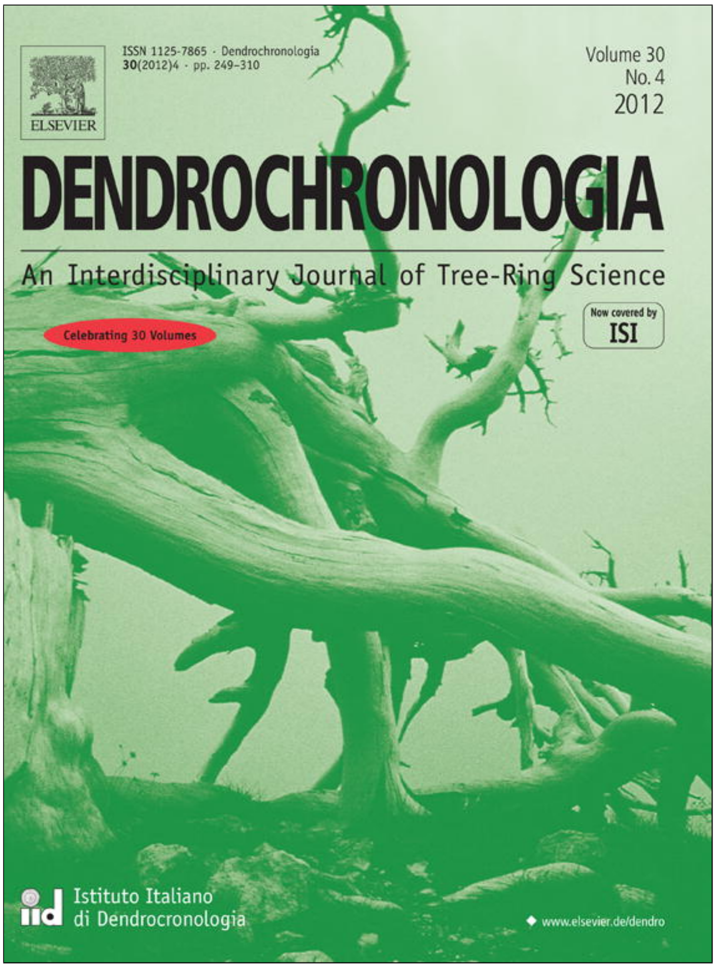

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Original article

Arboreal and prostrate conifers coexisting in Mediterranean high mountains differ in their climatic responses

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ABSTRACT

In contrast to most high elevation areas, plant growth at Mediterranean mountains is exposed to a summer drought period, which represents an additional climatic constraint to low temperatures. Although arboreal and shrubby conifers coexist at high altitudes, most dendroecological studies have focused on climatic responses of tree species, whereas those of shrubby species remain mostly unexplored. We built tree-ring width chronologies for two conifer species, a shrub (*Juniperus sabina*) and a tree (*Pinus sylvestris*), coexisting at three high-altitude localities of the Iberian System mountains, eastern Spain. We analyzed their climate–growth relationships for the period 1950–2009 using correlation analyses and multiple regressions. Coexisting species responded to year-to-year climatic variability in different ways. Radial growth in junipers and pines responded positively to April and May temperatures, respectively. Summer drought constrained growth in both cases, although its impact was stronger on junipers than on pines. Our findings suggest that junipers respond earlier than pines to spring temperatures due to their prostrate morphology which may enhance a fast warming of their cambial meristems after snowmelt. The higher dependence of *J. sabina* on summer rainfall as compared with co-occurring pines confirms that drought stress negatively impacts secondary growth in Mediterranean mountains. This sensitivity to water availability may be caused by the juniper shallow root systems, which mainly use superficial soil water. The climatic signal registered in *J. sabina* allows studying the response of other similar shrubby woody species growing in Mediterranean alpine areas to the ongoing climate warming, which could also reduce water availability.

Introduction

In mountains and cold continental areas, cambial resumption in spring is strongly influenced by air temperature (Rossi et al., 2006; Gričar and Čufar, 2008; Camarero et al., 2010). However, other factors such as snowmelt and related soil thawing may contribute to the onset of xylogenesis (Kirdyanov et al., 2003; Lupi et al., 2010); in fact, these factors may be modulated by topographical features like slope or exposure, modulating different growth patterns (Kirchhefer, 2000; Leonelli et al., 2009). Cambial activity during the growing period is also positively related to summer temperatures (Büntgen et al., 2010), thus leading to a strong link between secondary growth and temperature in high-elevation forests (Tardif et al., 2003; Frank and Esper, 2005). In contrast to most mountainous environments, plant growth at Mediterranean high mountains is exposed to a summer drought period (Nahal, 1981; Giménez-Benavides et al., 2005, 2010). Thus, growing season length in Mediterranean mountains is controlled by both temperature and precipitation, since dry periods can result in an earlier conclusion of xylogenesis (De Luis et al., 2007; Eilmann et al., 2011). This pattern is reflected in the secondary growth of conifers from continental Mediterranean climates, which show two major growing periods corresponding to spring and autumn, when cold and drought limitations of cambial activity are reduced (Camarero et al., 2010). Overall, conifers at Mediterranean mountains might show shorter growing seasons than mid-elevation mesic areas as a result of both low spring temperatures and summer droughts.

