Contrasting seasonal overlaps between primary and secondary growth are
linked to wood anatomy in Mediterranean sub-shrubs

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Abstract

Whole-plant approaches allow quantifying the temporal overlap between primary and secondary growth. If the amount of time available to grow is short there may be a high temporal overlap between shoot growth and wood formation. We hypothesize that such overlap depends on the duration of the growing season and it relates to wood anatomy. We evaluate wood anatomy, shoot longitudinal and radial growth rates, fine root production and the concentrations of non-structural carbohydrates (NSC) in wood of six sub-shrubs species growing in sites with contrasting climatic conditions (*Lepidium subulatum*, *Linum suffruticosum*, *Salvia lavandulifolia*, *Satureja montana*, *Ononis fruticosa*, *Echinopartum horridum*). Sub-shrub species living in sites with a short growing season displayed a high overlap between aboveground primary and secondary growth and formed wide vessels, whereas species from the warmest and driest sites presented the reverse characteristics. The highest overlap of the former species was linked to a rapid shoot extension and thickening performed through the enhanced hydraulic conductivity provided by wide vessels. The reductions in NSC concentrations when growth peaked were low or moderate which indicates that sub-shrubs accumulate NSC in excess as trees do. The temporal overlap among primary and secondary growth in woody plants may be connected to the duration and rates of shoot and wood growth, which in turn depend on the vessel lumen area.

1 **Introduction**

2 Integrated approaches are required to understand growth processes in woody plants.
3 However, research considering both primary and secondary growth in woody plants,
4 which are usually quantified separately, is extremely scarce (but see Yañez-Espinosa *et*
5 *al.* 2006). In particular, comparative approaches considering above and belowground
6 growth processes in different organs and using complementary may allow determining
7 how wood formation is related to other growth processes within the plant like shoot
8 extension and root production. Similarly, although several studies have analyzed the
9 impact of growth processes on the storage and use of non-structural carbohydrates
10 (NSC) by woody plants (Newell *et al.* 2002; Palacio *et al.* 2007a; Gruber *et al.* 2012),
11 integrative information at the whole-plant level is missing, and it is not know how
12 aboveground primary and secondary growth and root production affect NSC dynamics.

13 Trees pose practical difficulties to address questions at the whole-plant level in
14 mature individuals, often impossible to overcome because of their big size and usually
15 long lifespan. However, chamaephytes –hereafter termed as sub-shrubs– (plants that
16 develop buds at a maximum height of 80 cm in the case of Mediterranean species;
17 Orshan 1982), provide an opportunity to study how secondary growth interacts
18 simultaneously with primary aboveground (e.g., shoot growth) and belowground (e.g.,
19 fine-root dynamics) growth processes, because they are smaller and usually have
20 shallower root systems than trees (Palacio & Montserrat-Martí 2007). Hence, sub-
21 shrubs constitute a valuable model to test how primary and secondary growth interact, if
22 both tend to avoid overlapping with other growth components (e.g., root development)
23 and how growth components of woody plants interact with NSC use and storage. In
24 spite of the aforementioned advantages and despite they constitute the dominant plant
25 growth form in many regions of the world with harsh climatic conditions such as

