2025 ERDKUNDE Vol. 79 · No. 1 · 65–94

SYNTHESIS ON GROWTH PATTERNS AND MECHANISMS IN MEDITERRANEAN-ALPINE SHRUBS

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With 17 figures and 1 table
Received 20 November 2024 · Accepted 06 May 2025

Summary: In the context of open questions on the adaptability of alpine ecosystems to future global warming, we studied three Mediterranean-alpine shrub species using dendrometers. Here, we synthesize our research approach and the main findings from three previously published articles. Under climate change, cold-adapted Mediterranean-alpine shrubs might become exposed to severe summer droughts and milder winters. However, neither the physiological strategies for coping with winter cold and summer drought nor the adaptability of these shrubs to climatic variability are yet fully understood. Here, we used *Cytisus galianoi* as a target species, which was abundant at manifold sites across the Sierra Nevada. We compared the species' adaptation mechanisms to frost and drought with those of *Astragalus granatensis*, a shrub species co-occurring at exposed ridges, and those of *Genista versicolor*, a shrub species co-occurring at snow-covered slopes. Previous dendroecological studies on shrubs commonly used anatomical ring-width-based approaches. In contrast, we aimed at understanding stem diameter changes, water-related stem expansion and contraction, and physiological strategies for coping with winter cold and summer drought by combining long-term, high-resolution dendrometer measurements with soil temperature and soil moisture data recorded directly at the growing sites. From our findings, we deduced the species' strategies to cope with the climatic constraints. We show that the green-stemmed species *C. galianoi* is frost and drought tolerant, likely profiting from cold and snow-free winters by mobilizing assimilates from winter photosynthesis for major spring growth. *C. galianoi* showed severe summer stem contractions, and revealed strong water-related stem diameter increase due to rehydration in autumn, while growth rates were minor. Using this combined winter cold and summer drought tolerance strategies, *C. galianoi* showed great competitive advantages and performed best at all alpine sites due to its high growth plasticity. In contrast, we show that *G. versicolor* uses a winter-cold escape and summer-drought avoidance strategy and exhibits a far narrower ecological niche, which is restricted to snow-covered alpine slopes. The observed pattern of stem diameter change in *A. granatensis* suggests frost avoidance by osmoregulation and drought avoidance by maintaining high tissue water potential throughout summer, as indicated by constantly expanding stems. This makes it competitive at the highest, most exposed ridge sites where harsh conditions prevail during winter. Here, we synthesize how we derived the different growth strategies and address a) the overall growth performance in *C. galianoi* over its distributional range across the Sierra Nevada, b) the advantages and disadvantages of growth strategies in a green-stemmed and a seasonal dimorphic species, and c) the growth differences in comparison of two green-stemmed species at shared sites.

Keywords: Alpine ecology, climate–growth relationship, ecophysiology, growth plasticity, carry-over effects, high precision point dendrometers, adaptation strategies (drought and frost), green stems and seasonal dimorphism, *Cytisus galianoi, Astragalus granatensis, Genista versicolor*, Sierra Nevada (Spain)

1 Introduction

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 alpine environments provide such information on plant functional traits and growth patterns of dwarf shrubs (e.g., Warren-Wilson 1964, Bär et al. 2007, Weijers et al. 2018, Pereira et al. 2022, Francon et al. 2023). However, growth response and performance of dwarf shrubs in Mediterranean-alpine environments are still poorly investigated but have received more attention in recent years (e.g., Copenheaver et al. 2010, Gazol & Camarero 2012a, Olano et al. 2013, García-Cervigón et al. 2018). Knowledge is still lacking on temporal, spatial, and interspecific differences in cambium dynamics (Tumajer et al. 2021a), and the species' adaptability to a warmer climate. Such knowledge is necessary to obtain an understanding of overarching patterns and underlying physiological processes that

https://doi.org/10.3112/erdkunde.2025.01.04 ISSN 2702-5985 (Online)

might bring us closer to answering the question of when and how woody plants grow (Jevšenak et al. 2022). Here, analyses of spatio-temporal growth patterns and environmental drivers of growth are used to better understand changes in vegetation structure as well as productivity and performance of woody plants under ongoing climate change. Against this background, we studied three Mediterranean-alpine shrub species using dendrometers. Here, we synthesize our research approach and the main findings from our three articles on these shrubs (Albrecht et al. 2023, 2024a, 2024b).

Plant species richness is high in the Mediterranean, and the high phytodiversity is 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 topographic complexity may also be positively correlated with endemism in high mountain regions functioning as refugia (Crisp et al. 2001, Vetaas & Grytnes 2002). The Sierra Nevada in SE Spain is one of the most important biodiversity hotspots in the Mediterranean region (e.g., Blanca 1996, Médail & Quézel 1999, Barthlott et al. 2007, Cañadas et al. 2014). However, the spatial vegetation patterns are dominated by a small number of single species. The most dominant is *Cytisus galianoi* Talavera & Gibbs, which colonizes a large variety of sites across the entire alpine environment. It cooccurrs with *Astragalus granatensis* Lam. or *Genista versicolor* Boiss. depending on the topographic position. Due to their dominance, such shrub species play a crucial role concerning their potential distribution patterns in a changing environment (e.g., Pauli et al. 2012, Fernández Calzado & Molero Mesa 2013, Winkler et al. 2016, Tamudo et al.2024), 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 intra-annual plant performance under high climate variability. To our knowledge, studies focusing on Mediterranean-alpine shrub growth are rare (García-Cervigón et al. 2018, Dobbert et al. 2022a, Löffler et al. 2022). Such information, however, might help to understand climate-driven modifications in alpine plant life and their biogeographical patterns in the context of climate warming.

In general, alpine plants are exposed to a wide variety of environmental influences, as they are abundant over steep ecological gradients occurring over short distances (Benito et al. 2011, Körner 2021). In the Mediterranean-alpine, plant performance is constraint by both, low-temperature stress during winter, which is increasing with elevation, and drought stress during summer that declines with elevation (García-Cervigón et al. 2012, Gutiérrez-Girón & Gavilán 2013, Pescador et al. 2015, Magaña Ugarte et al. 2019). Cambium activity in alpine woody plants is likely to be maximized during spring and autumn but reduced during unfavourable conditions in summer and winter (Mitrakos 1980), as commonly observed in Mediterranean lowland species (Gutiérrez et al. 2011, Touchan et al. 2012, Pacheco et al. 2018). However, as reactivation of the cambium is not always observed after a dry summer, facultative bimodal growth has been proposed as the best way to describe growth patterns in the Mediterranean (Camarero et al. 2010, Battipaglia et al. 2014, Campelo et al. 2018). Such facultative bimodality in growth processes can be interpreted as a growth strategy that enables plants to restrict their growth to phases with favourable environmental conditions (cf., Tumajer et al. 2021b). As such, it is likely to enhance plant performance in the Mediterranean-alpine, where winter cold and summer drought are strongly pronounced (Albrecht et al. 2024a). However, it is assumed that physiologically effective drought and frost stress is rarely fatal in alpine plants (Körner 2021). Here, plant performance relies on well-adapted physiological strategies to withstand the various stressors to which they are exposed. These strategies help the species to survive during the two stress periods and allow them to increase their performance under favourable conditions (cf., Mitrakos 1980). The most commonly used approach by plants to cope with cold stress is cold acclimation, which enables them to survive freezing by accumulating cryo-protective polypeptides and osmolytes (Ritonga & Chen 2020). In addition, alpine woody plants adapt to frost by developing frost survival mechanisms. These include, for example, a) tolerance to extracellular freezing and freeze dehydration, b) establishment of life cycles that allow species to escape and/or avoid frost (Neuner 2014), and c) osmoregulation, in which osmotic forces cause cellular dehydration that help plants to avoid frost damage by preventing the formation of intracellular ice crystals (Ritonga & Chen 2020). Water availability is one of the most important limiting factors for shrub growth (Battipaglia et al. 2014, Szymczak et al. 2020), which is why, in addition to water shortage during periods of frozen ground (Dobbert et al. 2022a), the ability to adapt to summer drought is of crucial importance. 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 is based on delaying or even avoiding water scarcity in plant tissues, and the drought tolerance strategy is the result of maintaining physiological functionality despite significant dehydration of plant tissues (cf., Chaves et al. 2003, Chen & Wang 2009). However, little is known about the use of such strategies to protect against winter frost and summer drought in Mediterranean-alpine regions, and their effects on species performance during phases of actual growth are not yet fully understood.

Within the complex alpine topography, plant species are restricted to their specific ecological niche (e.g., Dobbert et al. 2021a, Löffler & Pape 2020), and therefore alpine vegetation patterns reflect these complex topographic structures (e.g., Gjærevoll 1956, von Büren & Hiltbrunner 2022). Consequently, the growth of alpine shrubs from different biomes is not only influenced by regional climate conditions (e.g., Bär et al. 2008, Gazol & Camarero 2012a, Li et al. 2013), but also by the local environment, which is considered to be the main driver for shrub growth (Dobbert et al. 2022b, Gazol & Camarero 2012b). In this context, plastic xylogenesis has been described as a competitive advantage under the Mediterranean climate regime, where the rate of secondary growth must be adapted to a wide range of climatic conditions (cf., Camarero et al. 2010). Accordingly, the spatiotemporal plasticity of secondary growth is generally assumed to be of particular importance in cold and dry ecosystems (c.f., Körner 2012, Pellizzari et al. 2017, Tumajer et al. 2021a). Furthermore, high plasticity has been emphasised as an advantage that allows biogeographically widespread species to colonise large areas (Ghalambor et al. 2007, McLean et al. 2014). However, measuring the spatiotemporal plasticity of secondary growth is challenging. It has been shown that continuous time-series of stem diameter change, measured with high-resolution dendrometers, are suitable for deriving the plasticity of cambial activity and the adjustment of wood formation to fluctuations in climatic conditions (Pacheco et al. 2018). In earlier studies related to our LTAER-NO program, we derived such continuous time-series of stem diameter change using high-precision point 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, 2022c). In this way, we already looked closely into growth responses of deciduous and evergreen species from the Norwegian alpine tundra contributing to long-term ecosystem research (e.g., Köhler et al. 1994, Löffler 2002, Bär et al. 2008, Pape et al. 2009, Wundram et al. 2010, Pape & Löffler 2017, Weijers et al. 2018, Frindte et al. 2019, Löffler & Pape 2020, Löffler et al. 2021). Here, we transposed the successful concepts from our projects in Norway to the Sierra Nevada in Spain, where we established a comparative scientific infrastructure. As such, we use a dataset of on-site micro-environmental drivers in combination with innovative dendrometer measurements mounted on Mediterranean-alpine shrub species to gain new insights into the alpine ecosystems of the Sierra Nevada. By synthesizing our three recently published articles based on continuous time-series of stem diameter change from numerous *C. galianoi*, *A. granatensis*, and *G. versicolor* specimens from a variety of different sites along several geographic gradients within the Sierra Nevada (Albrecht et al. 2023, 2024a, 2024b), we aimed to gain insights into the species' cambial activity and their adaptability to climatic variations. In this way, we wanted to understand growth strategies for coping with winter cold and summer drought in a common and widespread, green-stemmed Mediterranean-alpine shrubs species, and to compare its growth patterns and growth timing with those of two co-existing shrub species in the Sierra Nevada. Therefore, we initially focussed on the species *C. galianoi*, which we studied along its entire distribution along alpine elevational and microtopographic gradients. Then, we studied *C. galianoi* in comparison to *A. granatensis* at the alpine ridges only, where both species experience harsh environmental conditions especially during snow-free winters. Finally, we studied *C. galianoi* in comparison to *G. versicolor* at snow-covered slopes, where the latter species has its narrower niche within the alpine.