Shrub species can inhabit higher altitudes than trees, growing above the alpine tree line, i.e., above the uppermost location of trees at least 2-m high (Walter, 1973; Körner, 1998; Holtmeier, 2009). Despite that dendrochronology with shrubs is promising in ecological research (e.g., Liang and Eckstein, 2009; Blok et al., 2011), little is known about shrub climate–growth relationships in comparison

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to trees in this altitudinal limit (Tardif et al., 2003; Körner and Paulsen, 2004; Rossi et al., 2006, 2008). The few studies comparing shrub and tree species close to the tree line in alpine environments suggest that both life forms are similarly affected by temperature (Bär et al., 2007a). However, to the best of our knowledge, no scientific work has tested this assumption at Mediterranean high mountains, where climatic constraints are more complex than in temperate areas. Comparing climatic responses of shrubs and trees could contribute to understand if climatic factors constraining secondary growth might differ between coexisting woody life forms in these harsh environments. Moreover, this comparison would have an additional value considering the absence of reliable long-term climatic series from Mediterranean high mountains and the need of good proxies to evaluate climatic change in such areas.

Global warming is expected to result in warmer and drier climatic conditions in the western Mediterranean Basin (van Oldenborgh et al., 2009). Climatic change scenarios predict higher than average warming at most high-mountain areas (Meehl et al., 2007), where, additionally, complex interactions between altitude and topography determine abrupt climatic parameter changes over short horizontal distances (Beniston and Rebetez, 1996; Beniston, 2006). Noticeably, projected higher frequency and severity of extreme drought events would have more prominent impacts on vegetation than those caused by mean climate variations (Giorgi and Lionello, 2008; Jalili et al., 2010). Thus, high-mountain areas, where plant endemisms are abundant, are considered particularly threatened ecosystems in the frame of the ongoing climatic change (Theurillat and Guisan, 2001; Schröter et al., 2005). A possible consequence of global warming is the change in species' distribution areas; there is abundant scientific evidence suggesting recent altitudinal and latitudinal rising of shrub and tree species in response to warmer conditions (Sanz-Elorza et al., 2003; Hallinger et al., 2010; but see Büntgen and Schweingruber, 2010). Nevertheless, it remains unclear whether global warming is the main driver of this process or if other drivers such as changes in land use might be also involved in the rise of vegetation belts (Améztegui et al., 2010).

In Mediterranean high mountains, pine and shrubby juniper species coexist at the uppermost tree line (Adams, 2004). Juniper species usually show lower hydraulic conductivity and shallower root systems than pines (Willson et al., 2008). Furthermore, junipers also have more plastic cambial activity and longer summer cambial dormancy, which could result in different responses to water deficiencies than pines (Camarero et al., 2010). In this paper, we propose a comparative study of the dendroclimatic response of two conifer species with contrasting growth forms, a tree (Scots pine, *Pinus sylvestris* L.) and a large prostrate shrub (Savin juniper, *Juniperus sabina* L.), both inhabiting areas near the alpine tree line at three Mediterranean high-mountain sites. We hypothesize that radial growth is affected by both spring temperature and summer precipitation during the year of tree-ring formation for both species. We also expect a differential response to climate, with the juniper being less sensitive to air temperatures than the pine, since shrubs would be better coupled with soil microclimatic conditions than arboreal species due to their low stature. Furthermore, differences in climate–growth relationships between coexisting juniper and pine species might be also caused by contrasting xylogenetic patterns, i.e., different cambial dynamic phenologies (Camarero et al., 2010). Thus, our objectives were: (a) to assess the dendrochronological potential of Savin juniper, (b) to identify the main factors constraining the radial growth of Scots pine and Savin juniper inhabiting high elevations at Mediterranean mountains, and (c) to test whether climatic responses differ between both life forms.

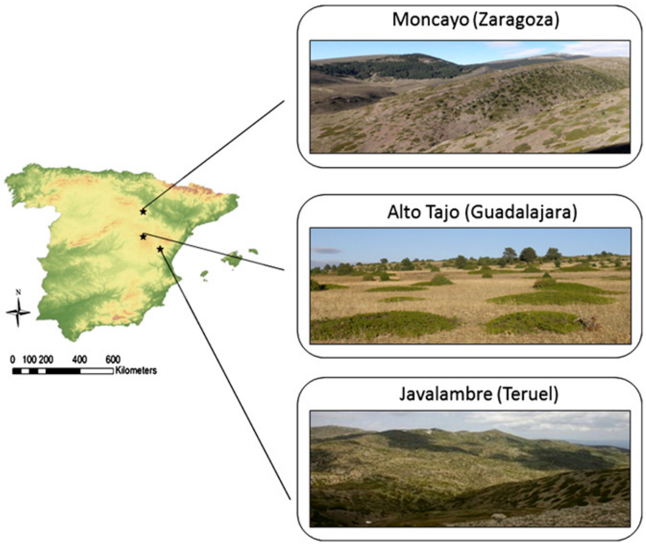

Fig. 1. Location and images of the three study sites.

