



Original article

Climate impact on growth dynamic and intra-annual density fluctuations in Aleppo pine (*Pinus halepensis*) trees of different crown classesJorge Olivar^{a,b,*}, Stella Bogino^c, Heinrich Spiecker^b, Felipe Bravo^a^a Sustainable Forest Management Research Institute, University of Valladolid-INIA, Avda. de Madrid 57, 34004 Palencia, Spain^b Institute of Forest Growth, Albert-Ludwigs-Universität Freiburg, Tennenbacherstr. 4, D-79106 Freiburg, Germany^c Departamento de Ciencias Agropecuarias, Facultad de Ingeniería y Ciencias Económico-Sociales, Universidad Nacional de San Luis, Avda. 25 de Mayo 384, 5730 Villa Mercedes, San Luis, Argentina

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ABSTRACT

Mediterranean environments are of special interest for the study of the relationships between climate, growth and anatomic features. Dendrochronological techniques were applied at eight sampling sites that were selected throughout the natural distribution area of *Pinus halepensis* in the Iberian Peninsula. The objectives of this paper were: (i) to identify relationships between radial growth and climate for different crown classes of Aleppo pine (*P. halepensis* Mill.); (ii) to quantify the presence of intra-annual density fluctuations (IADFs) according to crown class and cambial age; (iii) to establish the relationships between IADFs and climate. In the more mesic sites, dominant trees showed higher climatic sensitivity than suppressed trees, while in the more xeric sites suppressed trees showed higher sensitivity than dominant trees. Tree-ring growth of both crown classes correlated positively with precipitation during and prior to the growing season. IADFs were more frequent in young than in old stands without differences between crown classes. Precipitation in April and December was positively correlated to the occurrence of IADFs, while precipitation in July correlated negatively. A higher frequency in IADFs occurred in the last 50 years, which coincides with the increase in drought events in the Iberian Peninsula.

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Introduction

Tree radial-growth models are valuable for simulating the impacts of climate change on the future growth of forest species. Understanding how forest growth responds to climate is a key element for a deeper knowledge of forest dynamics in a changing environment. Trees growing in extreme conditions respond strongly to climate variations. Mediterranean regions, as transitional climate zones between arid and humid regions of the world, are areas where climatic changes may have the greatest effects (Lavorel et al., 1998).

Different Mediterranean pine species have been analyzed to detect relationship between climatic trends and tree growth. Growth of pine species is positively correlated to precipitation in the Iberian Peninsula: *Pinus pinea* in southern Portugal (Campelo et al., 2006), *Pinus pinaster* in central Portugal (Vieira et al., 2009)

and in central Spain (Bogino and Bravo, 2008), *Pinus nigra* in south-eastern Spain (Martin-Benito et al., 2008) and *Pinus sylvestris* in its southern and western distribution threshold (Bogino et al., 2009). In southern Italy, growth rate of *Pinus halepensis* is sensitive mainly to temperature variations during the wet season and to soil humidity variations during the dry season (Attolini et al., 1990). In France, Rathgeber et al. (2005) concluded that *P. halepensis* growth is mainly controlled by soil water availability during the growing season. In Greece, the growth of Aleppo pine was related positively with the winter and spring precipitations and negatively with the temperatures of the spring months (Papadopoulos et al., 2001, 2005, 2009).

Wood anatomical features in tree rings have been interpreted as indicators of environmental change (see for instance Briffa et al., 2003). 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 and Schweingruber, 1995). Their inclusion of IADFs in dendrochronological studies allows detailed analysis of climatic events within the

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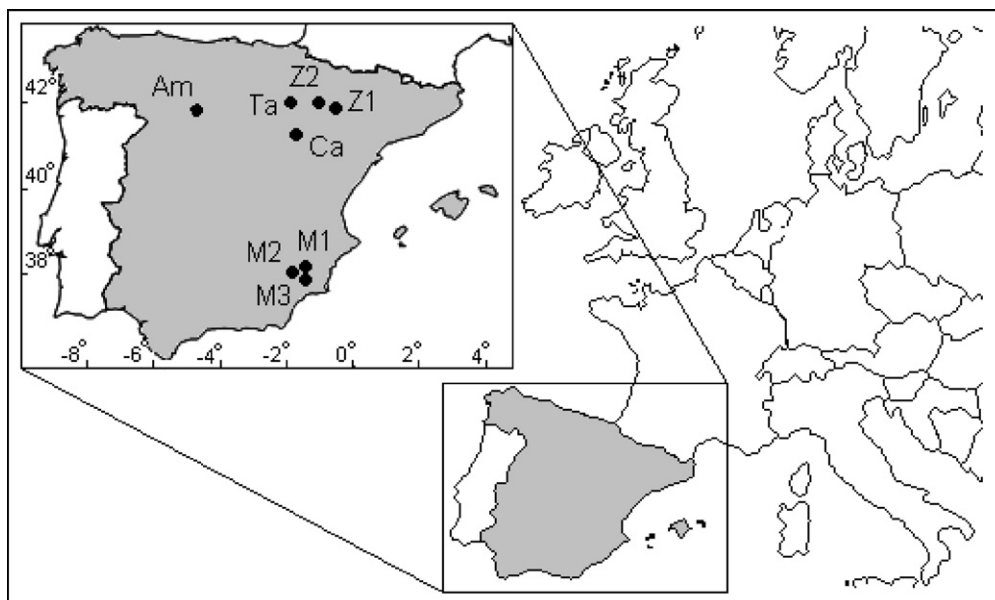


