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RESEARCH ARTICLE

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Changes in climate-growth relationships and IADF formation over time of pine species (*Pinus halepensis, P. pinaster* and *P. sylvestris*) in Mediterranean environments

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Abstract

Background: The Mediterranean basin has experienced an increase in the mean annual temperature, a decrease in the mean annual precipitation, and an increase in the frequency of severe drought periods during the second half of the 20th century. However, winter and spring precipitation has increased and summer precipitation has decreased in the western Mediterranean region.

Aim of the study: The objectives of the present study were: i) to compare changes in climate-growth relationships over time for *Pinus halepensis*, *P. pinaster* and *P. sylvestris* in Spain ii) to quantify the presence of intra-annual density fluctuations (IADFs) on the three species, and iii) to define the associated climatic variables.

Area of study: 26 sampling sites (8 *P. halepensis* sites, 8 *P. pinaster* sites and 10 *P. sylvestris* sites) were selected in their distribution area in Spain.

Main results: Precipitation is the main factor influencing growth and IADF occurrence in the three species. Wet periods during previous winter and spring induced higher growth rates on *P. halepensis* and *P. pinaster*, while *P. sylvestris* was mostly influenced by summer precipitation. However, the influence of these climatic variables on the growth of these species changed over the studied period. The increase of winter and spring precipitation combined with increasingly harsh summer climatic conditions in the second half of the 20th century may have enhanced the importance of precipitation at the beginning of the growing season on the growth of species subject to higher summer drought stress (*P. halepensis* and *P. pinaster)* and increased IADF occurrence.

Research highlights: Besides reflecting changes in the environmental conditions during the growing season, the inclusion of IADF detection in chronologies adds new information to ring-width chronologies, thereby improving its quality.

Key words: Aleppo pine; maritime pine; scots pine; dendroclimatology, IADFs.

Abbreviations used: IADF: Intra-annual density fluctuation; AIC: Akaike information criterion; ROC: Receiver operating characteristic.

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Introduction

Mediterranean environments, as transitional climate zones between arid and humid regions of the world, are of special interest for the study of the relationships between climate, tree growth and wood anatomical features. In addition, the Mediterranean is one of the areas where climatic changes may have the greatest effects (Lavorel *et al*., 1998). Mediterranean forests are the most important ecological infrastructure of the region, providing goods and services and acting as a key for resilience and adaptability. *Pinus halepensis, P. pinaster* and *P. sylvestris* are native pines in the Mediterranean region and dominate the current forested landscape. Previous studies on *P. halepensis* concluded that its growth rate is mainly controlled by soil water availability (Rathgeber et al., 2005). Radial growth of *P. pinaster* is positively correlated with precipitation in Portugal (Vieira *et al*., 2010; Campelo *et al.* 2013) and central Spain (Bogino & Bravo, 2008). This fact was also reported for *P. sylvestris* in its southern and western distribution limit in Spain (Bogino *et al*., 2009).

Climatic influences on tree growth are unstable, species specific and site dependent (Tardif *et al.,* 2003). Climate change is resulting in both positive and negative trends in tree growth, the latter frequently observed in drought-stressed environments (Camarero *et al*., 2010). The influence of climatic variables on growth can be modified over time (Andreu et al., 2007) and previous studies showed a changing association between climatic variables and growth of *Pinus* species in the Mediterranean area (Bogino & Bravo, 2008; Vieira *et al*., 2010; Campelo *et al*., 2013). During the second half of the 20th century, an overall increase of the mean annual temperature, a decrease of the annual precipitation and a higher frequency of severe drought periods have been observed in the Mediterranean area (Martrat *et al,*. 2004; Xoplaki *et al*., 2006). However, in the western Mediterranean basin, winter and spring precipitation increased and summer precipitation decreased during that period (Bradley *et al*., 1987; Maheras, 1988; Díaz *et al.,* 1989).