Materials and methods

Field sampling

J. sabina is a prostrate juniper species that is widely distributed along central and southern Europe, northern Africa, and western Asia at an altitudinal range ranking from 1400 to 2750 m a.s.l. (Adams, 2004; López González, 2004). This shrub may form prostrate canopies with an area around 1900 m^2 (personal observation) and although it can grow on siliceous soils, it is more abundant on calcareous substrates, being able to develop on particularly stony soils. *P. sylvestris* is a sub-boreal tree pine species up to 35 m tall with the widest distribution of all conifers. It grows in Europe and Asia, reaching its southwestern limit in the Iberian Peninsula (Amaral Franco, 1986). It is a dominant species in low-elevation forests at cold areas and high-elevation mountain forests in the circum-Mediterranean, where it may grow above 2100 m a.s.l. (López González, 2004).

Field sampling was conducted at three different sites located in the Iberian System, which extends between the Spanish central plateau and the Ebro Valley in eastern and northeastern Spain along more than 500 km. *P. sylvestris* and *J. sabina* coexisted at the uppermost tree line in the three selected sites, which are located in the oro-Mediterranean bioclimatic belt (Rivas Martínez, 1987): Moncayo (Zaragoza, MO hereafter), Alto Tajo (Guadalajara, AT hereafter), and Javalambre (Teruel, JA hereafter), following an elevation and continental gradient (Fig. 1; Table 1). Climatic conditions at the three study sites were described by using interpolated data obtained from the Digital Climatic Atlas of the Iberian Peninsula which is described below (Ninyerola et al., 2005). At the lowest site MO, Savin junipers coexist with *Juniperus communis* subsp. *alpina* and Scots pines are situated 6 km away. At site AT Savin junipers are located on flat areas where they favor the establishment and development of Scots pines, which form forests in surrounding areas. Finally, at the highest locality (JA), Scots pines are located at their altitudinal limit, and extensive areas are covered by Savin junipers above the tree line.

Dendrochronological methods

At each site, 20–30 individuals per species were sampled. Pines were bored at breast height using a Pressler increment borer,

Table 1
Geographical, topographical and climatic features of the three study sites. Site codes: MO, Moncayo; AT, Alto Tajo; JA, Javalambre. Summer seasonal variables were calculated considering June, July and August.

Site	Latitude	Longitude	Altitude (m a.s.l.)	Annual mean temperature (mean minimum–maximum) (°C)	Summer mean temperature (°C)	Annual (summer) precipitation (mm)
MO	41°43′N	1°46′W	1420	8.6 (2.5–14.7)	17.5	571 (112)
AT	40°34′N	1°49′W	1600	8.3 (1.7–14.9)	17.4	568 (112)
JA	40°06′N	1°01′W	1930	7.6 (1.3–14.0)	17.1	520 (109)

obtaining two perpendicular cores per individual. Complete basal and central branch sections of Savin junipers were also collected. Afterwards, pine cores were mounted into wood strips. Both pine cores and Savin juniper cross-sections were sanded using sandpapers of progressively finer grain to obtain clearly visible rings for stereomicroscopic analysis. Samples were visually cross-dated and ring widths were measured to 10-μm precision using a Velmex measuring device (2011 Velmex, Inc., USA). Visual cross-dating was statistically checked using the COFECHA program (Holmes, 1983), which determines the degree of synchrony between series based on correlation with the mean site series.

Ring-width series were doubly detrended using lineal or exponential negative fits followed by a 32-year-long polynomial spline in order to eliminate long- and medium-frequency signals and to retain high-frequency variability at annual scales. Then, they were standardized and their temporal autocorrelation was modeled and removed to obtain annual growth indexes. Finally, mean site chronologies of growth residual indexes were obtained for each species, and these residual chronologies were then used for subsequent analyses. All these processes were done with ARSTAN program (Cook and Holmes, 1996).

Several descriptive statistics were calculated to compare chronologies among localities and species for the common interval 1950–2009 (Cook and Kairiukstis, 1990; Fritts, 1976). Mean tree-ring width (MW), standard deviation (SD) and first-order autocorrelation (AC) were calculated for the raw tree-ring widths. Residual chronologies were used to calculate: mean sensitivity (ms_x), which is a measure of the relative variability in width of consecutive tree rings; mean series correlation between trees (r_{bt}); expressed population signal (EPS), a measure of the statistical quality of the mean chronology compared with a perfect infinitely replicated chronology; percentage of variance explained by the first principal component (PC1), which estimates the common growth variability among all trees at each site; and signal-to-noise ratio (SNR), a measure of the strength of the common high-frequency signal in the ring-width indexes of trees from the same site.

