAdam, and M. R. Mosquera-Losada, editors. Agroforestry in Europe: current status and future prospects. Springer, Dordrecht, Netherlands.

Rodríguez, V., C. Egea, and J. A. Nieto. 2002. Return migration in Andalusia, Spain. International Journal of Population Geography 8:233–254.

Rondeau, R. 2020. Long-term population trends and environmental attributes of the imperiled Chapin Mesa Milkvetch (*Astragalus schmolliae*). Doctoral dissertation, Colorado State University. USA.

Rondeau, R. J., D. G. Anderson, J. E. Handwerk, and T. Spector. 2022. Post-Fire Effects on the globally imperiled Chapin Mesa Milkvetch (*Astragalus schmolliae*), 2001–2019. Natural Areas Journal 42:4–17.

Rozas, V., I. García-González, and R. Zas. 2011. Climatic control of intra-annual wood density fluctuations of Pinus pinaster in NW Spain. Trees 25:443–453.

Sardans, J., and J. Peñuelas. 2013. Plant-soil interactions in Mediterranean forest and shrublands: impacts of climatic change. Plant Soil 365:1–33.

Sayadi, S., M. C. González-Roa, and J. Calatrava-Requena. 2009. Public preferences for landscape features: The case of agricultural landscape in mountainous Mediterranean areas. Land Use Policy 26:334–344.

Schenk, H. J., S. Jansen, and T. Hölttä. 2021. Positive pressure in xylem and its role in hydraulic function. New Phytologist 230:27–45.

Schulte, P. J. 1993. Tissue hydraulic properties and the water relations of desert shrubs. Pages 171–191 *in* J. A. C. Smith, and H. Griffiths, editors. Water deficits: plant responses from cell to community. BIOS Scientific Publishers, Oxford, UK.

Schwegman, J. E. 1998. Some aspects of the life history and population dynamics of *Astragalus tennesseensis* A. Gray in Illinois. Castanea 63:63–67.

Steinbauer, M. J., S. D. H. Irl, and C. Beierkuhnlein. 2013. Elevation-driven ecological isolation promotes diversification on Mediterranean islands. Acta Oecologica 47:52–56.

Talavera, S., and P. Gibbs. 1997. *Cytisus purgans* auct. (Leguminosae – Papilionoideae) comprises four distinct species. Botanical Journal of the Linnean Society 125:331–342.

Tarrega, R., L. Calvo, and L. Trabaud. 1992. Effect of high temperatures on seed germination of two woody Leguminosae. Vegetatio 102:139–147.

Touchan, R., C. Baisan, I. D. Mitsopoulos, and A. P. Dimitrakopoulos. 2012. Fire history in European Black Pine (*Pinus nigra* ARN.) forests of the Valia Kalda, Pindus Mountains, Greece. Tree-Ring-Research 68:45–50.

Troll, C. 1973. The upper timberlines in different climatic zones. Arctic and Alpine Research 5:A3–A18.

Tumajer, J., A. Buras, J. J. Camarero, M. Carrer, R. Shetti, M. Wilmking, J. Altman, G. Sangüesa-Barreda, and J. Lehejček. 2021. Growing faster, longer or both? Modelling plastic response of Juniperus communis growth phenology to climate change. Global Ecology and Biogeography 30:2229–2244.

UGR-IDR (Universidad Granada Instituto de Desarollo Regional). 2019. Total population of Alpujarra de la Sierra and Andalusia for the period from 1987 to 1995.

Valeriano, C., E. Gutiérrez, M. Colangelo, A. Gazol, R. Sánchez-Salguero, J. Tumajer, V. Shishov, J. A. Bonet, J. Martínez de Aragón, R. Ibáñez, M. Valerio, and J. J. Camarero. 2023. Seasonal precipitation and continentality drive bimodal growth in Mediterranean forests. Dendrochronologia 78:126057.