2 Material and methods

2.1 Study area

The study area is located in the Sierra Nevada (SE Spain), a typical Mediterranean mountain area where multiple variables such as climate, human impacted grazing, nature conservation, forestry, and wildfires are interacting in complex ways (Anderson et al. 2011, Gómez-Ortiz et al. 2013). However, since the establishment of the National Park Sierra

Nevada (1999) and the encircling Natural Park (1989) (Gómez-Ortiz et al. 2013), plant growth has experienced a period of relative stability without fire and with a moderate grazing regime, allowing the study of near-natural conditions and the environmental drivers of plant growth. This is especially the case above the local treeline at about 2000 m a.s.l. (Troll 1973), which is mainly built by autochthonous and planted, mainly Scots pines (Linares et al. 2014, Piper et al. 2016) partially intermitted by widespread holm oak forests, reaching up to 2000 m a.s.l. (Linares et al. 2014). Aiming to study shrub growth and its environmental drivers under the most near-natural conditions possible, we selected two pronounced elevational gradients located at the southern slope of the Sierra Nevada above the treeline. The western gradient ranged from 2400 to 3200 m a.s.l. and the eastern from 2100 to 2800 m a.s.l. (Fig. 1a). Our gradients cover the alpine environment, where near-natural conditions prevail at the latest with establishment of the National Park. We selected our study sites according to the spatial distribution of our three focal species *Cytisus galianoi*, *Astragalus granatensis* and *Genista versicolor*, which colonize the three major microtopographic positions within the complex alpine topography, namely ridges, slopes and snowbeds (Fig. 1b). As such, our study design represents the overall spatial gradients of the area.

2.2 Plant species, distribution and seasonality

2.2.1 *Cytisus galianoi*

In the Sierra Nevada, the alpine vegetation is dominated by *Cytisus galianoi* Talavera & Gibbs (Rivas-Martínez 1996, Talavera & Gibbs 1997, Valle 2003), an endemic shrub species of the southern Iberian Peninsula (Valle 2003, Giménez et al. 2004, Melendo et al 2003), occurring frequently across the heterogenous topography. 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., 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 5 mm), when the plant is flowering, and are shed towards the end of summer (Talavera & Gibbs 1997). The species' stems are elastic and its flexible cells shrink upon water loss while maintaining a high turgor (cf., Patakas & Noitsakis 1999). In combination with its extensive, highly branched root system (Fernández-Santos et al. 2004), the species' elastic stems allows it to absorb water from a large volume of soil (Arndt 2000), which indicates high water use efficiency. Overall, density and surface cover of *C. galianoi* differ with aspect, slope, and curvature of the local topography. 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 & Rejmanek 1992). Therefore, 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*, 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. It is well adapted to harsh climatic conditions characterized by hot and dry summers under strong solar irradiation and cold and wet winters with protection by snow cover or exposure to severe frosts without snow cover (Fig. 2).

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 earlywood vessels, 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. 3). Given this xylem anatomy, the difficulties described in identification and measuring annual rings in Mediterranean species, where two split growth periods are expected (Camarero et al. 2010), separated by drought-induced false rings (Copenheaver et al. 2010), did not occur in our samples. Assumably, *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).

2.2.2 *Genista versicolor*

Within the alpine vegetation, *Genista versicolor* Boiss. (Rivas-Martínez 1996, Blanca et al. 2009a), endemic to the South of the Iberian Peninsula (Melendo et al. 2003, Giménez et al. 2004), forms

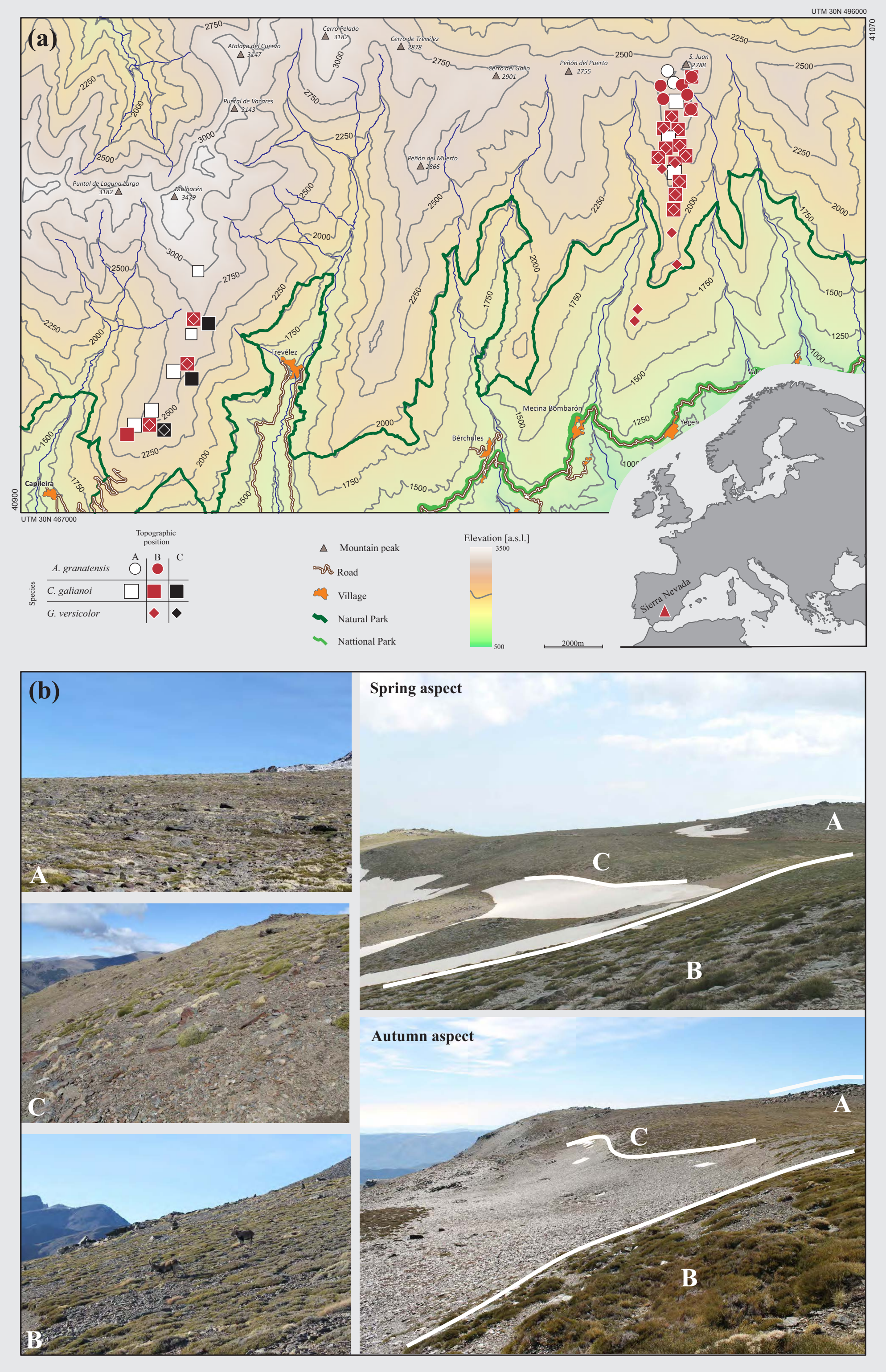


Fig. 1: (a) Topographic map of the Sierra Nevada showing the investigated mountain region and the locations of the sampling sites at ridges (A), slopes (B) and within snowbeds (C) along the elevational gradient (modified after Löffler et al. 2022). (b) Photos of the alpine environment showing the different topographic positions (modified after Albrecht et al. 2024a).

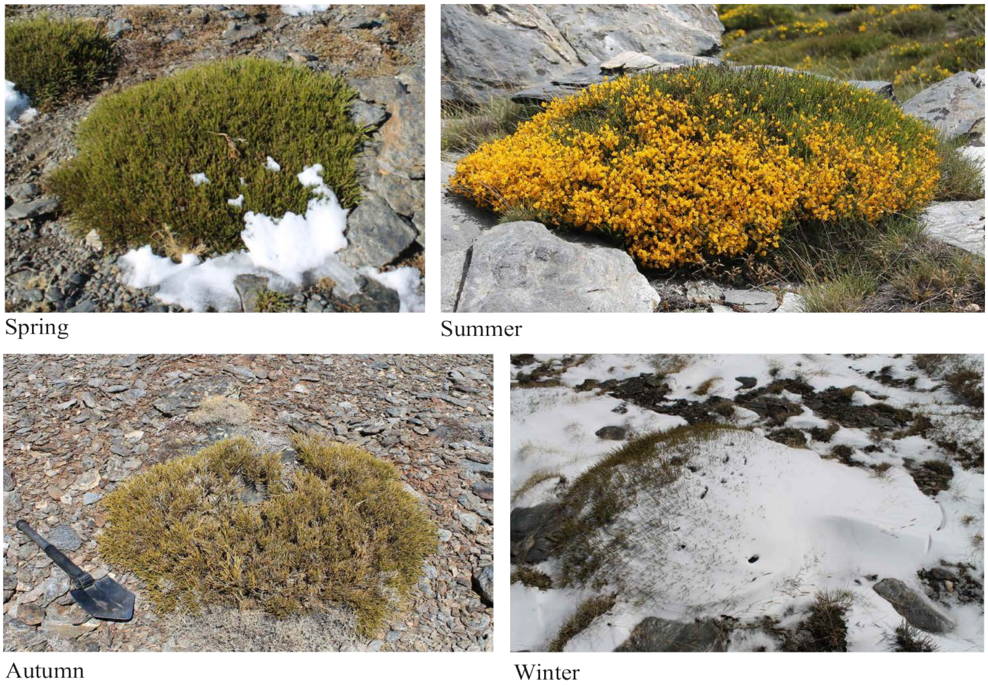


Fig. 2: Seasonal aspects of *C. galianoi*. In spring, when chlorophyll content is high, the species' stems appear intensely green, and in summer, its appearance is dominated by its yellow flowers. In autumn, it appears more brownish, and in winter, it is either covered by snow (slopes and snowbeds) or exposed to strong winds, low temperatures and occasional freezing conditions (ridges).