1 Mediterranean areas under continental conditions (Di Castri 1981), sub-shrubs have
2 been scarcely studied.

3 The amount of time available in the year for sub-shrubs to complete their growth
4 cycle under continental Mediterranean climatic conditions may be very limited, either
5 because of a marked summer drought or due to cold conditions in winter (Montserrat-
6 Marti *et al.* 2011). With these limitations, sub-shrubs have to develop shoots, roots,
7 flowers and fruits but also form their wood. In trees from continental Mediterranean
8 areas, the season of wood formation is shortened by cold and dry conditions (Cherubini
9 *et al.* 2003; Camarero *et al.* 2010). However, sub-shrubs may show a shorter growing
10 season than trees, thus avoiding hydraulic failure and plant collapse (Schenk *et al.*
11 2008). To date, it is not know how sub-shrubs arrange growth processes, including
12 wood formation (xylogenesis), to withstand the restrictive environmental conditions of
13 the inland Mediterranean sites where they dominate the woody flora. Pioneering studies
14 evidenced that Mediterranean sub-shrub species form less wood when water availability
15 decreases (Aljaro *et al.* 1972, Avila *et al.* 1975; Liphshitz & LevYadun 1986).
16 Nevertheless, data on wood-anatomical features (ring distinctiveness, vessel area, and
17 theoretical hydraulic conductance) and seasonal wood formation of Mediterranean sub-
18 shrub species as related to above- and belowground phenology are missing. However,
19 wood-anatomical data such as vessel lumen area, a proxy of hydraulic conductance,
20 may link primary and secondary growth dynamics.

21 In this study, we analyse how wood anatomy and radial growth are linked to
22 shoot growth, fine root production, and NSC concentrations in six sub-shrub species
23 growing in sites with contrasting climatic conditions and hence different duration of the
24 vegetative period. For instance, in the warmest sites the studied species attain maximum
25 photosynthetic biomass values in early spring, whereas in the coldest sites they are

attained in summer (Palacio *et al.* 2006). We expect that species from cold and relatively moister sites such as *Echinopartum horridum* and *Ononis fruticosa* will show the shortest vegetative periods, whereas others from warmer and drier sites (*Satureja montana*, *Lepidium subulatum*, *Linum suffruticosum*, *Salvia lavandulifolia*) will present longer vegetative periods. We aimed to: (i) determine their seasonal dynamics of secondary growth as related to shoot and root growth, and (ii) evaluate the relationship between secondary growth and NSC concentrations. In relation to the first objective, we hypothesized that wood formation and shoot growth will show the highest overlap in the coldest sites because low temperatures will constrain growth in autumn and winter. In addition, secondary growth and root formation will show a low temporal association since fine root production in Mediterranean sub-shrubs peaks in autumn (Palacio & Montserrat-Martí 2007). As related to the second objective, we expected that the high overlap among growth types in species from the coldest sites will also involve a strong but negative association between growth and NSC concentrations.

Materials and methods

Studied species and sites

The studied species were distributed along a climatic gradient in north-eastern Spain (latitude 41° 43'-42° 31' N, longitude 0° 26'-0° 44' W) subjected to continental Mediterranean climate and ranging from cold-wet to warm-dry conditions (Fig.1, Table 1). Sampling was conducted monthly in 2003 and 2004 for a minimum of 13 months per species. Weather conditions were similar between the two years of study. Three studied are seasonally dimorphic (*S. montana*, *L. suffruticosum*, *S. lavandulifolia*), i.e. they normally bear two different types of branches (short and long branches) with different types of leaves that cover the plant during unfavourable (summer to winter)

1 and favourable (spring) periods, respectively (Orshan 1989). Since wood anatomy may
2 change as a function of branch type in Mediterranean seasonal dimorphic species, we
3 restricted our analyses to long branches or dolichoblasts (De Micco & Aronne 2009).
4 The remaining species are the summer deciduous *L. subulatum*, the winter deciduous *O.*
5 *fruticosa* and the evergreen thorny cushion plant *E. horridum*. For further details on
6 studied species and sites see Palacio and Montserrat-Martí (2005, 2006).

7 ***Wood anatomy and growth***

9 On each sampling date, fifteen three-year-old branches were sampled from fifteen
10 individuals randomly selected within one population per species. To check for
11 differences in radial growth among different cohorts of shoots, the diameter of the three
12 cohorts of shoots included in each three-year-old branch was measured for each species
13 and sampling date including the bark (see Supporting Information, Fig. S1).