Valle, F. 2003. Mapa de series de vegetaciónde Andalucía. Escala1:400.000. Consejería de medio ambiente. Junta de Andalucía, Sevilla.

Verdú, J. R., M. B. Crespo, and E. Galante. 2000. Conservation strategy of a nature reserve in Maditerranean ecosystems: the effects of protection from grazing on biodiversity. Biodiversity and Conservation 9:1707–1721.

Vetaas, O. R., and J.-A. Grytnes. 2002. Distribution of vascular plant species richness and endemic richness along the Himalayan elevation gradient in Nepal. Global Ecology and Biogeography 11:291–301.

Wardle, D. A., R. D. Bardgett, J. N. Klironomos, H. Setälä, W. H. van der Putten, and D. H. Wall. 2004. Ecological linkages between aboveground and belowground biota. Science 304:1629–1633.

Warren-Wilson, J. 1964: Annual growth of *Salix arctica* in the High-Arctic. Annals of Botany 28:71–78.

Weeks, S. 2004. Factors limiting growth in *Astragalus michauxii* (sandhills milk-vetch). Doctoral dissertation, North Carolina State University, Raleigh, USA.

Weijers, S., N. Beckers, and J. Löffler. 2018. Recent spring warming limits near-treeline deciduous and evergreen alpine dwarf shrub growth. Ecosphere 9(6):e02328.

Winkler, M., A. Lamprecht, K. Steinbauer, K. Hülber, J.-P. Theurillat, F. Breiner, P. Choler, S. Ertl, A. Gutiérrez Girón, G. Rossi, P. Vittoz, M. Akhalkatsi, C. Bay, J.-L. Benito Alonso, T. Bergström, M. L. Carranza, E. Corcket, J. Dick, B. Erschbamer, R. Fernández Calzado, A. M. Fosaa, R. G. Gavilán, D. Ghosn, K. Gigauri, D. Huber, R. Kanka, G. Kazakis, M. Klipp, J. Kollar, T. Kudernatsch, P. Larsson, M. Mallaun, O. Michelsen, P. Moiseev, Dmitry Moiseev, U. Molau, J. Molero Mesa, U. Morra di Cella, L. Nagy, M. Petey, M.

Pușcaș, C. Rixen, A. Stanisci, M. Suen, A. O. Syverhuset, M. Tomaselli, P. Unterluggauer, T. Ursu, L. Villar, M. Gottfried, and H. Pauli. 2016. The rich sides of mountain summits – a pan-European view on aspect preferences of alpine plants. Journal of Biogeography 43, 2261–2273.

Wundram, D., R. Pape and J. Löffler. 2010. Alpine soil temperature variability at multiple scales. Arctic, Antarctic and Alpine Research 42:117–128.

Wyka, T. 1999. Carbohydrate storage and use in an alpine population of the perennial herb Oxytropis sericea. Oecologia 120:198–208.

Wyka, T. P., and J. Oleksyn. 2014. Photosynthetic ecophysiology of evergreen leaves in the woody angiosperms – a review. Dendrobiology 72:3–27.

Zambrana Pineda, J. F. 2006. El sector primario andaluz en el siglo XX. Instituto de Estadística de Andalucía, Sevilla, 2006. Ganado ovino y caprino en Andalucía 1906-2000. Junta de Andalucía: Instituto de Estadística y Cartografía de Andalucía. Consejería de Economía y Conocimiento. Atlas de Historia Economíca de Andalucía SS XIX-XX. Livestock (https://www.juntadeandalucia.es/institutodeestadisticaycartografia/atlashistoriaecon/atlas_cap_19.html) (Last Access: 01.09.2019)

Zimmerman G. T., and L. F. Neuenschwander. 1984. Livestock grazing influences on community structure, fire intensity, and fire frequency within the Douglas-fir/Ninebark habitat type. Journal of Range Management 37:104–110.

Zweifel, R. 2016. Radial stem variations - a source of tree physiological information not fully exploited yet. Plant, Cell and Environment 39:231–232.

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