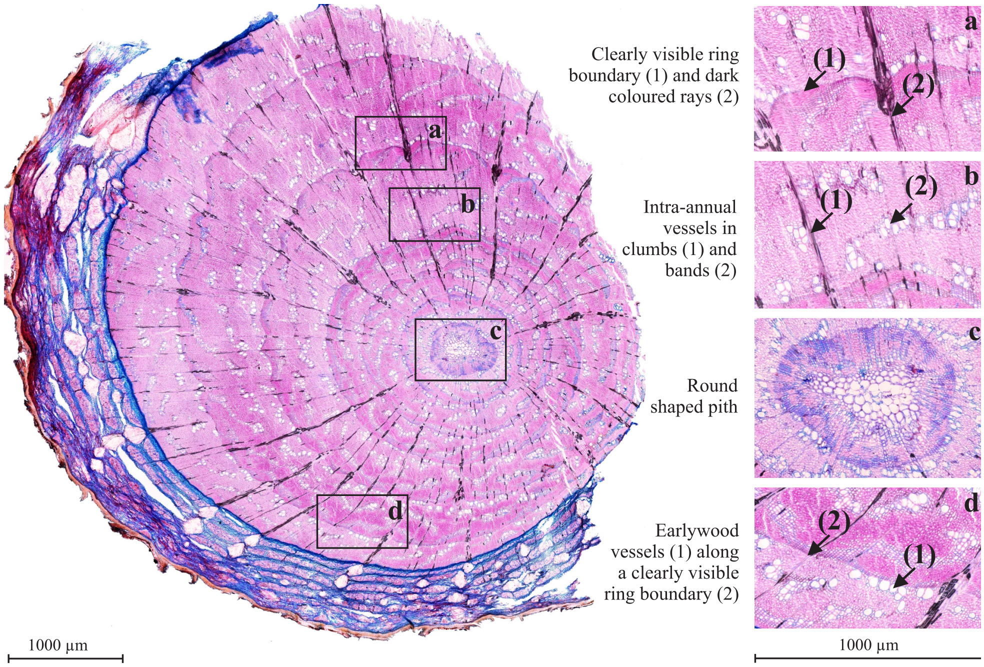


Fig. 3: Anatomical features in a base section of *C. galianoi*. The species' semi-ring porous xylem is characterized by a) clearly visible annual ring boundaries where thick-walled latewood cells merge into thin-walled earlywood cells. Narrow, dark coloured rays occur regularly and mostly range from 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.

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. Moreover, 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 5 mm) during anthesis in May/June (Fig. 4), which are shed towards the end of summer (Blanca et al. 2009a). The greyish-green photosynthetic stems (Bossard & Rejmanek 1992) are comparatively rigid and unbending, allowing increased water uptake (cf., Schulte 1993), further promoted by the species' taproot reaching deep into the soil (Albrecht et al. 2024b).

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. 5). The concentrically arranged first row of earlywood vessels helped 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 & Schweingruber 2013).

2.2.3 *Astragalus granatensis*

In our study region, *Astragalus granatensis* Lam. (Podlech 2008, Blanca et al. 2009a) only occurs at high elevations of the eastern gradient, between 2600 m a.s.l. and 2780 m a.s.l. (Fig. 1a). 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). This species is a long-living, cushion-forming, Iberian-North African chamaephyte that belongs to the Fabaceae family (Molina & 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 in the transition between autumn and winter

Spring

Summer

Autumn

Winter

Fig. 4: Seasonal aspects of *G. versicolor.* In spring, when chlorophyll content is high, the species' stems appear greyish-green, 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.

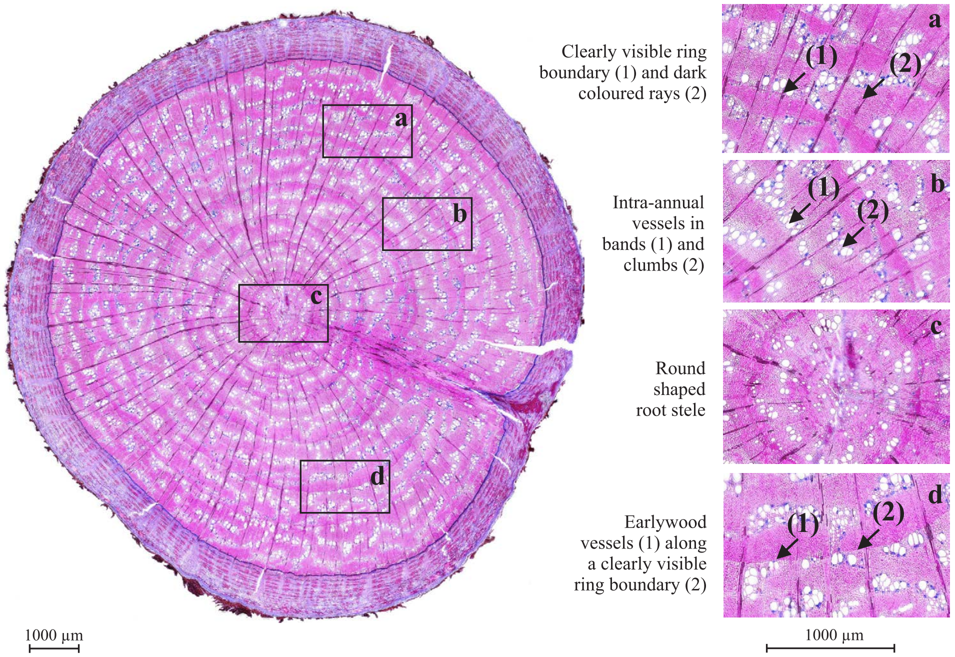


Fig. 5: Anatomical features in a root section of *G. versicolor*. The species' semi-ring porous xylem is characterized by a) clearly visible annual ring boundaries where thick-walled latewood cells merge into thin-walled earlywood cells. Narrow, dark coloured rays occur regularly and mostly range from 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.

Spring Summer

Autumn Winter

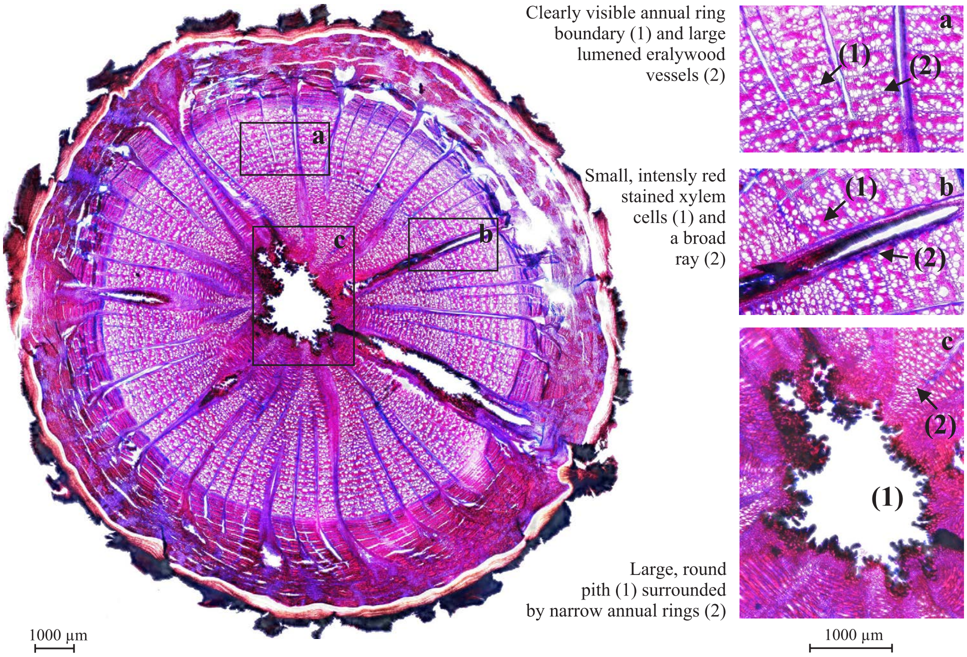
Fig. 6: Seasonal aspects of *A. granatensis*. In spring, the species is leafless, and at the beginning of summer, its appearance is dominated by its green summer leaves (first leaf cohort), which are shed towards the end of summer. At the beginning of autumn, it appears yellowish-brown, and towards the 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).

(November/December) (Fig. 6). Such seasonal leaf dimorphism has long been described for a variety of Mediterranean plant species (e.g., Liphschitz & Lev-Yadun 1986, Puglielli 2019) and interpreted as an adaptation strategy to the typical seasonality in the Mediterranean biome characterized by seasonal 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 plays an important role. It 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. As such, it allows the species to effectively buffer seasonal drought by dew condensation 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).

A. granatensis has ring-porous to semi-ring porous wood and annual ring boundaries are distinct by marginal parenchyma bands (Fig. 7). Thick-walled vessels occur in bands or clusters, and fibers are thick- to very thick-walled. The pith is round-shaped and surrounding cells contain dark staining substances (c.f., Crivellaro & 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 & Biçer 2016) exudes when twigs, stems and roots are incised. Since the amount of sap exuding is highest at the beginning of winter, we assume that it may play an important role in osmoregulation (e.g., Braun 1984, Blackman 1991, Boughalleb et al. 2016).

2.2.4 Distribution and seasonality of investigated shrubs

The geographical distribution of the target species (Fig. 1a) corresponds with complex environmental patterns characteristic to the study area (Fig. 1b), and seasonally changing site conditions (Fig. 8). Along the elevational gradient, the dense shrub vegetation of the lower alpine belt (at 1800–



Clearly visible annual ring boundary (1) and large lumened eralywood vessels (2)

Small, intensely red stained xylem cells (1) and a broad ray (2)

Large, round pith (1) surrounded by narrow annual rings (2)

Fig. 7: 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.

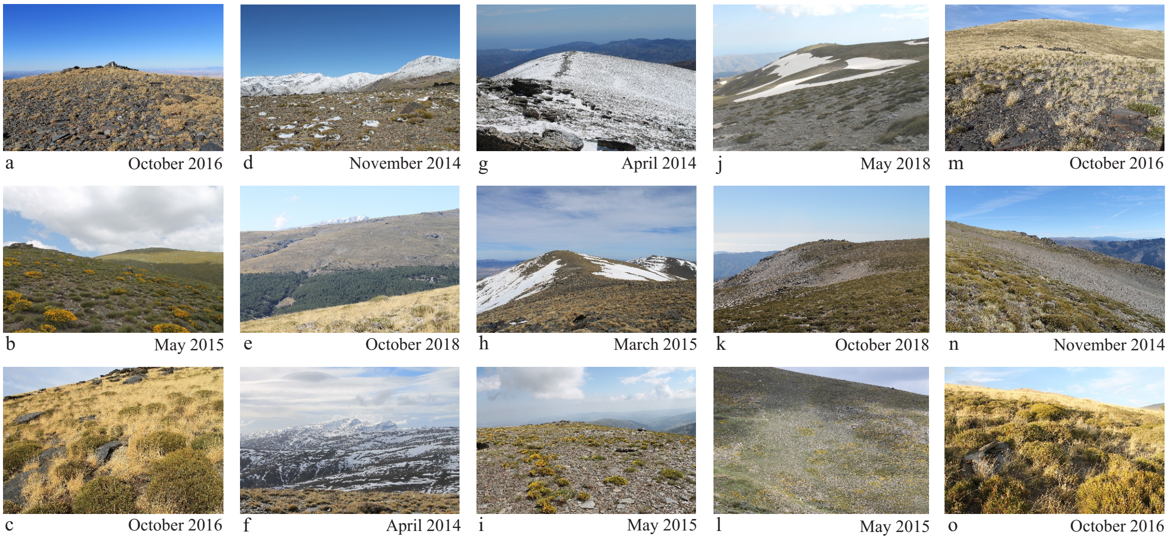


Fig. 8 Elevation and topography drive complex biogeographical patterns in our species. Vegetation cover and density increases along the elevation gradients from a) highest to b) intermediate and c) lowest elevations. During d) early winter and during f) spring, the highest peaks usually display a complex 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. j) and l) Aspects of snowbeds during May, and k) during October indicate high inter-annual climate variability. Vegetation cover changes in dependence to topography from m) hilltops and n) snowbeds with low density to increasing density and thickness at o) slopes.