14 Cross sections of branches were cut (10-20 μm in thickness) near the middle
15 longitudinal shoot position with a sliding microtome (Anglia Scientific AS 200, UK)
16 following Schweingruber and Poschlod (2005). They were stained with 1% aqueous
17 solutions of safranin O, methylene blue or astra blue and embedded permanently in
18 synthetic resin (Eukitt®, Merck, Darmstadt, Germany). Mounted cross-sections were
19 photographed under a light microscope (Olympus BH2) at 100-400 magnification with
20 a digital camera (Leica DFC 290). Photographs of each ring were processed and
21 converted into black-and-white images and processed with Adobe Photoshop CS2
22 (Adobe Systems Inc., San Jose, USA) after excluding the pith and the bark.

23 Vessel area and number were analyzed for each annual ring using the ImageJ
24 software (Rasband 2011) (Supporting Information, Fig. S2). We measured all vessels
25 whose area was within the 0.0001-0.01 mm^2 range. The vessel area (%) was calculated

as the ratio between the sum of the areas of all individual vessels and the measured xylem area. The predicted hydraulic conductance (Kh) was calculated, according to the Hagen-Poiseuille law, as the sum of the fourth power diameters of all the vessels from each species assuming vessels had a circular shape. The relative contribution of each vessel class, according to their area, to the total Kh , was also obtained and expressed as percentage for 1-, 2- and 3-year-old branches. Radial growth was calculated by measuring the ring width in two opposite radii in the latest formed ring of photographed cross-sections from 3-year-old branches.

Primary shoot and root growth

Data of primary shoot and root growth were obtained from published studies on the same species and sites (Palacio & Montserrat-Martí, 2005, 2006, 2007). These were calculated as mean values for each sampling date and for the same studied populations and years.

Chemical analyses

Data of non-structural carbohydrate (NSC) concentrations in stems and roots (SS, soluble sugars; starch and total NSC) were obtained from studies on the same species and sites but they were fully re-analysed as a function of growth data (Palacio *et al.* 2007a; 2007b). Carbohydrate data were expressed as means for each sampling date and for the same studied populations and years. NSC concentrations were measured on the main roots and stems of five individuals per species as described in Palacio *et al.* (2007a, b).

Statistical analyses

To compare the distribution of vessels according to their transversal lumen area among species we used G tests. To quantify growth patterns cumulative shoot length and radial increment were converted into growth rates by subtracting consecutive growth data and dividing them by the elapsed time between sampling dates (mean = 30 days). We evaluated the associations among growth variables (longitudinal and radial growth rates, fine root production), and NSC (SS, starch and NSC separately) concentrations in stems and roots using the non-parametric Spearman correlation coefficient (r_s). Finally, to estimate the temporal overlap between primary and secondary growth we calculated the area below the curves corresponding to monthly longitudinal and radial growth rates. The rates were converted to relative values (0-1) by dividing by the maximum rate of each growth type. Then, we estimated graphically the temporal overlap as the percent non-overlapping and overlapping areas between the areas underneath longitudinal and radial growth-rates curves.

Results

Wood-anatomical features

All studied sub-shrub species formed distinct rings and had semi-ring-porous wood (Fig. 2). *L. subulatum* presented highly packed vessels in radial multiples and ring shake (rings break along the ring boundary) was common in old branches (Fig. 2). In all species most vessels showed areas smaller than 0.0005 mm². The vessels with widest lumens (up to 0.004 mm² in area) were observed in *E. horridum* followed by *O. fruticosa* and the highest frequency of smaller vessels occurred in *S. lavandulifolia* and *L. suffruticosum* (Table 2, Fig. 3). The highest vessel area (3.4%) was recorded in *E. horridum* and *O. fruticosa*, whereas the minimum (1.1%) value corresponded to *L. subulatum*. The vessels distributions according to their lumen area differed significantly

among species ($P < 0.001$ in all cases) for the three analysed ages (1-year old vessels, $G = 116$; 2-year old vessels, $G = 527$; 3-year old vessels, $G = 608$).