Climatic data

Given the absence of meteorological stations, we used the Digital Climatic Atlas of the Iberian Peninsula (Ninyerola et al., 2005) to describe the climatic conditions prevailing at each study site. These climatic data were interpolated with a spatial resolution of 200 m using regressions between climatic data obtained from local meteorological stations and geographical variables (Ninyerola et al., 2007; detailed description at http://opengis.uab.es/wms/iberia/en_index.htm). Although these are the most precise available climatic data at the study sites, they only provide an average for the period used in the calculations (1950–1999), but not for individual years. Thus, in order to establish climate–growth relationships at the regional scale we used annual and monthly records from the TS 3.0 data set produced by the Climate Research Unit (CRU) (Mitchell and Jones, 2005). Data consisted of 0.5° resolution gridded monthly mean temperature (T) and total precipitation (P) from 1950 to 2006 and were downloaded by means of Climate Explorer of the Royal Netherlands Meteorological Institute (http://climexp.knmi.nl). The CRU database is formed by interpolated values from data of local meteorological stations. It must be remarked that most meteorological stations are located at low altitudes in Spain, with high-elevation stations lacking. The effect of altitude on climatic variables can be interpolated with more reliability in terms of temperature than precipitation. Temperature shows a well-established altitudinal gradient and has similar temporal and spatial variability at broad spatial scales. But precipitation presents high spatial heterogeneity at high-elevation environments, particularly during summer months (Barry, 2008).

Statistical analyses

Common variance among the six residual chronologies was quantified by means of a principal component analysis (PCA), an ordination technique used to extract series of orthogonal components expressing the variance contained in a data set (Legendre and Legendre, 1998). A scatter plot of weighting coefficients for the first two principal components (PCs) graphically displayed the inter-relationship. PCA was performed with the vegan package (Oksanen et al., 2011) in R environment (R Development Core Team, 2010). Pearson correlation coefficients between pairs of chronologies were calculated.

To determine the main climatic drivers of secondary growth of both considered species, we performed correlations between annual growth indexes of residual chronologies and monthly climatic data (mean temperature and total precipitation). Since radial growth may partially depend on climatic conditions of the previous year (Fritts, 1976), we calculated Pearson correlation coefficients and multiple forward stepwise regressions by considering climatic records from August of the year before tree-ring formation up to October of the growth year. Moreover, we performed a climatic analysis over two separate periods (1950–1978 and 1979–2006) in order to assess how stationary were the influences of climatic variables on growth. For each of these two periods, we calculated correlations between individual growth indexes and significant climatic variables based on multiple regression results. Mean correlations of both periods were compared by means of a t-test for paired samples. These analyses were performed using PASW Statistics v. 18 (SPSS Inc., Chicago, 2009).

Results

Dendrochronological features

Ring-width chronologies were successfully built for each species and study site providing reliably replicated series for the period 1950–2009 (Table 2; Fig. 2). Mean ± SE ring widths of all sites indicated that radial growth in Scots pines (1.96 ± 0.92 mm) was nearly seven times higher than in coexisting Savin junipers (0.28 ± 0.15 mm). Radial growth of both species largely differed among sites with the highest values of tree-ring width of Scots pines being observed at site MO (2.29 mm) and the highest values of Savin junipers being found at site AT (0.32 mm).

Table 2
Summary of dendrochronological statistics calculated for the common period 1950–2009: mean ring width (MW) and its standard deviation (SD); first-order autocorrelation (AC); mean sensitivity (ms_x); mean inter-tree correlation (r_{bt}); expressed population signal (EPS); variance explained by the first principal component (PC1); signal-to-noise ratio (SNR); percentage of variance of radial-growth indexes explained by climatic variables after multiple regression (R^2_{adj} climate). Site codes: MO, Moncayo; AT, Alto Tajo; JA, Javalambre. Species codes: JS, *Juniperus sabina*; PS, *Pinus sylvestris*.