2200 m a.s.l.), interspersed with individual trees and groups mainly of *Quercus rotundifolia* and planted *Pinus sylvestris* and *Pinus pinaster* species, opens up into the middle alpine belt (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 into the high-alpine belt where single low-growing shrubs co-occur with grasses in a matrix of open rock and debris (Rivas-Martínez 1981, Rivas-Martínez & Loidi 1999, Löffler et al. 2022). In the middle-alpine belt, *C. galianoi* co-occurs with *G. 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 *A. granatensis* (Lorite 2001), but is replaced in the latest snowbeds and at highest elevations. At the highest, most exposed ridges, where snow is usually blown out and vegetation cover is patchy with open rock and debris at the surface, *A. granatnesis* remains the exclusive shrub species (Löffler et al. 2022). Nomenclature and taxonomy of the plant species followed Blanca et al. (2009a, 2009b).

2.3 Study design, data collection, and climatic conditions

2.3.1 Study design

We designed this study to represent the full complexity of Mediterranean-alpine shrub communities from the local treeline to the highest peaks. Aiming at understanding of the climatic control of plant performance in the Mediterranean biome, we measured stem diameter variation and on-site environmental conditions at an hourly basis from January 1, 2015 to December 31, 2020, including additional data from 2014. In this way, we obtained a comprehensive six-year dataset for our three focal species across their respective spatial ranges (for the entire dataset cf., Löffler et al. 2022). This dataset offers numerous opportunities to explore climate-growth relations at different scales within Mediterranean-alpine ecosystems (Löffler et al. 2022). By partitioning this comprehensive dataset into three data subsets comprising stem diameter changes and on-site environmental data of a) *Cytisus galianoi* across its spatial range (Albrecht et al. 2024a), b) *C. galianoi* compared to *Astragalus granatensis* at ridges (Albrecht et al. 2023), and c) *C. galianoi* compared to *Genista versicolor* at slopes (Albrecht et al. 2024b), we were able to better understand the species' growth mechanisms. Here, we synthesise the most relevant findings based on these data subsets to shed light on the physiological mechanisms of radial stem growth and to infer the species' adaptation strategies to winter cold and summer drought from the complex patterns of stem diameter change in relation to environmental conditions at the microsites.

2.3.2 Dendrometer measurements, setup and data

Since the first studies using dendrometers to monitor continuous radial stem change in trees in the 1930s and the 1940s (Reineke 1932, Daubenmire 1945) dendrometers have been widely used to monitor secondary growth responses to environmental fluctuations (cf., Dobbert et al. 2022b for a brief review of related studies). Meanwhile, they are able to capture radial stem dimensions at hourly or even shorter intervals (Drew & Downes 2009, Liu et al. 2018), making them an effective technique for capturing intra-annual growth variability in trees. As modern dendrometers are designed for measurements at a micrometer scale, they can also be used on shrubs to provide fine scale, intra-annual, continuous, and highly comparable information, as recently presented (Löffler et al. 2022, Dobbert et al. 2021a, 2021b, 2022a, 2022b, 2022c). Here, we used such high-precision point dendrometers (type DD-RO; Ecomatik, Dachau, Germany, temperature coefficient <0.2 μm K^{-1}) to obtain dendrometer measurements of *Cytisus galianoi*, *Astragalus granatensis* and *Genista versicolor* at 1-minute sampling intervals, aggregated and stored as hourly data. To continuously monitor the species' radial stem diameter variations, we mounted our dendrometers to the main stems of the selected specimens using UV-resistant rubber band. The obtained stationary system consisted of a T-shaped aluminium bar placed horizontally above the ground surface (~1 cm above ground). Before attaching the dendrometers, we removed the outermost layers of the dead periderm (0.5 mm) (Dobbert et al. 2022c) to minimize the influence of hygroscopic swelling and shrinkage of the bark (Zweifel & Häsler 2001). We took care to place our dendrometers as close as possible to the root collar of the specimens (Albrecht et al. 2023, 2024a, 2024b), which is assumed to integrate the growth of all plant parts (Bär et al. 2007; Ropars et al. 2017). However, it should be noted here that the extent to which changes in radial stem diameter vary within specimens and between multiple stems of the same specimen, as well as along individual stems, is not yet fully understood (Dobbert et al 2021b). Given this enormous variation, we firstly ensured that all selected specimens were growing at locations representative of the conditions observed at each study site, and secondly monitored as many specimens as possible at each site, usually 1 to 3 specimens. In this way, the variation between individual shrubs should also be taken into account. This is important because, due to the high climatic variability in the Mediterranean biome, the shrubs likely exhibit pronounced temporal plasticity, as secondary growth must be adapted to a wide range of climatic conditions (Camarero et al. 2010). As we found significant correlations and clear matches in the growth patterns, despite the small sample size in some cases, we were able to infer general trends. From our raw dendrometer measurements collected in this way, we obtained daily mean values by averaging the hourly dendrometer data following the 'daily mean approach' (Deslauriers et al. 2007). In a next step, we normalized the annual stem diameter curves by removing the initial stem diameter from the annual curves (for ranges of removed initial stem diameters cf., Albrecht et al. 2024a for *C. galianoi*, Albrecht et al. 2023 for *C. galianoi* and *A. granatensis*, and Albrecht et al. 2024b for *C. galianoi* and *G. versicolor*). This step is necessary because dendrometers measure changes in stem diameter relative to the start of the measurement cycle. Finally, we checked for outliers, defining the interquartile range (IQR) and the 25th (Q1) and 75th (Q3) percentiles (Q1/Q3 ± 1.5 × IQR) as cutoff ranges. Since we did not find any outliers, all daily values per curve were retained. By performing these processing steps, we obtained 77 dendrometer curves of *C. galianoi* across its spatial range (Albrecht et al. 2024a). From these 77 curves, we selected 16 curves of *C. galianoi* specimens for comparison with 10 curves of *A. granatensis* specimens that co-occurred at ridges (Albrecht et al. 2023). In addition, we selected 29 curves of *C. galianoi* specimens for comparison with 29 curves of *G. versicolor* specimens that co-occurred at slopes (Albrecht et al. 2024b).

2.3.3 Environmental data collection

To assess the potential drivers of the monitored radial stem diameter variations, we recorded on-site environmental data, namely soil temperatures (°C, T_{RZ}) and volumetric soil water content (m^3/m^3, SM_{RZ}), reflecting the exact root zone conditions of each specimen. Therefore, we installed our thermistors (type S-TMB-002, 0.2°C accuracy) and soil moisture probes (type S-SMD-M005, 3% accuracy) at 10 cm soil depth in the root zone of each specimen directly below the main stem selected for the dendrometer measurements, taking care not to damage the roots (cf., Löffler & Pape 2020, Dobbert et al 2021a, 2021b). Both the T_{RZ} and SM_{RZ} were recorded at 1-minute intervals and stored as hourly averages using ONSET's HOBO loggers (type H21-002). Complementary, we recorded the following environmental variables at 2692 m a.s.l., reflecting the climatic conditions in our study area: Relative air humidity (rH, %) and air temperature (AT, °C) at 2 m above ground using Skye rht sensors (SKH 2065) with ± 2% accuracy for rH and ± 0.2°C for T, global radiation (GRSZ, W/m²) at 1 cm above ground in the shoot zone of one specimen using a silicon pyranometer (type S-LIB-M003) with ±10 W/m² accuracy, air pressure (AP, hPa) at 2 m above ground using a barometric air pressure sensor (type Meier-NT-MNT10025) with ± 0.01 hPa accuracy, and precipitation (mm, P) at 100 cm above ground, using a precipitation sensor (type LAMBRECHT-meteo-15189) with ± 2% accuracy. Sensors were mounted to an ADL-MX data logger that recorded data at hourly intervals. All environmental data were collected for the period January 1st, 2015 to December 31st, 2020. There were no missing data and additional data from 2014 were used to calculate the previous year's environmental conditions for 2015. This non-invasive design generates comparable data across large elevational and topographic gradients. In addition, it assumes that in the generally shallow alpine soils where deeper roots penetrate the parent rock, lateral roots at shallow depths are most important for access to surface moisture and nutrients and thus have a major impact on plant health (Muktadir et al. 2020). Most of the lateral and fine roots of our focal species are distributed at these shallow depths (Albrecht et al. 2023, 2024a, 2024b), allowing us to capture a large part of the relevant soil conditions. As such, our data provide site-specific information about the amount of water available for the plants.

2.3.4 Regional climate and micro-environmental conditions

The Mediterranean climate is associated with severe summer droughts and torrential precipitation, abruptly introducing the cool but mild and humid winter period. This bimodality of the Mediterranean climate (Mitrakos 1980, Camarero et al. 2012) is reflected in the data we recorded at our alpine climate station at 2692 m a.s.l. They show the overall climate regime (Fig. 9), including a whole series of variables that characterize the general weather conditions (Fig. 10). 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 & 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). However, corresponding studies on patterns of stem diameter changes and growth mechanisms are rare for Mediterranean-alpine plant species (Dobbert et al. 2022a) and 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 & 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 & 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 11, also our micro-environmental conditions (SM_{RZ} and T_{RZ}) 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

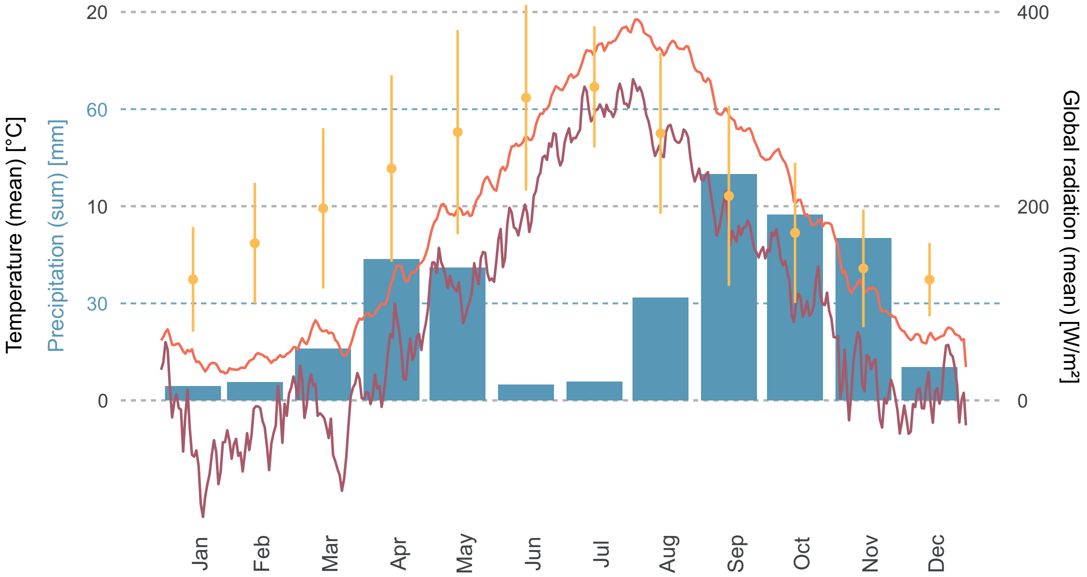


Fig. 9: Illustration of the overall climate regime. Monthly means of hourly measurements of global radiation (+/- SE, indicated by vertical lines), and precipitation (without snow), as well as daily means of air temperature (2 m above ground) measured at 2692 m a.s.l. and averaged over the period from 2015 to 2020, and soil temperatures measured at slopes across the entire elevation gradient and also averaged over the study period.

mild, humid winters (ANDERSON et al. 2011, GÓMEZ-ORTIZ et al. 2013). 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 topographic positions but pronounced inter-annual differences in timing of the dry period in summer (LÖFFLER et al. 2022). The dry period usually begins in May/June, when SM_{RZ} drops due to increased atmospheric demands such as high VPD, wind and high solar radiation, and lasts until August/September, when the first autumn rains replenish the soil water and make water available to the plants again (Fig. 11). Importantly, here we refer to physiological drought, i.e., a water deficit in the soil that is directly related to the water potential of our plants (cf., ALBRECHT et al. 2023, 2024b). Just as the dry period can be identified from the SM_{RZ} data, the T_{RZ} curve makes it possible to identify frost periods (T_{RZ} below 0°C) and snow cover (absence of daily fluctuations in the data curves).