Considering the predicted hydraulic conductance (Kh), vessels whose lumen showed an area smaller than 0.001 mm^2 accounted for all of the Kh in *L. suffruticosum* while, on the other extreme, wide-lumen vessels with areas from 0.001 up to 0.005 mm^2 accounted for most (89% in 3-year old shoots) of the Kh in *E. horridum* (Fig. 3). In *S. montana* and *O. fruticosa* vessels with lumen of intermediate area (0.001 - 0.002 mm^2) also accounted for ca. 40% of the Kh .

Wood formation and radial growth

Studied species started their radial growth between March and April (Fig. 4). The maximum increase in vessel area was observed in the early phases of cambial growth in spring (April-May), i.e. when the widest vessels were formed, and at that time vessel area varied between 2% (*S. lavandulifolia*, *S. montana*, *L. suffruticosum*, *L. subulatum*) and 5% (*O. fruticosa*, *E. horridum*). All species presented the maximum radial-growth rates from May (*L. subulatum*, *L. suffruticosum*, *S. lavandulifolia*, *E. horridum*) to June (*S. montana*, *O. fruticosa*) while most of the ring (at least 80%) was formed before summer drought started in July (Fig. 4). Mean radial-growth rates ranged from 0.003 - $0.004 \text{ mm day}^{-1}$ (*L. subulatum*, *L. suffruticosum*) up to ca. $0.005 \text{ mm day}^{-1}$ (*S. montana*, *S. lavandulifolia*, *O. fruticosa*, *E. horridum*). In some of the studied species there were differences in the timing of maximum radial-growth rates when comparing shoots of different ages. For instance, in the case of *S. lavandulifolia*, *O. fruticosa* and *E. horridum* the youngest shoots showed the highest radial increment one month later than the oldest ones (Supporting Information, Fig. S1).

Relationships between growth types and NSC concentrations

The period comprising the most active shoot extension occurred from April to May in *L. subulatum* and *L. suffruticosum*, and from May to June and July in *E. horridum* and *O. fruticosa*, respectively (Fig. 4). This period of active primary growth extended up to August in *S. montana* and *S. lavandulifolia*. In autumn and winter fine roots grew actively in all species, and spring was also an important period of belowground growth in *L. suffruticosum*, *S. montana* and *S. lavandulifolia*. Only *S. montana* presented root growth in summer, probably because the site where this species was studied was located near a riverbed.

Secondary and primary above-ground growth clearly overlapped in all studied species (Fig. 4). The rates of both growth types were positively associated in all species except in *L. suffruticosum*, which presented a very rapid shoot extension (Table 3). The temporal overlap between primary and secondary growth was maximum (98.5%) in *E. horridum* (the species growing in the coldest site) and minimum (38.5%) in *L. suffruticosum* (the species growing in the warmest site; Fig. 5). The other species from cold sites (*O. fruticosa*) also presented a very high overlap between both growth types (92.9%), being followed by *S. lavandulifolia* (71.5%), whereas the remaining species showed intermediate overlap values (*L. subulatum*, 61.2%; *S. montana*, 50.2%). In *L. suffruticosum* and *L. subulatum* secondary-growth rates and root production were negatively related (Table 3).

Stem NSC reached maximum concentrations in late summer and autumn (e.g., *L. suffruticosum*, *S. montana*, *O. fruticosa*), winter (*S. lavandulifolia*, *E. horridum*) or late spring (*L. subulatum*) (Fig. 6). The SS and NSC concentrations in the stems, and also the SS concentrations in roots, were inversely related to radial-growth rates in all species but *L. suffruticosum* and *L. subulatum* (Table 3). Primary shoot and root growth

were not significantly related to SS, starch and NSC concentrations in any of the six studied species ($P>0.10$ in all cases, *results not presented*), except in the case of *S. montana* which presented a negative correlation between shoot longitudinal growth rates and SS concentrations in the stems ($r_s=-0.57$, $P=0.05$).

Discussion

We found that Mediterranean sub-shrubs displayed different temporal overlaps between primary and secondary growth. Such diverse overlapping patterns seem to be linked to the different durations of the growing season in the diverse environmental conditions where sub-shrubs grow, which has implications for their contrasting wood anatomical properties and growth rates. The highest overlap between growth types occurred in species growing in sites characterized by a short vegetative period.