The analysis of temporal and seasonal dynamics of intra-annual cell formation and wood density profiles is a relevant topic in the recent literature (Edmondson, 2010; Bender *et al*., 2012; Harley *et al*., 2012). Species growing under Mediterranean climate, with summer droughts and high inter-annual variability in precipitation and temperature, commonly show special anatomical characteristics in tree rings (Schweingruber, 1993). Intra-annual density fluctuations (IADFs) are defined as a layer of cells within a tree ring identified by different shape, size and wall thickness (Kaennel & Schweingruber, 1995). Previous studies in *P. halepensis* (e.g. Moreno-Gutiérrez *et al*., 2012; Olivar *et al*., 2012; Novak *et al*., 2013), *P. pinaster* (e.g. Rozas *et al*., 2011; Campelo *et al.,* 2013) and *P. sylvestris* (Panayotov *et al*., 2013), have shown good correlations between IADF formation and climate around the Mediterranean. The consistency of the climatic signal among different pine species and areas suggests that a large-scale network of IADFs could be developed in the Mediterranean region to study intra-annual climate variability (Campelo *et al*., 2013). A more detailed analysis of climatic events may detect effects on inter-annual density fluctuations as determined by a logistic model that includes the stabilized IADF frequency assessed in relation to calendar year.

In order to understand the responses of Mediterranean pine species to climate change and which anatomical structures can be used to document it, the present work investigates: i) radial growth-climate relationships over time for *P. halepensis, P. pinaster* and *P. sylvestris* in Spain, ii) the presence of intra-annual density fluctuations (IADFs) on the three species and, iii) the climatic variables that are associated with the occurrence of IADFs.

Materials and Methods

Study area

Twenty-six sampling sites (8 *P. halepensis* sites, 8 *P. pinaster* sites and 10 *P. sylvestris* sites) were selected in their distribution area in Spain (Figure 1; Table 1). *Pinus halepensis* sampling sites consist of an upper storey of *P. halepensis* and an understorey formed by broadleaved Mediterranean species (*Quercus ilex* L., *Q. coccifera* L. and *Q. faginea* Lamk.). Silviculture in the sampling area of *P. pinaster* is traditionally based on natural regeneration following a seed tree system and focused on multifunctional uses (recreation, timber and resin). *Pinus sylvestris* sampling sites are at its southern and western distribution threshold. These dry areas of distribution of this species that usually grows in humid environments are the logical places to investigate the effects of increased aridity (Martínez Vilalta & Piñol, 2002). Besides, in assessing the impact of global warming on ecosystems, any changes in tree growth are likely to occur first in those tree stands placed at the ecological boundary of the species (Tess-

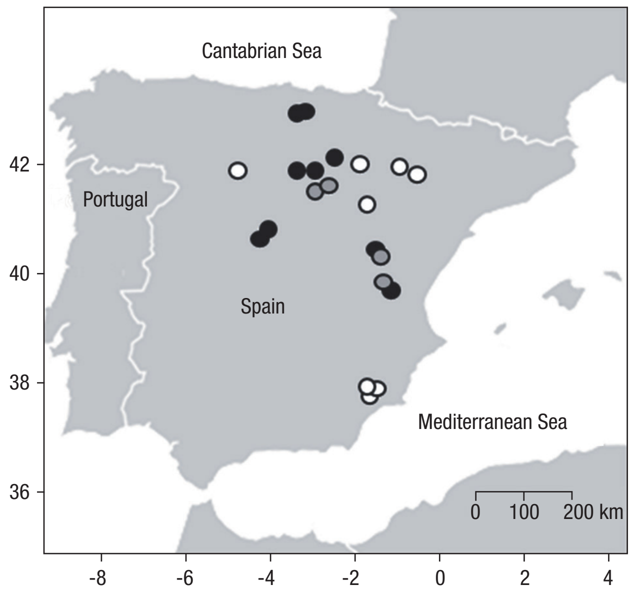

Figure 1. Study areas of the three pine species in the Iberian Peninsula. White: *Pinus halepensis*; grey: *P. pinaster*; black: *P. sylvestris*.

Table 1. Sampling sites description of *Pinus halepensis, P. pinaster* and *P. sylvestris* in Spain. Alt = Altitude; Temp. = Annual temperature; Precip. = Mean monthly precipitation. Correlation coefficients ($p < 0.05$) between radial growth of *Pinus halepensis, P. pinaster* and *P. sylvestris* and seasonal climate (mean temperature and precipitation). White: 0-0.24; light grey: 0.25-0.49; dark grey: 0.5-0.74; black: 0.75-0.99.