For information on specific micro-environmental conditions measured within the root zone of a) *Cytisus galianoi* across its spatial range cf., ALBRECHT et al. (2024a), b) *C. galianoi* at ridges compared to *Astragalus ganatensis* cf., ALBRECHT et al. (2023), and c) *C. galianoi* at slopes compared to *Genista versicolor* cf., ALBRECHT et al. (2024b).

2.4 Analysis of growth patterns

To detect the species' seasonal growth patterns from the measured dendrometer curves, we defined two growth phases, one in the first and one in the second half of the year. In this way, it is possible to consider the bimodal rhythm of the Mediterranean climate (MITRAKOS 1980), which is known to induce bimodal growth patterns in several Mediterranean lowland tree species (CAMARERO et al. 2010) and possibly in Mediterranean-alpine plants (OLANO et al. 2013). These two phases of radial stem increment are intermitted by a first phase of stem contraction during summer and a second phase of stem contraction during winter. We calculated growth semi-annually by defining growth-induced irreversible stem expansion (hereafter growth) as the cumulative stem diameter maximum of the current half-year minus the most recent maximum of the previous study period (cf., ALBRECHT et al. 2023, 2024a, 2024b). Growth is therefore equivalent to an increase in stem diameter that is greater than at any point in the past (ZWEIFEL 2016, ZWEIFEL et al. 2021). According to this approach, which is inspired by the 'zero-growth approach' proposed by ZWEIFEL (2016), growth can only assume positive values, but does not necessarily occur in every growth phase or in every year. If growth failed to occur during certain growth phases or years, these are referred to as dormant phases or years. Whenever

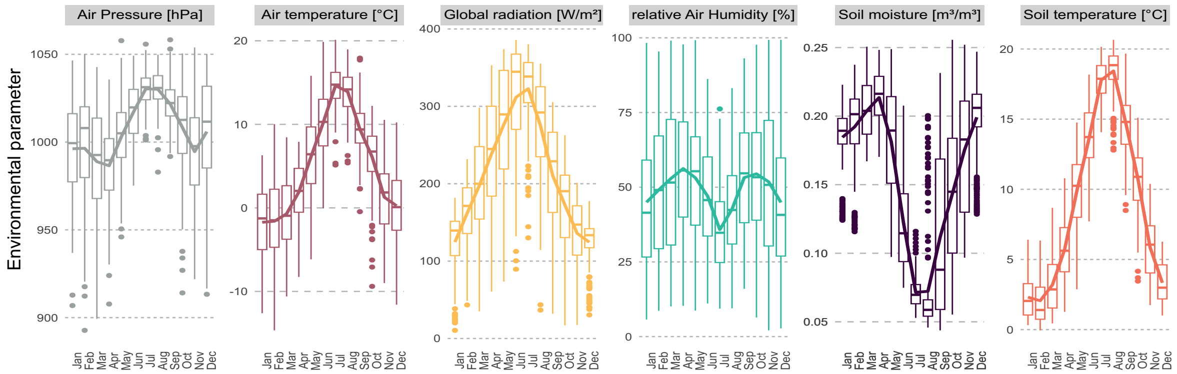


Fig. 10: Boxplots of hourly measurements of air pressure (AP), air temperature (T, 2 m above ground), global radiation (GRSZ, at 1 cm above ground in the shoot zone of one specimen), and relative humidity (rH) measured at 2692 m a.s.l. and averaged over the period from 2014 to 2020, and soil moisture and soil temperatures measured at slopes across the entire elevation gradient and also averaged over the study period.

growth occurred, we calculated both the change in stem diameter and the temporal duration of the respective phase, defined as the period from the first day of growth to the last day of growth during the respective period for all specimens and years. Finally, to draw conclusions about the species' strategies for coping with winter cold and summer drought from the derived stem diameter patterns, cumulative growth curves and timing of growth, we visually compared the patterns between both the different species and the different topographic positions. In combination with the micro-environmental data measured within the species' root zone (cf., Albrecht et al. 2023, 2024a, 2024b), we were able to work out the growth patterns and strategies of the species.

3 Results

By grouping and averaging the dendrometer measurements derived from individually installed dendrometers, we were able to derive the patterns of stem diameter change, growth and growth timing of the investigated species *Cytisus galianoi*, *Astragalus granatensis* and *Genista versicolor*.

All 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. 12). Focusing on the differences between the species, we found that *C. galianoi* revealed a more pronounced stem contraction during summer but a less pronounced stem contraction during winter compared to *A. granatensis*. Moreover, we found that stem contraction during summer and winter was more pronounced in *C. galianoi* compared to *G. versicolor*. Focusing on the differences between the three contrasting topographic positions, we found that most pronounced differences occurred within snowbeds, most likely reflecting the highly variable snowpack distribution within the complex alpine topography. Moreover, stem contraction during summer and winter was most pronounced at ridges.

Differences in bimodality were primarily 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* revealed least summer stem contraction. Likewise, the species showed different patterns of stem diameter changes during winter, which were driven by differences of the species' response to winter cold (Fig. 12). We found that the changes in stem diameter of *C. galianoi* during winter were characterized by moderate variability, while in *A. granatensis* winter stem contraction was strongly pronounced, whereas it was practically absent in *G. versicolor*. 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.

By separating growth from water-related stem diameter changes, we derived irreversible stem diameter increments (growth) resulting from cell division and expansion. These cumulative growth curves showed that *C. galianoi* achieved the highest growth rates during spring, particularly at the slopes. In contrast, *A. granatensis* and, to a lesser extent, *G. versicolor* showed higher growth rates in autumn (Fig. 14).

In addition to the cumulative growth curves showing the general growth pattern in our three alpine species, the absolute growth rates revealed

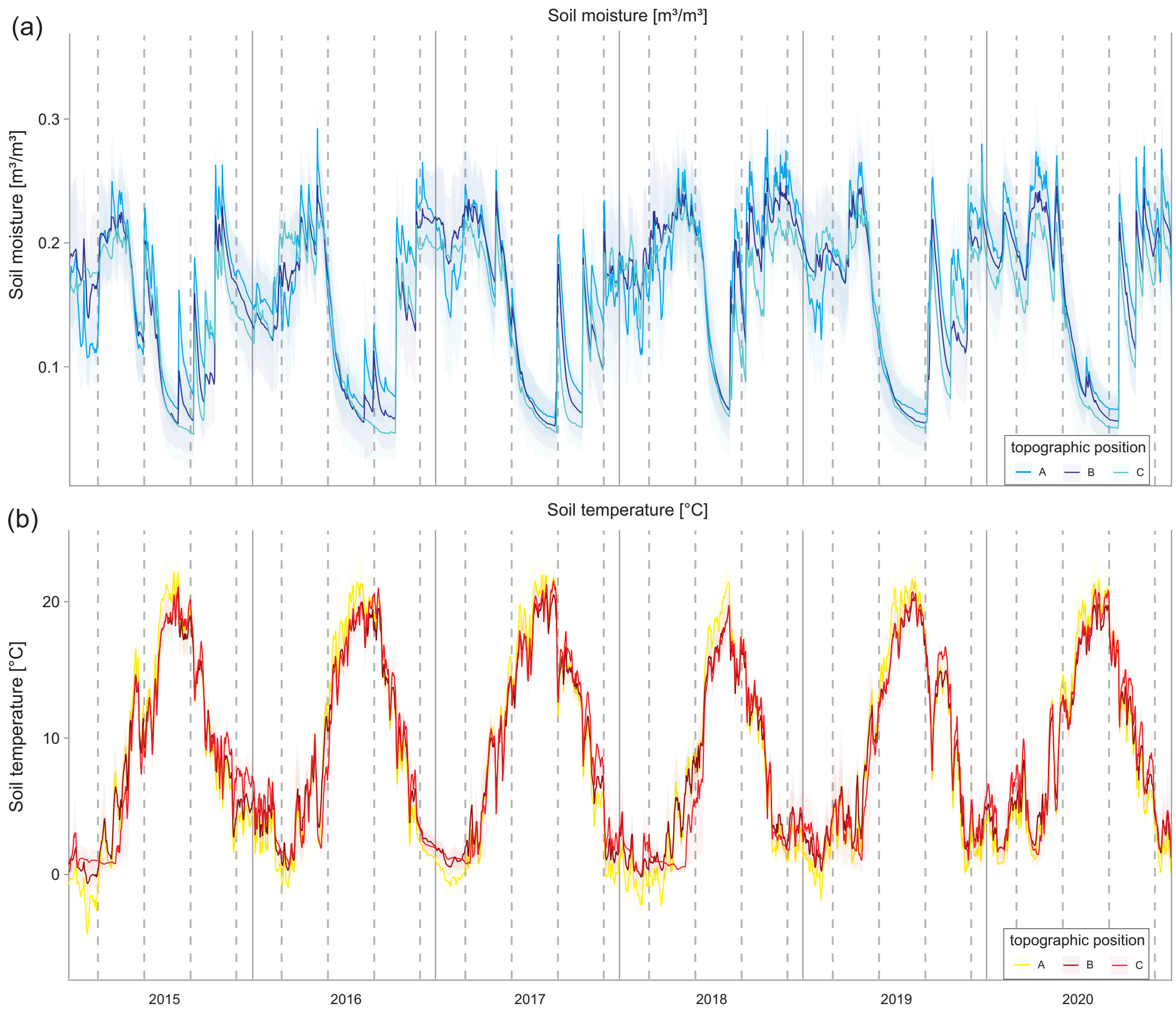


Fig. 11: Micro-environmental data, namely (a) soil moisture (SM_{RZ}) and (b) soil temperature (T_{RZ}), from three topographic positions (A = exposed ridges, B = slopes, and C = snowbeds). The presented curves represent averaged series and transparency indicates standard deviation. Vertical dashed grey lines indicate the seasons (namely: spring = March, April, May; summer = June, July, August; autumn = September, October, November; winter = December, January, February) and vertical black lines mark the years (modified after Löffler et al. 2022).

a high inter- and intra-annual variability as well as differences between the topographic positions (Fig. 15). Overall, *A. granatensis* showed the highest growth rates, followed by *G. versicolor* and *C. galianoi*. At the slopes, growth rates of *C. galianoi* and *G. versicolor* were similar, while at ridges *C. galianoi* achieved significantly lower growth rates than *A. granatensis*. Interestingly, maximum growth rates of co-occurring species, i.e., *C. galianoi* and *A. granatensis* at ridges and *C. galianoi* and *G. versicolor* at slopes, were achieved at seasonally differing times. While *C. galianoi* achieved the highest growth rates in spring, the other two species achieved the highest growth rates in autumn. This suggests that timing of resource acquisition and growth are maximally decoupled, allowing the co-occurrence of alpine shrub species, which are generally competitors for the same resources.