Wood anatomy and secondary growth

All studied Mediterranean sub-shrub species presented semi-ring-porous wood and distinct annual rings but formed vessels with varied lumen size and showed contrasting seasonal patterns of radial growth. Species from the warmest and driest sites (e.g., *L. suffruticosum*, *L. subulatum*) formed narrow vessels along an extended xylogenesis period while species from the coldest and moistest sites (e.g., *O. fruticosa*, *E. horridum*) formed wide vessels over a short period of secondary growth. The wide vessels of Fabaceae species in the high-elevation sites may also be a response to increasing water availability (Table 1) which strongly affects xylem structure in Mediterranean sub-shrubs, usually leading to wide earlywood vessels (De Micco *et al.*, 2008). However, drought stress is absent in those cold sites, and the highest vessel area values were observed there in either deciduous (*O. fruticosa*) or evergreen (*E. horridum*) species

1 suggesting that xylem properties seem to be tuned to the length of the growing season.
2 This suggests that the length of the growing season for the studied species is more
3 constrained by low temperatures than by drought period usually occurring in summer.

4 Overall, in the studied species most secondary growth occurred from early to
5 late spring, i.e. a pattern that matches that described for seasonally dimorphic species by
6 Liphshitz and LevYadun (1986). All species performed most wood formation almost
7 one month before summer drought started. However, some local deviations from this
8 pattern were also observed. For instance, primary and secondary growth were recorded
9 in autumn in *S. montana*, which was sampled near a riverbed where soil water
10 availability is high and may allow growing even during the dry summer (Palacio *et al.*
11 2006). In this species and also in *S. lavandulifolia* and *E. horridum*, radial growth
12 peaked before in the oldest than in the youngest shoots, which may be due to either
13 hydraulic or growth constraints. For example, the rapid extension of current-year shoots
14 of *E. horridum* (Palacio & Montserrat-Marti 2006) may require an increased amount of
15 water and thus enhanced hydraulic conductivity supplied by the firstly-formed wide
16 vessels (Palacio *et al.* 2008). Indeed, young shoots in species with fast shoot extension
17 are fully elongated before starting their lignification, whereas in species with a more
18 extended period of shoot growth lignification and extension partly overlap. Hence, there
19 seems to be a more pronounced delay in the secondary growth of young shoots as
20 compared with old ones in species with high overlap between primary and secondary
21 growth such as *S. lavandulifolia*, *O. fruticosa* and particularly *E. horridum*.

22 Phylogenetic constraints on xylem characteristics and phenology must also be
23 taken into account, since the two species with the largest vessel lumens and highest
24 relative vessel areas belong to the Fabaceae family, whereas the two Lamiaceae species
25 formed the smallest vessels. It is also remarkable that Brassicaceae woody species

living under cold conditions and supporting a short growing season usually form distinct rings as we observed in *L. subulatum* (Schweingruber 2006). This author also noted a trend towards ring-porosity by forming wide vessels and enhancing hydraulic transport under arid conditions in the latter family.

Temporal overlap among growth types and changes in NSC concentrations

We found that secondary growth overlapped with primary above-ground growth in all studied sub-shrubs species. As expected, the major periods of shoot extension and thickening overlapped more in sub-shrubs from the coldest site (e.g., *E. horridum*) than in those from warm ones (e.g., *L. suffruticosum*). *E. horridum* showed a short period of wood growth which allowed developing shoots quickly (Palacio & Montserrat-Martí 2007). This species and *O. fruticosa* present the widest vessels and they are characterized by a rapid shoot during short growing seasons in cold sites. Our findings indicate that the wide vessels of these species allow them to increase the hydraulic conductivity, performing an efficient rapid growth with a high overlap between primary and secondary growth. According to our results, such overlap seems to be linked to a fast consumption of the available carbohydrates for growth, leading to a sharper reduction in the NSC concentrations during shoot growth (Table 3).