Species	Site code	Alt. (m)	Time span	Temp. (ºC)	Precip. (mm)	Growth-Temp. Correlation				Growth-Precip. Correlation			
						Win.	Spr.	Sum.	Aut.	Win.	Spr.	Sum.	Aut.
P. halep	H30101	811	1932-2008	12.7	617						+		+
	H30102	957	1915-2008	12.7	617		–				+		
	H30103	1118	1914-2008	12.7	617					+	+		
	H34001	849	1975-2008	12.1	441	+		–		+	+		–
	H50009	976	1978-2008	12.3	344					+	+	+	
	H50001	695	1975-2008	13.1	395								
	H50101	535	1919-2007	12.4	616			–					
	H50102	706	1926-2007	12.4	587								
P. pin	P16106	970	1880-2005	8.3	901				–	+	+		
	P16108	920	1948-2005	8.3	901				–	+	+		
	P16201	1078	1948-2005	8.3	901	+			–	+	+		
	P16202	1010	1978-2005	8.3	901			–			+	+	
	P16208	1090	1887-2005	8.3	901	+							
	P42002	1059	1918-2005	8.3	487							+	
	P42201	1012	1948-2005	10.2	484			+					
	P44002	1437	1846-2005	10.4	563					+	+	+	
	P44005	1364	1849-2005	10.4	563					+	+		
	P44204	1232	1953-2005	10.4	563					+	+		
P. sylv	S05006	1438	1813-2005	7.5	559							+	
	S09005	888	1867-2005	9.2	632								
	S09209	1097	1848-2005	10.2	487	+	+					+	–
	S09501	814	1935-2005	10.3	527	+				–		+	
	S40006	1440	1891-2005	9.7	466			–					
	S42415	1165	1951-2005	10.2	487							+	
	S42504	1431	1960-2005	10.2	487		+					+	
	S42505	1659	1946-2005	10.2	487							+	

ier *et al*., 1997). At each sampling site, 15 dominant trees were randomly selected. Two cores were extracted at 1.30 m above ground from each selected tree. The increment cores were air dried, mounted on wooden supports and dated according to standard dendrochronological techniques (Stokes & Smiley, 1968).

Climate analysis

Absolute dating is essential for any dendroclimatological study, and it is impossible to compare climatic variables in one specific year with tree-ring growth if the individual tree-ring series are not dated correctly (Fritts, 2001). To assess measurement and dating accuracy, the v6.06P COFECHA program (Holmes, 2001; Grissino-Mayer, 2001; available at www.ltrr.arizona.edu) was applied. This program calculates the Pearson correlation indices between the indexed tree-ring series and a master reference chronology in a series of consecutive, partially overlapped segments of a length specified by the user. According to standard dendrochronological methods, tree-ring series exhibiting correlation values with the master chronology below 0.4 were excluded.

Standardization removes geometrical and ecological trends while preserving inter-annual high-frequency variations that are presumably related to climate. To eliminate biological trends in tree-ring series and to minimize growth variations that are not shared by most trees, the v6.05P ARSTAN program (Cook & Holmes, 1984; Holmes, 2001; available at www.ltrr.arizona.edu) was used. The long-term trend was removed from each time series of ring width measurements by fitting and calculating an index defined as actual ring-width for each year divided by the curve-fit value. The standardized series were averaged in order to obtain a master chronology at each study site.

IADF determination

The accurately dated cores were visually examined for IADF using a stereomicroscope (magnification up to 25x). In contrast to the annual rings, IADFs show a non-sharp transition boundary between earlywood and latewood cells (Fritts, 2001). IADFs were only counted when present in both cores in the same tree ring, and they were identified by considering the position of the density fluctuation within the ring. Only IADF type E (latewood-like cells within the earlywood) were considered for our study since IADF type L (earlywood-like cells within the latewood) were rarely present in our sample (Figure 2). As the number of samples changed over time, the relative frequency was calculated with the following formula [1]:

$$F = n/N \quad [1]$$

where F is the relative frequency of IADF in a particular year; n the number of trees that formed the IADF and N the total number of trees analyzed. The bias in the frequency was assessed by calculating the stabilized IADF frequency (f), according to the formula of Osborn et al. (1997) [2]:

$$f = F^{0.5} \quad [2]$$

The nonlinear logistic equation form was chosen to model the probability of occurrence of IADFs [3]:

$$P = (1.0 + e^{(-z)})^{-1} \quad [3]$$

where P is the probability of IADFs and $Z = b0 + b1(x1) + b2(x2) + \ldots\ldots + bk(xk) + \varepsilon$; where x1; x2..... xk are the climatic variables and b0; b1; b2 ….. bk are unknown parameters of the model and ε is a normal random error N (0,1); and *e* is the exponential operator. The logistic equation can be formulated to accept a binary variable such as occurrence of IADFs, and the parameters can be estimated by maximum-likelihood methods. The resulting prediction is bounded by 0 and 1. Monthly rainfall and mean monthly temperature were used as explanatory variables. The hydrological year was defined as a period of 12 months, from October of the previous year to September of the current growth year. A stepwise selection method was used to find the best model.

The alternative fits were evaluated on the basis of Akaike information criterion (AIC), the –2*Log Likelihood, the area under the receiver operating characteristic (ROC) curve, and the expected behavior as indicated by the signs of the estimated parameters. The ROC curve is displayed for the models and the area underneath was calculated as a value of the accuracy of the model. Values greater than 0.80 indicate an excellent fit (Hosmer & Lemeshow, 2000). This curve relies on false/true positive/negative tests, and the sensitivity is indicated by the proportion of correctly classified events and the specificity by the proportion of correctly classified non-events (Hair *et al.* 1998). Logistic regression was previously successfully used to estimate the probability of occurrence of IADFs in *P. pinaster* subsp. *mesogenesis* and *P. halepensis* in the Iberian Peninsula (Bogino and Bravo, 2009; Olivar et al., 2012). PROC LOGISTIC of SAS 9.1 (SAS Institute Inc. 2004) was used to fit the model.

We grouped the climatic variables (monthly precipitation and mean monthly temperature) recorded at the closest meteorological stations (Agencia Estatal de Meteorología, Spain) in climatic seasons: winter (December, January and February), spring (March, April and May), summer (June, July and August) and fall (September, October and November). The climatic data were regressed against ring-width indices and the stabilized IADF frequency. In order to calculate Pearson correlation coefficients and response functions we used DENDROCLIM 2002 (Biondi & Waikul, 2004). Moving correlation function was used to test stationarity and consistency through time with a 20-year interval.

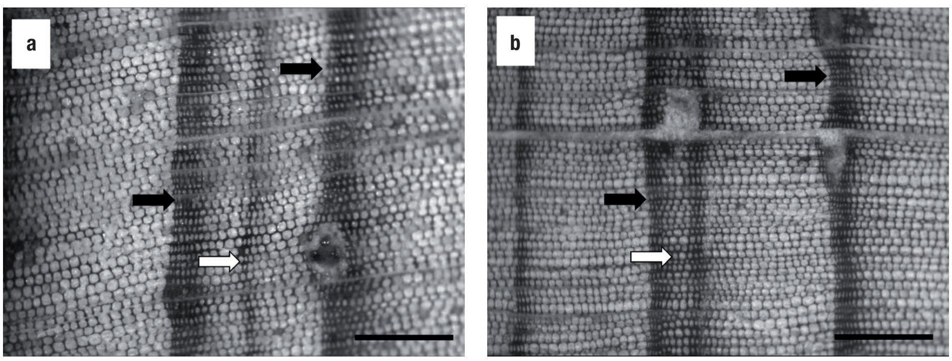

Figure 2. Intra-annual density fluctuations (IADF) in *Pinus pinaster (*Bogino & Bravo, 2009*)*. IADF type E (a): Latewood-like tracheids within the earlywood. IADF type L (b): Earlywood-like tracheids within the latewood. Annual tree rings grew from right to left. Black arrows indicate the true tree-ring boundary and white arrows the IADFs. *Scale bars* 1 mm.