Apart from the magnitude of growth, the cumulative growth curves uncovered the timing of growth by both visualizing the timing of irreversible stem expansion and enabling the calculation of the temporal phases of irreversible stem expansion (Fig. 16). Here, we observed high inter-annual variability, which was reflected by the different species with the most striking differences at the ridges during the first growth phase. In *C. galianoi* at ridges, growth onset of the first growth phase was usually in February/March and cessation in late May. In contrast, in *A. granatensis* the timing was highly variable, with growth onset usually occurring at the end of

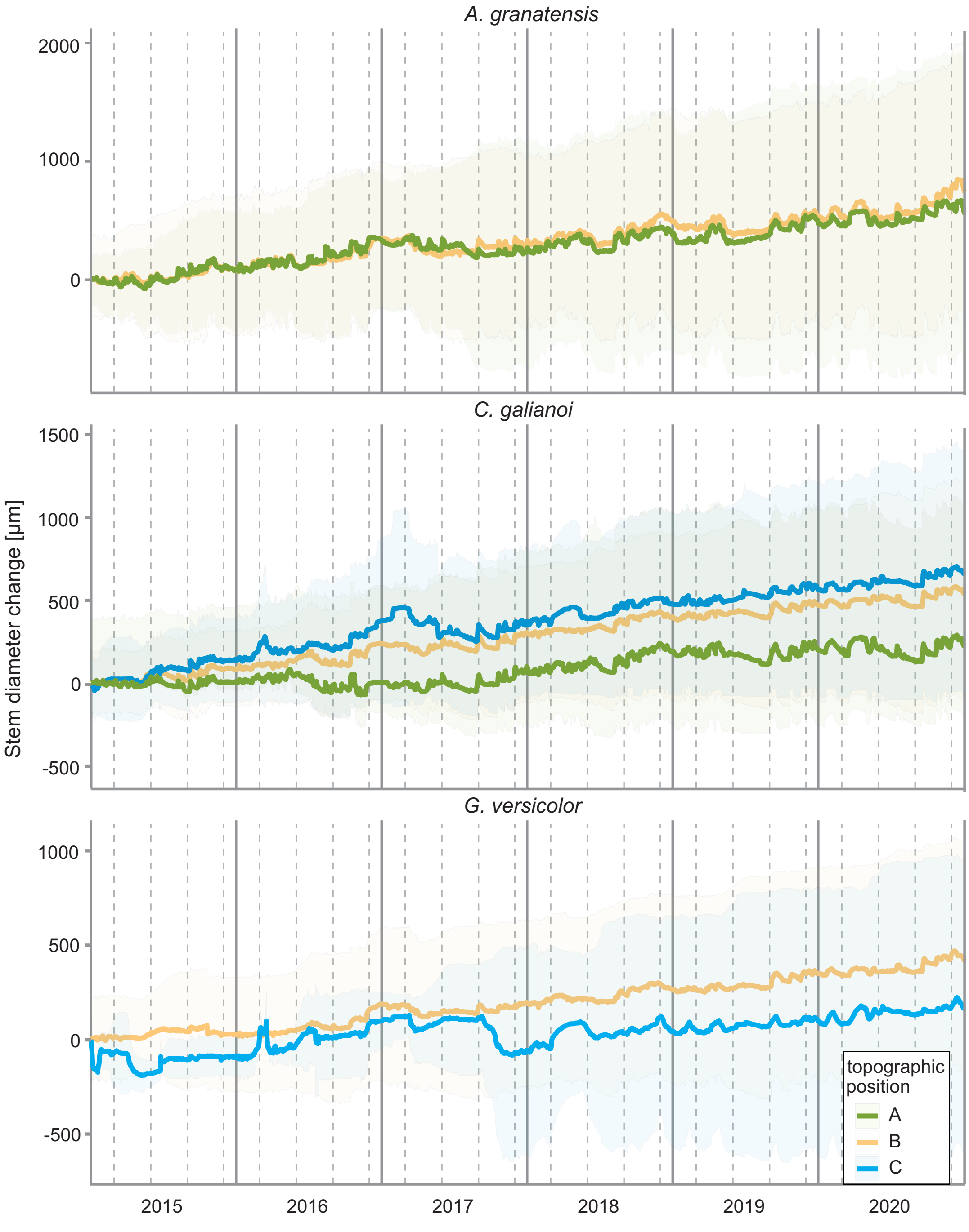


Fig. 12: Dendrometer curves representing averaged series of stem diameter change between *A. granatensis*, *C. galianoi* and *G. versicolor* as well as between ridges (A), slopes (B) and snowbeds (C); transparency indicates standard deviation among specimens. Vertical dashed lines indicate the meteorological seasons (namely: spring = March, April, May; summer = June, July, August; autumn = September, October, November; winter = December, January, February) and vertical solid lines mark the years (modified after Löffler et al. 2022).

March/April and cessation between mid-April and late May. At slopes, onset of the first growth phase was usually in February/March and cessation in May/June. In general, it was slightly earlier for *G. versicolor* than for *C. galianoi*. In *C. galianoi* at ridges, the onset of the second growth phase was highly variable, usually occurring in September/October, whereas in *A. granatensis* it took place between middle and end of

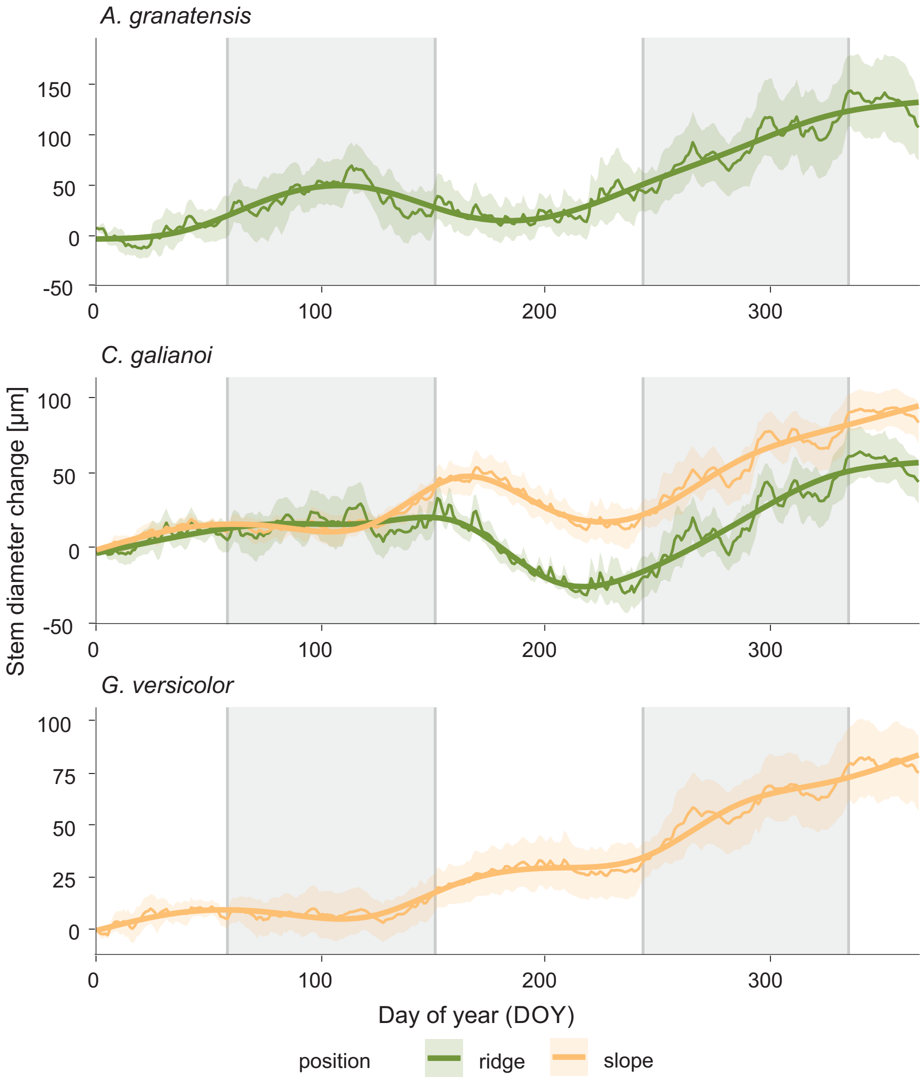


Fig. 13: Seasonal patterns of stem diameter change in *A. granatensis, C. galianoi,* and *G. versicolor* at different topographic positions (ridges and slopes, see Fig. 12) averaged over the studied period 2015 – 2020 and represented by generalized additive models (GAMs). Alternating grey and white background markers highlight the meteorological seasons.

August, while growth cessation usually occurred in November/December for both species. In *C. galianoi* at slopes, growth resumption after summer drought usually took place in August/September, several weeks after *G. versicolor* (July/August), while the timing of growth cessation was similar in both species (November/December). Overall, the interannual variability in the duration of the two growth phases was high, but the growth rates were independent of the duration of the growth phases. The observed variability of growth onset, duration and cessation reflected site-specific differences and the species' trait-based coping strategies.

Overall, by grouping and averaging our dendrometer measurements, we found that changes in stem diameter of *C. galianoi* during winter were characterised by moderate variability, which apparently allowed early stem expansion (February), usually peaking in May/June. This suggests that early water uptake with the resulting high turgor pressure promotes an early onset of growth processes. Moreover, we found that both, summer and winter stem contraction were most pronounced at the ridge positions, and that *A. granatensis* had a more pronounced winter stem contraction, while *C. galianoi* had more pronounced summer stem contraction. This suggests a) winter dehydration in

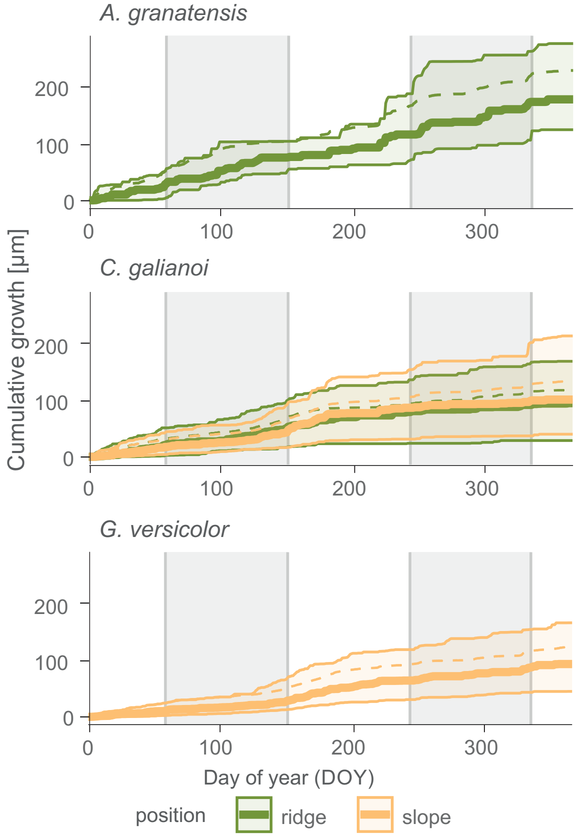


Fig. 14: Cumulative growth in *C. galianoi, A. granatensis* and *G. versicolor* at different topographic positions (ridges and slopes, see Fig. 12) shown as median (solid line), average (dashed line) and the 25% and 75% quartiles (shaded), over the days of the year using growth data of six consecutive years (2015 – 2020). Alternating grey and white background markers highlight the meteorological seasons.