Fig. 1. Study areas of *Pinus halepensis* in the Iberian Peninsula.

growing season. Different studies of pine species showed a good correlation between IADF formation and climate in the Mediterranean area. IADFs were mainly correlated with precipitation in autumn in *P. pinaster* in Portugal (Vieira et al., 2009) and with precipitation in late winter and spring and higher temperatures in central Spain (Bogino and Bravo, 2009). IADFs were caused by precipitation events early in summer following a water deficit early in the growing season in *P. pinea* in southern Portugal (Campelo et al., 2006). Until now, the information about the impact of climate on IADFs of *P. halepensis* is scarce.

The Aleppo Pine (*P. halepensis* Mill.) is a native pine of the Mediterranean region, where it is one of the main species in the present landscape. Therefore, the study of the impact of climatic variables (temperature and precipitation) on its radial growth becomes of major interest. The objectives of the present study were: (i) to identify relationships between radial growth and climate for different crown classes of Aleppo pine (*P. halepensis* Mill.); (ii) to quantify the presence of intra-annual density fluctuations (IADFs) according to crown class and cambial age; (iii) to establish the relationships between IADFs and climate.

Materials and methods

Sites

Eight sampling sites were selected throughout the natural distribution area of *P. halepensis* in the Iberian Peninsula (Fig. 1 and Table 1).

The site index, a relative measure of forest site quality based on the height of the dominant trees at a specific age, was determined by using site index curves. The site index was defined as the top height (m) at age 80 (Montero et al., 2001).

Chronologies

Fifteen trees from each crown class (dominant and suppressed) were selected on each sampling site. Dominant trees were defined as those standing above all other trees in its vicinity and receiving full light from above, whereas suppressed trees were defined as those growing below the tree canopy. In sites Za1 and Za2 only dominant trees were sampled. Therefore, a total of 14 tree-ring chronologies (eight dominant and six suppressed) were analyzed. On each tree two cores were extracted at 1.30 m above ground. The increment cores were air dried and mounted on wooden supports and dated according to standard dendrochronological techniques (Stokes and Smiley, 1968). The preparation of the samples was done by use of the diamond flycutter (Kugler F500). This machine was designed specifically for single point diamond flycutting of plan surfaces requiring an optical quality surface finish, precise flatness and exacting parallelism.

The v6.06P COFECHA program (Holmes, 2001; Grissino-Mayer, 2001; available at www.ltrr.arizona.edu) was applied to assess measurement and dating accuracy. 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.

Table 1
Sampling sites and meteorological stations.

Site	Location	Latitude	Longitude	Altitude (m)	Site index	Met. station	Longitude	Latitude
Am	Palencia	41°51'36"	4°45'36"	849	Q17	Palencia E.C.A.	42°00'30"	4°33'27"
Ca	Aragón	41°18'16"	1°44'52"	976	Q14	Calatayud aguas	41°19'51"	1°38'49"
Ta	Aragón	41°59'31"	1°50'09"	695	Q20	Tarazona	41°54'28"	1°43'54"
Za1	Aragón	41°48'58"	0°32'15"	535	Q11	Sos del rey catolico	42°29'34"	1°12'52"
Za2	Aragón	41°56'04"	0°56'25"	706	Q11	Sos del rey catolico	42°29'34"	1°12'52"
M1	Murcia	37°52'51"	1°30'36"	811	Q11	Moratalla "benizar"	38°16'25"	1°58'59"
M2	Murcia	37°52'50"	1°32'15"	957	Q20	Moratalla "benizar"	38°16'25"	1°58'59"
M3	Murcia	37°51'13"	1°32'34"	1118	Q17	Moratalla "benizar"	38°16'25"	1°58'59"

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. According to standard methods in dendrochronology trees exhibiting correlation values with the master chronology below 0.4 were excluded.

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 and Holmes, 1984; Holmes, 2001; available at www.ltrr.arizona.edu) was used. Standardization removes geometrical and ecological trends while preserving inter-annual high-frequency variations that are presumably related to climate. To obtain a master chronology at each study site and crown class, the standardized series were averaged.