Results

Precipitation is the main factor influencing tree growth of the three Mediterranean tree species. Bootstrap correlation significant values ($p < 0.05$) between radial growth of *P. halepensis, P. pinaster* and *P. sylvestris* and seasonal climate are shown in Table 1. Despite site variability, there was a correspondence between the higher correlation values and seasonal climate indicating that wet periods during winter previous to the growth season and spring induced high growth rates on *P. halepensis* and *P. pinaster*, while the growth of *P. sylvestris* was mostly influenced by summer precipitation. *Pinus pinaster* showed the highest correlations ($p < 0.005$) between precipitation and growth ($r = 0.12$ in average)

The analysis of the influence of the climatic variables over time on *P. halepensis* shows that this positive influence of winter, spring and summer precipitation on its growth began increasing in the 1980s. During that period, spring temperature shifted its influence from negative to positive, while summer temperature shifted from positive to negative (Figure 3a). In the case of *P. pinaster*, the greatest increase in the influence of the climatic variables on growth occurred during the 1970s, when spring precipitation became the dominant influence followed by summer and winter precipitation. Also during that period, winter temperature increased its positive influence, while the influence of spring, summer and autumn temperature became negative (Figure 3b). Summer precipitation had the highest correlation values (0.33) with *P. sylvestris*, and they remained essentially stable during the study period. Winter and spring temperature also had a positive influence on its growth, while summer temperature shifted its influence from positive to negative around 1980 (Figure 3c).

Pinus pinaster had the highest accumulated mean stabilized IADF frequency (0.12), followed by *P. halepensis* (0.03). The logistic function estimated that the