Species	Site	Period	MW (mm)	SD (mm)	No. of trees/radii	AC	ms_x	r_{bt}	EPS	PC1 (%)	SNR	R^2_{adj} climate (%)
JS	MO	1863–2010	0.28	0.14	18/32	0.61	0.23	0.27	0.87	34.27	6.65	44.0
JS	AT	1896–2009	0.32	0.17	14/25	0.66	0.24	0.36	0.89	40.28	7.74	28.5
JS	JA	1887–2010	0.26	0.15	14/23	0.64	0.19	0.31	0.86	36.11	6.42	25.7
PS	MO	1934–2010	2.29	1.05	12/19	0.72	0.21	0.59	0.95	62.58	17.60	35.6
PS	AT	1918–2009	2.19	1.01	17/25	0.75	0.15	0.28	0.87	31.49	6.51	32.3
PS	JA	1766–2010	1.41	0.70	15/25	0.70	0.21	0.51	0.95	53.76	15.33	15.6

Mean sensitivity (ms_x) was similar between species (0.22 in junipers vs. 0.19 in pines). Accordingly, growth variance explained by climatic variability was rather similar between species (33% in junipers vs. 28% in pines; see Table 2). However, the statistics related to common growth signal and mean correlation among individuals within each site (r_{bt}, EPS, PC1, SNR) were usually higher for pines than for junipers.

We found a higher coherency among chronologies of the same species, despite the geographical distance among them, in comparison with juniper and pine chronologies located at the same site. Mean intraspecific correlation values were higher within (Savin junipers, $r = 0.46$; Scots pines, $r = 0.36$) than among co-occurring species ($r = 0.31$) (Table 3). This result was confirmed by the PCA with juniper and pine chronologies appearing in two distinct groups in the ordination diagram (Fig. 3). Nevertheless, interspecific comparisons within each site were significant in all localities except in site AT, where correlations were marginally significant ($P = 0.071$), thus suggesting some degree of site-related shared climatic signal.

Climate–growth relationships

Current spring temperatures had a positive effect on radial growth. This effect was more important in April in the case of junipers (AT, JA, and marginally in MO), and in April (site MO) or May (sites AT and JA) in the case of pines (Fig. 4). Radial growth of junipers was also enhanced by summer rainfall, being significant in June (MO), July (AT), and August (JA), whereas pines only showed a

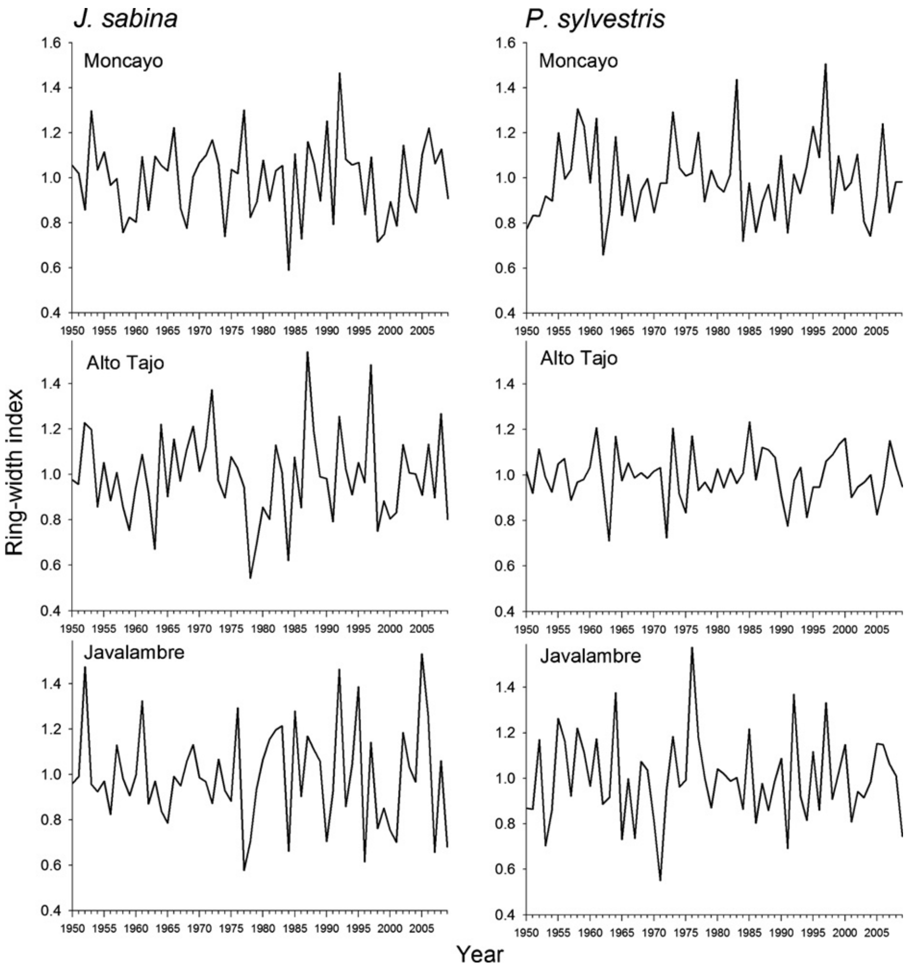

Fig. 2. Residual chronologies of *Juniperus sabina* and *Pinus sylvestris* built for the period 1950–2009 at the three study sites.

Table 3
Pearson correlations and their corresponding *P*-values in brackets calculated among *Juniperus sabina* (JS) and *Pinus sylvestris* (PS) chronologies. Significant ($P < 0.05$) correlations are shown in bold. See Table 2 for site and species codes.