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. Comparing patterns of stem diameter change at the slope positions it became obvious that both, winter and summer stem contraction was least pronounced in *G. versicolor*. This suggests a) that frost protection gets less relevant where species are protected by snow during winter, and b) 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.

4 Discussion

Here, we synthesize the main results of our three research articles on the patterns of stem diameter change and growth of three Mediterranean-alpine shrub species in the Sierra Nevada (Spain) (Albrecht et al. 2023, 2024a, 2024b). In these studies, we inferred the species' strategies for coping with winter cold and summer drought, with the overall aim of drawing conclusion on the adaptive capacity of these shrubs to possible future climate variability.

In our three alpine shrub species, we observed bimodal patterns of annual stem diameter change and growth, with differences in bimodality between species being primarily due to differences in the species' response to summer drought. Strong stem contraction and dehydration during summer observed in *Cytisus galianoi* suggest drought tolerance at the expense of reduced performance during autumn, i.e., growth (Bacelar et al. 2012), when rehydration is prioritized to increase the water potential before growth resumption (Albrecht et al. 2023, 2024b). We assume that the species' ability to absorb low daily dew precipitation (cf., Mooney et al. 1980) is compensated by relatively high transpiration loss. The latter is probably regulated by the anisohydry of the photosynthetically active green stems (cf., Bossard & Rejmanek 1992), leading to long-term shrinkage at high water potential (cf., Albrecht et al. 2023, 2024b). In contrast, the observed early peak of stem contraction in *Astragalus granatensis* suggests that drought is avoided without compromising performance, while physiological functionality for carbon fixation is maintained at high tissue water potential throughout the summer (cf., Chaves et al. 2003, Bacelar et al. 2012). This allows the species to maximize growth during autumn rains (cf., Albrecht et al. 2023). The species' ability to capture and absorb low daily dew precipitation and to store it in their tissues (Guarino et al. 2005) via stem succulence (Griffiths & Males 2017) is probably controlled by isohydric summer leaves. Overall, this physiological behaviour leads to a long-term, steady increase in their water potential (Albrecht et al. 2023). The observed less pronounced summer stem contraction in *Genista versicolor* suggests a high water potential throughout the summer (Albrecht et al. 2024b). This in turn suggests that drought is avoided without compromising performance, while physiological functionality for carbon fixation is maintained at high tissue water potential throughout summer (Chaves et al. 2003, Bacelar et al. 2012). Here, the observed marginal diurnal changes in stem diameter indicate such a high water potential for this species, allowing it to maximize its growth during autumn rains, likely significantly extending the period for growth (major growth in autumn) (Albrecht et al. 2024b).

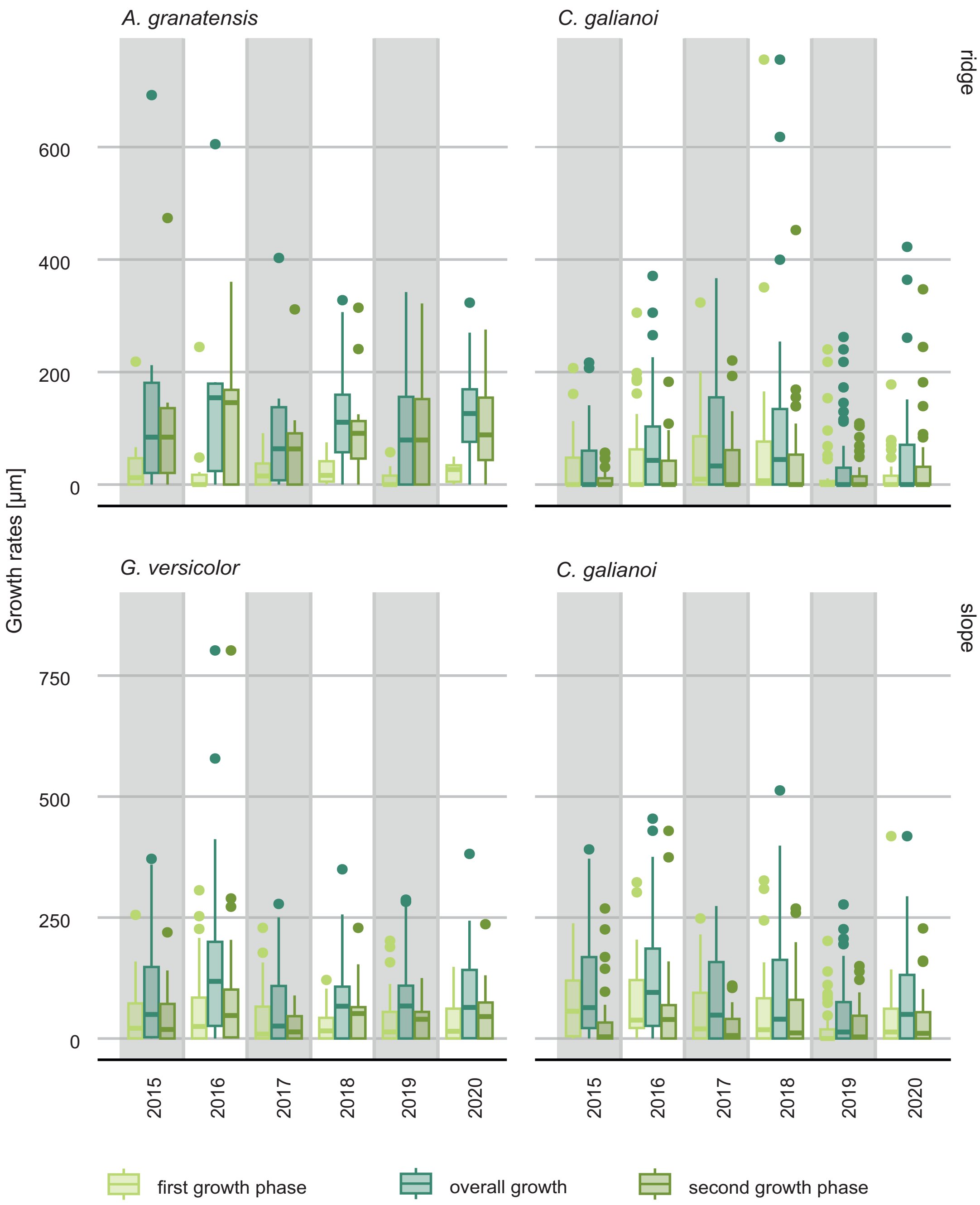


Fig. 15: Boxplot of growth phases showing the distribution of total annual growth (overall growth) as well as growth in the first and second growth phase in *A. granatensis, C. galianoi* and *G. versicolor* at different topographic positions. Alternating grey and white background markers highlight the years.

Similar to the summer, the observed differences in the species' patterns of stem diameter changes during winter were driven by differences of the species' response to winter cold. Here, the moderate variability of stem diameter changes in *C. galianoi* suggests that it tolerates frost with the advantage of benefiting from carbon fixation during winter, allowing it to maximize growth at high water potential in spring (BOSSARD & REJMANEK 1992). In contrast, the winter stem contraction observed in *A. granatensis* indicates that the species avoids winter frost because it is able to induce water efflux by osmoregulation (cf.,

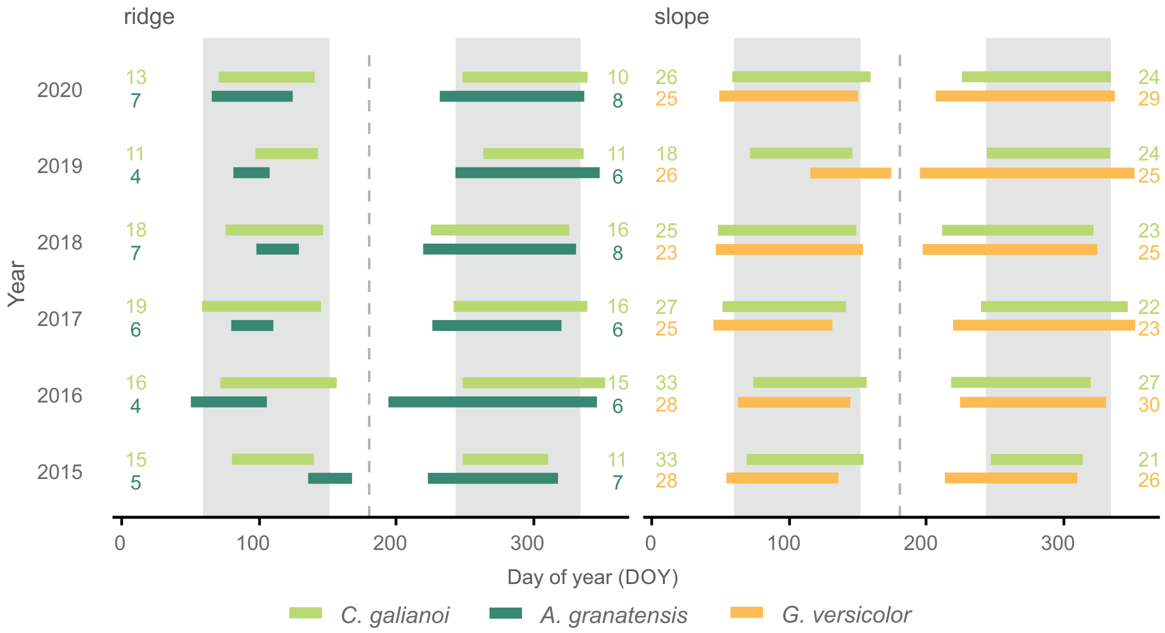


Fig. 16: Average growth onset and cessation in *A. granatensis, C. galianoi,* and *G. versicolor* at different topographic positions for the first and second growth phases in 2015 – 2020, derived from stem diameter curves. Numbers indicate the number of growing specimens. Alternating grey and white background markers highlight the meteorological seasons.

Boughalleb et al. 2016). In this way, it is able to protect its cells from frost damage, making it competitive at the most extreme sites in the area (Albrecht et al. 2023). *G. versicolor* showed the least winter stem contraction, suggesting that it simply does not experience frost at the snow protected alpine slopes, i.e., escapes frost by establishing itself only in a narrow niche that guarantees frost protection by snow (Albrecht et al. 2024b).