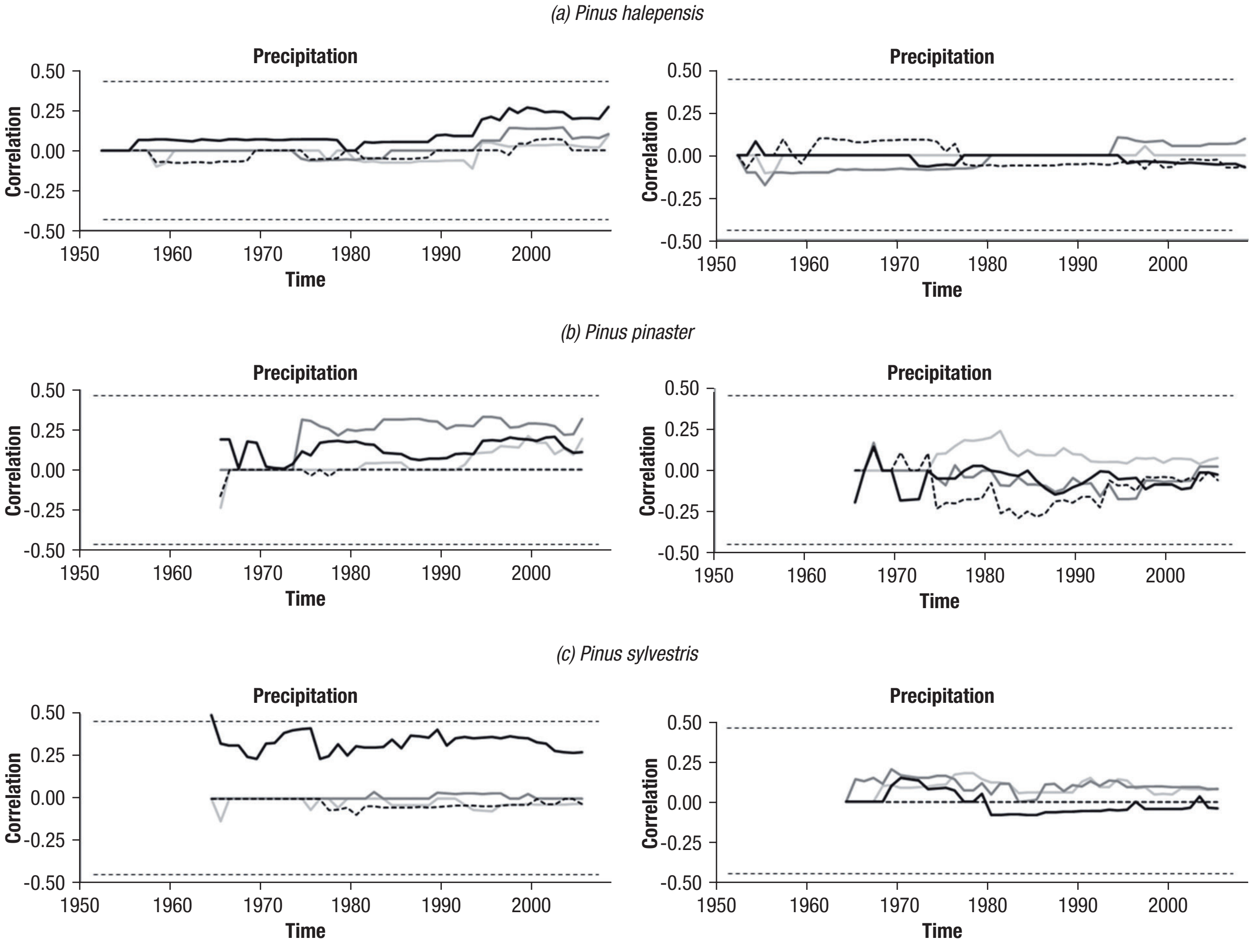

Figure 3. Influence of the climatic variables (precipitation and mean temperature) over 20 years running intervals on radial growth of *Pinus halepensis, P. pinaster* and *P. sylvestris* ($p < 0.05$). Light grey: winter; dark grey: spring; black: summer; black dashed line: autumn. Grey dashed lines indicate the lowest significant ($p < 0.05$) correlation coefficient. Horizontal dashed lines indicate the $p < 0.05$ ($n = 20$) significance limits.

occurrence of IADFs is mainly influenced by precipitation on the three species. Precipitation in the winter previous to the growing season and spring was associated with the occurrence of IADFs in *P. halepensis*, while this influence was delayed in the case of *P. pinaster*, influenced by spring and early summer precipitation. Both species showed a negative influence of precipitation in July. The IADF frequency of *P. sylvestris* was the lowest of the three species (0.004). IADF frequency in relation to calendar year (Figure 4) showed an increase in IADFs in the second half of the century. The years 1961, 1983, 1995 and 1999 had a higher occurrence of IADFs, with a stabilized frequency higher than 0.8.

Discussion

Climate-growth relationship along time

Precipitation is the main factor influencing tree growth of pine species in semiarid Mediterranean conditions (Raventós *et al.,* 2001). In our study sites, the growth of *P. halepensis, P. pinaster* and *P. sylvestris* is mainly controlled by precipitation at different times of the year. Despite the lack of biological significance of some low correlation values and the site variability, higher correlation values between seasonal climatic conditions and species reflect differences in the influence of climatic conditions between species. Winter and spring precipitation is related positively with tree-ring growth in *P. halepensis* and *P. pinaster,* while the growth of *P. sylvestris* is mostly influenced by summer precipitation. These results are consistent with those of previous studies in *P. halepensis* in Greece and Spain (Papadopoulos *et al.* 2008; Olivar *et al.* 2012), *P. pinaster* in Portugal (Vieira *et al*., 2010; Campelo *et al*., 2013) and central Spain (Bogino & Bravo, 2008), and

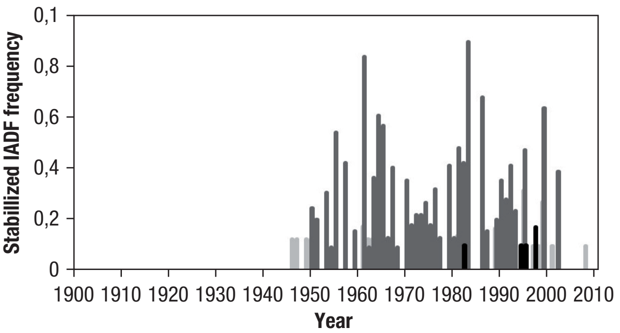

Figure 4. Mean stabilized IADF frequency in relation to calendar year of the three species. White: *Pinus halepensis* (1914-2008), grey: *P. pinaster* (1880-2005), black: *P. sylvestris* (1813-2005).

P. sylvestris at its southern and western distribution limits (Bogino *et al*., 2009).

However, the influence of these climatic variables on the growth of these species changed over the studied period. The positive influence of winter and spring precipitation on *P. halepensis* growth increased beginning in the 1990s and the positive influence of spring precipitation on *P. pinaster* growth increased beginning in the 1970s, while the positive influence of summer precipitation on *P. sylvestris* growth remained stable. These results agree with previous reports on pine species in the Mediterranean area, which suffered a change in growth response to climatic conditions in the second half of the 20th century (Andreu *et al.,* 2007; Bogino & Bravo, 2008; Vieira *et al*., 2010; Campelo *et al*., 2013).