Species	Site	JS			PS	
		MO	AT	JA	MO	AT
JS	AT	**0.569 (<0.001)**				
	JA	**0.334 (0.009)**	**0.470 (<0.001)**			
PS	MO	**0.304 (0.018)**	**0.278 (0.032)**	0.211 (0.106)		
	AT	−0.017 (0.895)	0.234 (0.071)	0.126 (0.339)	0.139 (0.290)	
	JA	0.249 (0.055)	**0.262 (0.043)**	**0.384 (0.002)**	**0.517 (<0.001)**	**0.413 (0.001)**

positive effect of summer rain at MO. Growth of both species was negatively related to previous September temperatures at most sites except for junipers at site JA, and to previous August temperatures in the case of pines from site AT. Finally, a negative effect of winter rainfall was detected both in pines (February) and junipers (March) at sites MO and AT.

At site MO all the significant climatic parameters showed changes on their intensity over the two split periods of analysis, most of them (4) increasing its responsiveness to climatic parameters (Fig. 4). At site AT only 5 out of 9 significant variables changed, 3 of which increased and 2 decreased, whereas at site JA only 1 out of 6 increased. The intensity of correlations with summer rainfall increased for both juniper and pine in the second period (1979–2006) respect to the first one (1950–1978). However, the rest of variables significantly related to growth (spring temperature, previous September temperature and winter rainfall) did not show remarkable temporal changes.

Discussion

Our results confirm that in Mediterranean high mountains, secondary growth suffers a double climatic constraint that shifts from temperature in spring to water availability in summer for both species independently of their life forms. To our knowledge, this is one of the first studies documenting a negative impact of drought stress on secondary growth in Mediterranean alpine and subalpine environments. However, there were notable differences between the climatic responses of the shrubby *J. sabina* and the coexisting tree *P. sylvestris*. Junipers showed an earlier response to spring temperatures than pines, suggesting an earlier onset of cambial activity. Moreover, although both species showed similar strength in their climatic responses, the common growth signal was higher in pines than in junipers, which can be partially attributed to the different situations of the species in relation to their geographical and altitudinal distribution areas. It is known that when climatic conditions become limiting, similarities between individual chronologies are enhanced till a certain threshold (Tardif et al., 2003). Consequently, Scots pines, which were located near their southern and higher distribution limits, may show higher coherence among growth series of different individuals, more tightly reflecting regional climatic conditions than Savin junipers, which were growing closer to their optimal range.

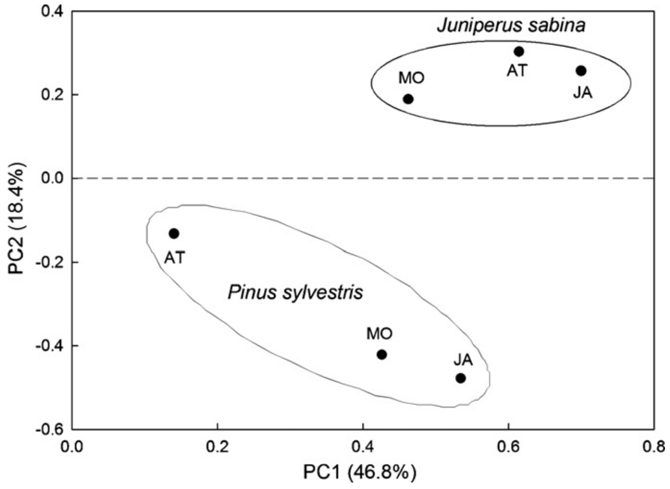

Fig. 3. Position of the different chronologies along the first two axes of the principal component analysis. The percentage of variance explained by each component is indicated in brackets. AT, Alto Tajo; MO, Moncayo; JA, Javalambre; PC1, variance explained by the first principal component; PC2, variance explained by the second principal component.

Spring temperatures positively affected radial growth of both species, but this effect occurred one month earlier in junipers than in pines (April vs. May), except at the lowest locality (MO). In arboreal conifers growing in cold climates, minimum spring temperatures are the critical factor limiting production and differentiation of xylem cells as well as growing season length (Rossi et al., 2008; Moser et al., 2010). Despite no literature available on juniper xylogenesis, it is known that radial growth in a congener tree species (*Juniperus thurifera*) is also highly dependent on spring temperature and occurs before coexisting Scots pines (Camarero et al., 2010). Thus, the earlier response of Savin junipers compared to Scots pines refutes our hypothesis that the juniper prostrate morphology would result in a more pronounced thermal inertia related to soil microclimate. Following this hypothesis, juniper would have shown a delayed onset of cambial reactivation due to lower spring temperatures of soil. Contrarily, the observed climate–growth relationship matches the climatic hypothesis of tree line formation (Körner, 1998), stating that trees exert a strong negative influence on their own soil temperature compared to low-stature vegetation due to the shadow that they project, which induces a substantial decrease in root-zone temperature. This finding is in agreement with experimental works showing a direct effect of increasing tree stem temperature on cambial activity initiation in evergreen conifers (Oribe and Kubo, 1997; Oribe et al., 2003). Thus, and against our initial expectations, low stature and reduced shading effect of high-mountain shrubs would improve their thermal conditions, allowing them to show relatively early cambial resumption in spring and possibly a prolonged growing season extending into early autumn. Further xylogenesis studies monitoring cambial activity might test this hypothesis.