Our results highlight that the observed discrepancy between the timing of growth onset in spring and growth resumption in autumn in our three species is most likely related to the differences in the species' strategy for coping with winter cold and summer drought (Albrecht et al. 2023, 2024a, 2024b). As such, these strategies are key to understanding the species' growth patterns. Here, we hypothesize that the combined frost and drought tolerance strategy of *C. galianoi* enables an early growth onset after winter (February/March) and leads to the observed delayed growth resumption after summer drought (Albrecht et al. 2024a, 2024b). The early growth onset in spring is probably due to early water uptake promoted by the species' photosynthetically active green stems (Bossard & Rejmanek 1992), which are characterized by high stomata conductance and high photosynthetic capacity (Meinzer et al. 2017). As such, the species' green stems allow an early increase in turgor pressure and thus an early onset of growth (Albrecht et al. 2024b). Conversely, the delayed growth resumption in autumn is probably due to decelerated rehydration of the stems, which are severely dehydrated after summer. This is presumably due to weak stem stomata regulation (Tardieu & Simonneau 1998), which indicates an anisohydric behaviour of the species (Attia et al. 2015, Albrecht et al. 2024b). In contrast, the combined frost and drought avoidance strategy of *A. granatensis* leads, on the one hand, to the observed late and highly variable onset of spring growth and, on the other hand, explains the immediate resumption of growth after summer drought in autumn (Albrecht et al. 2023). While the late and variable onset of spring growth is likely based on osmotic water uptake after winter dehydration (Albrecht et al. 2023), the immediate growth resumption in autumn is likely based on the species' ability to regulate transpiration-induced water loss and thus to minimize fluctuations in tissue water potential (Franks et al. 2007). This is typical for plants with stomata-controlled isohydric drought avoidance (Attia et al. 2015, Eyland et al. 2022). As such, *A. granatensis* maintains high osmotic water potential throughout summer, eliminating the need for rehydration processes and allowing immediate resumption of growth. Finally, the combined frost escape and drought avoidance strategy of *G. versicolor* allows both early growth onset in spring and early growth resumption in autumn. Here, early spring growth is probably due to the absence of winter stem contraction below snow, eliminating the need for rehydration processes and allowing growth onset as soon as snow melts. The equally early resumption of growth after summer drought is likely due to reduced stomata conductance of the species' greyish-green stems, allowing it to maintain a consistently high water potential throughout summer (Albrecht et al. 2024b), as is typical in plants with rather isohydric behaviour (Attia et al. 2015). This assumed behavior ultimately leads to faster rehydration after summer drought and thus earlier growth resumption (Albrecht et al. 2024b). Overall, our results on the timing of growth confirm that the duration of rehydration processes may depend on the duration and intensity of drought associated with embolism risk (Cochard & Delzon, 2013), as well as on the species' ability to withstand negative water potential before cavitation occurs (Ennajeh et al. 2008).

5 Synthesis and conclusion

The alpine area of the Sierra Nevada is dominated by *Cytisus galianoi*, which is abundant at all sites (cf., topographic positions (A, B, C) in Fig. 1) and shows a wide ecological range along multiple biogeographical gradients. In comparison, the two shrub species *Astragalus granatensis* and *Genista versicolor* show narrower ecological niches. Therefore, in our three articles, we focussed on ridges and slopes where *C. galianoi* co-occurred with one of the other species (Albrecht et al. 2023, 2024a, 2024b). Consequently, snowbeds (C) are not discussed separately here. Our dendrometer measurements revealed species-specific patterns of stem diameter change (Figs. 12, 13), from which we derived growth, defined as irreversible stem increment. Growth differed strongly between species and topographic positions, as represented by the cumulative growth curves (Fig. 14). The timing of growth varied both, between species and sites (Fig. 16), and growth pattern were bimodal, showing two distinct growth phases (Fig. 15). However, growth rates during the different phases did not correspond with the length of the growth phases (Figs. 15, 16).

From our overall findings on growth patterns in each species, we were able to infer 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 (Albrecht et al. 2023, 2024a, 2024b). By applying various statistical approaches, robust and significant driver constellations were uncovered, allowing us to argue for pronounced carry-over effects for both growth phases (Albrecht et al. 2024a, 2024b). Such effects were clearly visible for *C. galianoi*, which, as a green-stemmed, frost-tolerant species, benefitted from cold and snow-free winters by mobilizing assimilates from winter photosynthesis for major spring growth (cf., Bossard & Rejmanek 1992). As a drought tolerating species, *C. galianoi* showed severe summer stem contractions and strong water-related stem diameter increase in autumn, caused by rehydration rather than growth. Using these growth strategies to adapt to winter-cold and summer-drought, *C. galianoi* proved to perform best at all alpine sites and showed high growth plasticity.

Compared to the two co-occurring shrub species, the combined cold- and drought tolerant growth strategies of *C. galianoi* resulted in high competitive advantages. Here, we synthesized the different growth strategies in Table 1 and illustrate the species' most relevant traits that determine the respective underlying physiological mechanisms in Figure 17. Based on our knowledge of the underlying mechanisms, we addressed here a) the overall growth performance of *C. galianoi* across its distributional range in the Sierra Nevada (Albrecht et al. 2024a), b) the advantages and disadvantages of the strategies in the green-stemmed species *C. galianoi* compared to the seasonal dimorphic species *A. granatensis* (Albrecht et al. 2023), and c) the growth differences in two co-existing green-stemmed species *C. galianoi* and *G. versicolor* (Albrecht et al. 2024b).

Focusing on the patterns observed in *C. galianoi* across its distributional range (i.e., at ridges and slopes), our results highlight that growth in this species is maximized during spring, as is usually observed in other Mediterranean woody plants (Pellizzari et al. 2017, Alday et al. 2020, Camarero et al. 2021). Accordingly, radial increment in spring is primarily due to growth. In contrast, both, growth and water-related swelling cause autumn radial increment (Mäkinen et al. 2008, Zweifel 2016). Furthermore, our recently published results based on these patterns underpin the importance of pre-growth environmental conditions with carry-over effects (Albrecht et al. 2024a), helping the plant to decouple growth from carbon uptake (cf., Iwasa & Kubo 1997, Wyka 1999, Meloche & Diggle 2003). As such, for our alpine species, the spatio-temporal environmental drivers of bimodality should be scrutinized and common assumptions on the actuality

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

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

of driver – growth relations should be interpreted with caution (Albrecht et al. 2024a). Moreover, the high year-to-year variability of climatic constraints for growth in *C. galianoi* led to adjusted growth responses that reveal overall high temporal plasticity (Albrecht et al. 2024a). Such high temporal plasticity 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. 2021a, Valeriano et al. 2023). This is of general importance in alpine ecosystems, particularly under future climate change (Löffler et al. 2011). To the latter, *C. galianoi* is probably well adapted, as it takes advantage from warmer winters and tolerates even longer summer droughts (Albrecht et al. 2024a).

Our results on the patterns observed in our two physiologically distinct species *A. granatensis* and *C. galianoi*, shed light on contrasting bimodal growth patterns. 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 & Rejmanek 1992, Wyka & Oleksyn 2014). In contrast, 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 & 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 (Albrecht et al. 2023). The temporal decoupling of growth from photosynthetic opportunities was, to our knowledge, not yet shown in the literature.

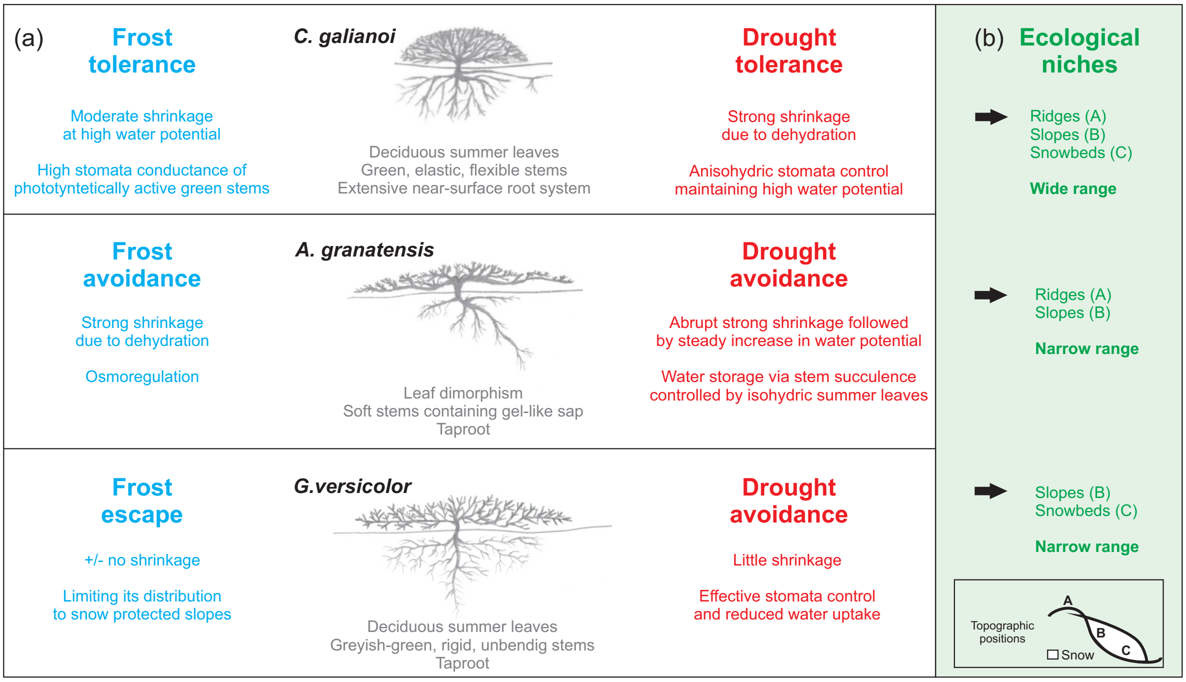


Fig. 17: (a) Growth strategies and mechanisms for coping with frost (blue) and drought (red) including drawings of the species *C. galianoi, A. granatensis* and *G. versicolor* and their most relevant traits (grey) determining the respective growth strategies and mechanisms. (b) Realised ecological niches of our focus species resulting from the respective growth strategies and mechanisms.

Interestingly, the patterns observed in our two coexisting green-stemmed alpine shrub species, *C. galianoi* and *G. versicolor*, also show contrasting bimodal growth patterns despite physiological similarities. In comparison to frost and drought tolerance in *C. galianoi*, patterns of stem contraction in *G. versicolor* suggested a drought avoidance strategy during summer without compromising performance (cf., Chaves et al. 2003, Bacelar et al. 2012) and a frost escape strategy during winter, forcing the species into the snow-protected sites (Albrecht et al. 2024b). As we recently showed (Albrecht et al. 2024b), despite common traits, our species showed contrasting responses to winter soil temperatures. This likely explains 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. 2024b).

Overall, we succeeded in deriving seasonal growth patterns and understanding the species' growth strategies in the Mediterranean-alpine (Albrecht et al. 2023, 2024a, 2024b), contributing to the ongoing scientific debate on future ecosystem responses to global change (Löffler et al. 2011). Our results help to 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.

Acknowledgements

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

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