In the opposite extreme, primary and secondary growth in warm but dry sites showed a relatively lower temporal overlap either because of the protracted period of shoot thickening as compared to shoot extension (*L. suffruticosum*) or because the primary growth extended from spring to autumn in humid conditions (*S. montana*). For instance, *L. suffruticosum* forms vessels with narrow lumens, it presents small leaves and shows a low overlap among growth types which may explain why radial-growth rates were not related to changes in NSC concentrations in this species. It must be also

1 indicated that species with high growth rates (e.g., *E. horridum*) also presented high
2 branching intensity, so that the overall growth rate per individual plant was also high.

3 In the warmest and driest sites, primary and secondary growth overlapped less in
4 the summer deciduous *L. subulatum* than in *L. suffruticosum*. This may be related to the
5 relatively longer shoot extension period of *L. subulatum* owing to the need to rebuild its
6 whole canopy after summer drought (Palacio *et al.* 2006). Nevertheless in these species,
7 wood formation and root growth clearly occurred in the two favourable seasons of the
8 year, namely spring and autumn. This suggests that *L. suffruticosum* and *L. subulatum*
9 finish most of their xylem development before summer drought, arrest most growth
10 processes during summer (but bud formation, see Palacio & Montserrat-Martí 2005),
11 and resume growth in autumn, probably by diverting carbohydrates for active root
12 growth to uptake the water and nutrients available in the soil (Palacio & Montserrat-
13 Martí, 2007).

14 Although we observed a negative relationship between stem NSC concentrations
15 and secondary growth in plants with increasingly shorter vegetative periods and the
16 highest overlaps between primary and shoot growth, the observed seasonal change in
17 NSC concentrations was only moderate. This may indicate that sub-shrubs accumulate
18 NSC in excess, similarly to trees (Millard *et al.* 2007). Possible explanations for
19 immobilizing NSC in the stems may be to use them as a safeguard against potential
20 disturbances or to maintain hydraulic integrity (Sala *et al.* 2012). The lack of strong
21 associations between primary shoot growth rates and SS, starch and NSC concentrations
22 may be caused by the fact that recently formed shoots and leaves are carbon sinks only
23 during their initial development, becoming net C sources afterwards (Keel & Schädel
24 2010).

To conclude, Mediterranean sub-shrubs displayed different degree of temporal overlap between primary and secondary growth processes, which seems to be linked to their wood anatomical properties and their growth rates. The highest overlap between growth types occurred in species from cold and relatively moister sites characterized by a short vegetative period (*E. horridum* and *O. fruticosa*). These plants showed rapid shoot extension and radial growth rates and formed vessels with relatively wide lumen. In fact, the temporal overlap among primary and secondary growth seems to be positively associated to the mean vessel diameter in the youngest stems ($r = 0.75$, $P = 0.09$). This association was marginally significant and based only in six species, but it opens up interesting questions as to how xylem anatomy is linked to the temporal arrangement of the different growth processes of woody species. Owing to our results, this syndrome was also related to a more negative relationship between stem NSC concentrations and secondary growth in species with a higher overlap between primary and secondary growth processes, which may indicate a more intense consumption of stem carbohydrates for wood growth in these species.

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Figure captions

Figure 1. Views of three study sites dominated by (a) cushion *E. horridum* individuals, (b) tagged *S. montana* plant, and (c) *L. suffruticosum* and *L. subulatum* populations. The climatic diagrams were built using data from nearby meteorological stations (see Table 1) and correspond to cold (upper graph), mild (middle graph) and warm (lower graph) climatic conditions.

Figure 2. Cross-sections of 1-, 2- and 3-year old branches of the six studied species (shown from left to right). Triangles indicate spring growth in the case of the selected 1- and 2-year-old *S. montana* and *E. horridum* branches, respectively. Scale bars correspond to 250 μm .