According to our expectations, secondary growth in Mediterranean high mountains was constrained by water availability during summer, as it has also been observed in juniper species in semi-arid areas (Sass-Klaassen et al., 2008; Camarero et al., 2010). Surprisingly, this effect was stronger in junipers than in pines, suggesting high growth responsiveness to precipitation in high-mountain Savin juniper. This may reflect the ability of the shallow juniper root systems to rapidly respond to superficial water deriving from sporadic storms, whereas deep pine roots are likely

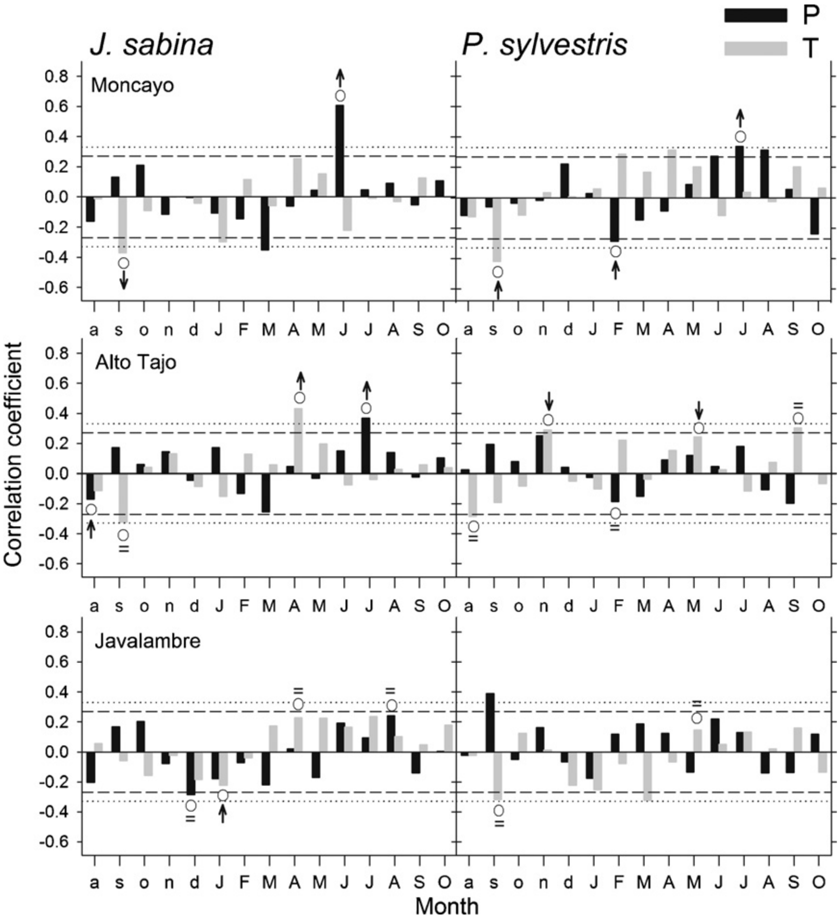

Fig. 4. Correlations between radial growth (ring width indexes) and climatic variables (*P*, total precipitation; *T*, mean temperature) for both species at the three study sites. Dashed and dotted lines indicate $P < 0.05$ and $P < 0.01$, respectively. Significant ($P < 0.05$) coefficients of multiple regression analysis are indicated with circles. Upward (downward) arrows indicate increased (decreased) absolute correlations for the period of 1979–2006 as compared with the period of 1950–1978. Equal signs indicate no significant differences on correlations between both periods at $\alpha = 0.05$. Lowercase and uppercase letters correspond to months of the previous and current years, respectively.

more dependent on deeper water layers accumulated previously to spring growth (Willson et al., 2008). This pattern is in accordance with the highly plastic phenological patterns of cambial dynamics observed in other juniper species, which adjust their xylogenesis to the length of the favorable growing season and may present pronounced cambial dormancy in summer (Camarero et al., 2010). In fact, a negative relationship between altitude and the onset of summer drought stress on juniper growth was also clearly shown, with the first significant month shifting from June in the lowest locality (MO) to August in the highest one (JA), suggesting that plastic xylogenesis may be an inherent feature of junipers. In contrast, secondary Scots pines growth may be maintained during summer due to their high hydraulic conductivity and deep roots, helping them to reach higher growth rates than junipers (Camarero et al., 2010), although probably at the expense of higher post-drought mortality rates (Allen and Breshears, 1998; Mueller et al., 2005). Along the studied period, both species became more responsive to summer rainfall, particularly in sites at lower altitudes (MO, AT). Non-stationary climatic signals have already been described for other juniper and pine species in Spain (Tardif et al., 2003; DeSoto et al., 2012), and may be related to increasing evapotranspiration trends derived from warmer temperatures (Appendix A). In any case, further research is ongoing to determine the causes of this pattern.