Global studies around the Mediterranean basin indicate that winter and spring precipitation increased and summer precipitation decreased during the second-half of the 20th century (Bradley *et al*., 1987; Maheras, 1988; Díaz *et al.,* 1989). Mediterranean pines evolved during the Pliocene under tropical-like climate, before the onset of the Mediterranean climate, as a component of the pre-Mediterranean Arcto-Tertiary flora (Verdú *et al.,* 2003; Petit *et al*., 2005). This species survived to a gradual increase of aridity during the transition to Mediterranean conditions, which may have led to its characteristic growth plasticity (Chambel *et al*., 2007). Mediterranean *Pinus* species are considered well adapted to withstand drought by reducing growth as water availability decreases and increasing growth as conditions become favourable (Pasho *et al.*, 2012). This increase of winter and spring precipitation combined with the increasingly harsh climatic conditions during summer may have enhanced the importance of precipitation at the beginning of the growing season on the growth of species subject to higher drought stress conditions during summer, such as *P. halepensis* and *P. pinaster.* On the other hand, *P. sylvestris*, growing in mountainous environments with higher water availability during the whole year, didn't suffer that severity under the climatic conditions.

IADF occurrence

The occurrence of IADFs is mainly influenced by precipitation in these species. IADFs may appear at different positions within a tree-ring depending on the time of the year when the triggering factor occurred (Campelo *et al*., 2007; Edmondson, 2010; de Micco *et al*., 2012). IADF type E is triggered by dry periods during spring and early summer. In contrast, IADF type L is triggered by precipitation during late summer and (or) early autumn (Wimmer *et al.,* 2000). Previous studies in the Mediterranean area showed a high frequency of IADFs in latewood (de Luis *et al*., 2007; Vieira *et al*., 2010; Rozas *et al.*, 2011; Campelo *et al*., 2013; Novak *et al*., 2013). However, the low frequency of IADF type L and the high frequency of IADF type E observed in our samples indicate a higher occurrence of water stress episodes inhibiting cell division and enlargement during the first part of the growing season. The ability of species to produce different types and forms of cells in different periods may also be interpreted as an important adaptation of trees for maintaining the balance among the capacity to conduct water, resistance to cavitation and mechanical stability (Novak *et al.,* 2013).

The formation of IADFs is triggered by above-average precipitation in the previous winter and spring in *P. halepensis* and in spring and early summer in *P. pinaster* and negatively influenced by precipitation in July. These climatic conditions (precipitation at the beginning of the growing season and summer droughts) have been increasingly favoured over the second half of the 20th century, explaining the increasing occurrence of IADFs our study area. This result agrees with previous studies that found an increase in IADF frequencies after 1980 in *P. pinaster* in Spain (Bogino & Bravo, 2009) and Portugal (Vieira *et al*., 2010; Campelo *et al*., 2013). Despite being at its southern distribution threshold, where a species that usually grows in humid environments could suffer from the effects of increased aridity (Martínez Vilalta & Piñol, 2002), *P. sylvestris* showed the lowest IADF frequency of the three species on our sample. As pointed out by Battipaglia *et al*. (2010), the frequency and the triggering climatic factors promoting different anatomical characteristics may vary among populations, depending on different environmental conditions.

Conclusions

Precipitation is the main factor influencing tree growth and its fluctuation determines IADF occurrence in the three pine species. *Pinus pinaster* showed the highest correlations between precipitation and growth. Wet periods during winter previous to the growth season and spring induced higher growth rates in *P. halepensis* and *P. pinaster*, while the growth of *P. sylvesteris* was mostly influenced by summer precipitation. Precipitation in the winter previous to the growing season and spring was associated with the occurrence of IADFs in *P. halepensis*, while this influence was delayed in the case of *P. pinaster*, influenced by spring and early summer precipitation. However, the influence of these climatic variables on the growth of these species changed over the studied period. During the second half of the 20th century, the increase of winter and spring precipitation combined with the harsher climatic conditions during summer may have enhanced the importance of precipitation at the beginning of the growing season on the growth of species growing under drought conditions, increasing the occurrence of IADFs in *P. halepensis* and *P. pinaster*. The incorporation of special ring features such as IADFs and their association with climatic variables in any dendrochronological study provides a useful proxy for complementing and enhancing the dendroclimatological data.

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