Figure 3. Distribution of vessels in 1-, 2- and 3-year-old branches (bars of different colours) according to their area and their relative contribution to the total predicted hydraulic conductance (Kh) in the six sub-shrub species studied. Numbers located below species names indicate total numbers of samples and vessels measured. A scheme showing the general morphology of the branches of each species is also displayed.

Figure 4. Monthly radial (circles) and longitudinal (triangles) growth rates as compared to fine root growth (bars, percentage scales) of the six studied sub-shrubs. The lower black lines indicate the periods of active primary shoot growth. Data are means $\pm$ SE ($n = 15$).

Figure 5. Periods of overlapping (green area) and non-overlapping (yellow areas) primary and secondary growth types. The periods were calculated by graphically estimating the areas below the curves corresponding to the indexed longitudinal and radial-growth rates (range 0-1) of sub-shrub species.

Figure 6. Radial growth rates (circles) and seasonal dynamics of non-structural carbohydrate concentrations (soluble sugars - white portion- and starch - grey portion of bars) in the main stems of the six studied sub-shrubs. Data are means $\pm$ SE ($n = 15$).

Tables

Table 1. Characteristics of the studied sub-shrub species and sites. Height values are means $\pm$ SE.

Species (Family)	Study site	Sampling period (sampling frequency in days)	Elevation (m)	Mean annual temperature ¹ (°C)	Total annual precipitation (mm)	Soil	Life form	Height (cm)
<i>Linum suffruticosum</i> L. (Linaceae)	Villamayor	Oct 2002 – Jan 2004 (29)	320	14.6	335	gypsum	Seasonally dimorphic	40 $\pm$ 90
<i>Lepidium subulatum</i> L. (Brassicaceae)	Villamayor	Oct 2002 – Jan 2004 (29)	320	14.6	335	Gypsum	Summer deciduous	30 $\pm$ 70
<i>Salvia lavandulifolia</i> L. (Lamiaceae)	Villamayor	Sep 2002 – Nov 2003 (30)	420	14.0	453	limestone, gypsum	Seasonally dimorphic	30 $\pm$ 50
<i>Satureja montana</i> L. (Lamiaceae)	Lasieso	Jan 2004 – Jan 2005 (31)	670	12.1	654	calcareous alluviums	Seasonally dimorphic	20 $\pm$ 40
<i>Ononis fruticosa</i> L. (Fabaceae)	Bernués	Dec 2003 – Dec 2004 (30)	1030	10.9	735	marl	Winter deciduous	60 $\pm$ 100
<i>Echinospartum horridum</i> (Vahl.) Rothm. (Fabaceae)	S. Juan de la Peña	Oct 2002 – Nov 2003 (32)	1380	8.0	1247	limestone	Evergreen cushion	50 $\pm$ 80

¹ Climatic data were obtained from the following meteorological stations (site): Zaragoza-Aeropuerto (41° 40' N, 1° 00' W, 247 m) and Perdiguera (41° 45' N, 0° 38' W, 452 m) (Villamayor); Apies (42° 14' N, 0° 24' W, 680 m) (Lasieso), Arguis (42° 19' N, 0° 26' W, 1039 m) (Bernués), and Santa Cruz de la Serós (42° 31' N, 0° 41' W, 820 m) (San Juan de la Peña).

Table 2. Morphological and wood-anatomical characteristics of the sub-shrubs studied. Mean ($\pm$ SD) values ($n = 15$).