An additional effect of climatic conditions during the year before cambial initiation was found in both woody species: previous September temperatures (August for pines at AT) negatively affected their radial growth. This finding is consistent with results obtained for Iberian pine species (Richter et al., 1991; Tardif et al., 2003; Andreu et al., 2007). It probably results in both species experiencing either a long growing season or being subjected to an extended summer drought, consequently limiting accumulation of carbohydrates to be invested in earlywood formation the following year (Kagawa et al., 2006). On the contrary, late-winter precipitation in March showed a negative effect, particularly in junipers at the less continental locality (MO). This is probably related to prolonged snow cover and low temperatures, which have been shown to affect other alpine shrub species (Bär et al., 2007b). Additionally, late-winter precipitation may have two complementary impacts: (a) the mentioned cooling effect and related increases in cloud cover, which would delay the onset of cambial growth and reduce carbohydrate acquisition for earlywood development (Oribe and Kubo, 1997; Gimeno, 2010) and (b) an increase in late-winter snow depth which could affect photoperiod-related triggering of cambial onset in shrubby Savin junipers, as observed in other low-stature alpine plants (Keller and Körner, 2003).

Differing climatic responses would imply differing responses of coexisting shrubs and trees to climatic change. Warmer and drier conditions are projected for the circum-Mediterranean mountains (Giorgi and Lionello, 2008; Nogués Bravo et al., 2008). Under a scenario of increasing temperatures and climatic stability, an upward rise in tree lines and encroachment of high-elevation forests are

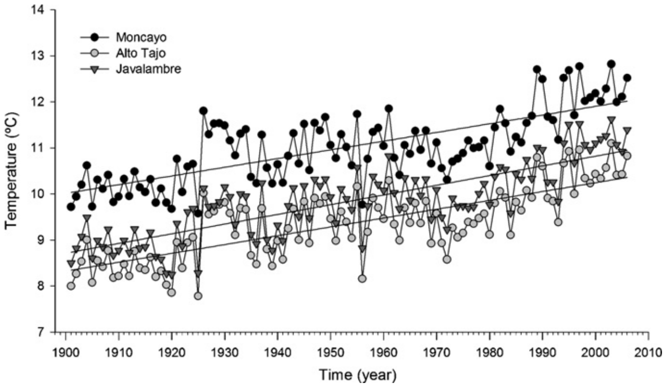

Fig. A1.

expected (Camarero and Gutiérrez, 2004; Harsch et al., 2009; Hallinger et al., 2010). Rising temperatures without a parallel rainfall increase would result in longer summer drought periods in Mediterranean mountains, since evapotranspiration rates would also raise, thereby increasing physiological water stress. In such cases, pines would be more negatively affected than slow-growing junipers since the latter can stop growing in the midst of summer, whereas the former probably cannot (Camarero et al., 2010). However, it is necessary to consider that microtopographic variations at mountain areas could have much more influence on thermal changes than regional, broad-scale climatic variations (Löffler et al., 2006; Scherrer and Körner, 2010).

Conclusions

To the best of our knowledge, this is the first study that has found that juniper species inhabiting Mediterranean high-elevation environments possess a strong climatic signal related to precipitation and water availability during the growing season. Hence, the radial growth of similar woody species living in Mediterranean mountains may be negatively impacted by drought stress. This novel finding differs from the response of other shrubby junipers inhabiting Eurasian cold areas which mostly showed responses to temperature (Esper et al., 2007; Hallinger et al., 2010; Hantemirov et al., 2011). Our results show that the prostrate shrub *J. sabina* is a good potential candidate for conducting dendroclimatic reconstructions of water availability in Mediterranean alpine areas. We consider this an important outcome of the present work since this species is one of the longest living plants that form annual rings at high altitudes (1400–2750 m) in circum-Mediterranean mountains. Moreover, differential climatic response compared to pine trees reinforces the value of *J. sabina* growth as a proxy for past climatic reconstructions in high elevation areas above the tree line. *J. sabina* growth can also be used as a source of future climatic and ecological forecasts for these elevated areas, which have high biodiversity values (e.g., high numbers of endemisms and relict populations), and where climatic series are scarce or absent.

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Appendix A.

Trends in mean annual temperatures for the 20th century at the three studied sites based on 0.5°-gridded data (Mitchell and Jones, 2005).

Fig. A1

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