Species	Shoot length (cm)			Shoot diameter (mm)			Vessel area (%)			Vessel area (mm ² 10 ⁻³)		
	Age (years)			Age (years)			Age (years)			Age (years)		
	1	2	3	1	2	3	1	2	3	1	2	3
<i>Linum suffruticosum</i>	5.2 $\pm$ 2.4	4.8 $\pm$ 1.8	4.3 $\pm$ 1.7	1.0 $\pm$ 0.2	1.5 $\pm$ 0.5	2.2 $\pm$ 0.5	1.9 $\pm$ 1.2	2.0 $\pm$ 0.8	2.1 $\pm$ 1.0	0.19 $\pm$ 0.09	0.20 $\pm$ 0.11	0.21 $\pm$ 0.11
<i>Lepidium subulatum</i>	5.3 $\pm$ 2.3	4.5 $\pm$ 1.8	4.8 $\pm$ 2.0	0.7 $\pm$ 0.1	1.1 $\pm$ 0.3	1.5 $\pm$ 0.4	1.1 $\pm$ 0.6	1.2 $\pm$ 0.7	1.2 $\pm$ 0.2	0.21 $\pm$ 0.16	0.24 $\pm$ 0.18	0.25 $\pm$ 0.32
<i>Salvia lavandulifolia</i>	3.3 $\pm$ 1.0	2.6 $\pm$ 1.1	2.7 $\pm$ 1.1	1.2 $\pm$ 0.3	1.5 $\pm$ 0.3	1.8 $\pm$ 0.4	1.5 $\pm$ 1.3	1.6 $\pm$ 0.8	1.8 $\pm$ 1.0	0.16 $\pm$ 0.06	0.17 $\pm$ 0.07	0.19 $\pm$ 0.09
<i>Satureja montana</i>	6.0 $\pm$ 2.6	4.1 $\pm$ 1.4	3.0 $\pm$ 1.1	0.7 $\pm$ 0.2	1.0 $\pm$ 0.2	1.5 $\pm$ 0.4	1.1 $\pm$ 0.4	1.5 $\pm$ 0.7	1.8 $\pm$ 1.2	0.18 $\pm$ 0.08	0.26 $\pm$ 0.16	0.27 $\pm$ 0.17
<i>Ononis fruticosa</i>	5.0 $\pm$ 1.3	5.1 $\pm$ 1.4	4.4 $\pm$ 1.5	1.0 $\pm$ 0.2	1.3 $\pm$ 0.2	1.6 $\pm$ 0.3	3.1 $\pm$ 0.9	3.5 $\pm$ 1.1	3.7 $\pm$ 1.3	0.25 $\pm$ 0.12	0.26 $\pm$ 0.17	0.30 $\pm$ 0.20
<i>Echinopartum horridum</i>	3.7 $\pm$ 1.1	2.4 $\pm$ 0.9	3.0 $\pm$ 1.2	1.1 $\pm$ 0.2	1.3 $\pm$ 0.2	1.4 $\pm$ 0.2	2.6 $\pm$ 1.0	2.9 $\pm$ 1.0	3.0 $\pm$ 0.6	0.33 $\pm$ 0.23	0.50 $\pm$ 0.24	0.53 $\pm$ 0.30

Table 3. Main relationships (Spearman correlation coefficient) between the radial-growth rates of studied species and the primary growth (shoot longitudinal growth rate), fine root growth and non-structural carbohydrates (SS, soluble sugars; starch and total NSC) concentrations of their main stems and roots ($n = 13$). Only correlations with $P \leq 0.05$ are shown.

Species	Shoot growth	Fine root growth	SS		Starch		NSC	
			Root	Stem	Root	Stem	Root	Stem
<i>L. suffruticosum</i>		-0.50 (0.05)						
<i>L. subulatum</i>	0.56 (0.03)	-0.52 (0.04)	-0.49 (0.05)		0.55 (0.03)			
<i>S. lavandulifolia</i>	0.78 (0.004)		-0.48 (0.05)	-0.49 (0.05)				-0.51 (0.05)
<i>S. montana</i>	0.72 (0.005)		-0.68 (0.03)	-0.65 (0.04)	-0.58 (0.05)		-0.72 (0.006)	-0.57 (0.05)
<i>O. fruticosa</i>	0.64 (0.03)	no data	-0.79 (0.001)	-0.72 (0.005)				-0.65 (0.03)
<i>E. horridum</i>	0.60 (0.05)		-0.63 (0.04)	-0.79 (0.003)				-0.64 (0.04)