The 14 master chronologies were analyzed separately to analyze differences in radial growth. Series from dominant and suppressed trees were averaged in two separate general chronologies. Chronology quality was evaluated using the mean sensitivity (MS), which is a measure of the mean relative changes between adjacent ring widths (Fritts, 2001); the signal-to-noise ratio (SNR), the proportion of the variability explained by climate or other casual factors divided by the residual or unexplained variability (Fritts and Swetnam, 1989); and the expressed population signal (EPS), which indicates the degree to which the particular sample chronology portrays a hypothetically perfect chronology (Wigley et al., 1984). The master chronologies were normalized by subtracting the mean and dividing by the standard deviation. Values far from zero mean higher reactions. The Normalized Difference Index was calculated by subtracting the normalized values of the suppressed trees to the normalized values of the dominant trees. Positive NDI values mean stronger reactions from dominant trees, while negative NDI values mean stronger reactions from suppressed trees.

Relationships between climatic data and tree-ring widths

Mean monthly air temperatures and total monthly precipitations were recorded at the closest meteorological stations (Agencia Estatal de Meteorología, Spain) (Table 1). Climatic data were grouped in climatic seasons: winter (December, January and February), spring (March, April and May), summer (June, July and August) and fall (September, October and November). These seasonal data were regressed against ring-width indices in order to assess climate-growth relationships. DENDROCLIM 2002 (Biondi and Waikul, 2004) was applied to calculate correlation and response functions by bootstrapped error estimates (Guiot, 1991).

Intra-annual density fluctuations

The correctly dated cores were visually examined for IADFs. IADFs show a non-sharp transition in opposite to the annual rings boundary (Fritts, 2001). Because of the variability of IADFs tangentially and vertically within the tree ring along the stem the IADFs were only considered when present in both cores, in the same tree ring. As the number of samples changed over time, the relative frequency was calculated with the following formula (1):

$$F = \frac{n}{N} \quad (1)$$

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 $Z = b_0 + b_1(x_1) + b_2(x_2) + \dots + b_k(x_k) + \varepsilon$; where x_1, x_2, \dots, x_k are the climatic variables and $b_0, b_1, b_2, \dots, b_k$ 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 -2Log Likelihood , the area under the receiver operating characteristic (ROC) curve and the expected behavior – as indicated by the signs of the estimated parameters. ROC curve is displayed for the models and the area underneath was calculated as a value of the accuracy of the model. Value over 0.80 indicates an excellent discrimination (Hosmer and 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). This model was successfully used to estimate the probability of occurrence of IADFs in *P. pinaster* subsp. *mesogenesis* in the Iberian Peninsula (Bogino and Bravo, 2009). PROC LOGISTIC of SAS 9.1 (SAS Institute Inc., 2004) was used to fit the model. Samples were first grouped according to site location (Palencia, Aragón and Murcia), age (younger than 80 years and older than 80 years) and crown class (dominant and suppressed).

Results

Chronologies

The master chronologies of *P. halepensis* and the number of samples used at each sampling site are shown in Fig. 2. The master chronologies from Ampudia showed higher mean sensitivity values (0.40 for dominants and 0.37 for suppressed) than the other locations. The master chronology of the dominant trees in Ampudia also showed higher SNR and EPS (66.08 and 0.98, respectively) than the rest of the locations (Table 2).

The mean chronology of the suppressed trees showed slightly higher mean sensitivity values (0.30 for dominants and 0.33 for suppressed) and higher SNR values (26.64 for dominants and 12.77 for suppressed) than the mean chronology of the dominant trees. The mean chronology of the dominant trees also showed higher variance and mean correlation values than the mean chronology of the suppressed trees (Table 3).

Looking at the normalized curves (Fig. 3) it can be observed that dominant trees react stronger than suppressed trees in favourable years in Ampudia while in Tarazona suppressed trees react stronger than dominant trees in favourable years, the other sites show no patterns. The Normalized Difference Index (Fig. 4) showed that, from 1980 to 2000 suppressed trees reacted stronger in Murcia and Aragón, while since 2000 no clear tendency was found.

Relationships between climatic data and tree-ring widths

Relationships between mean seasonal temperatures mean seasonal precipitation and radial growth of the different crown classes in the eight sampling sites are presented in Figs. 5 and 6. Precipitation appeared to be the main factor influencing tree growth with significant values in all seasons, while temperature showed weak correlation values showing significant values in only two of the

five seasons. Spring precipitation showed the most significant positive correlations followed by summer and winter previous to the growing season.

Intra-annual density fluctuations

A total of 13,502 tree rings were analyzed from trees from the eight sampling sites and a total of 107 IADFs were found. Samples

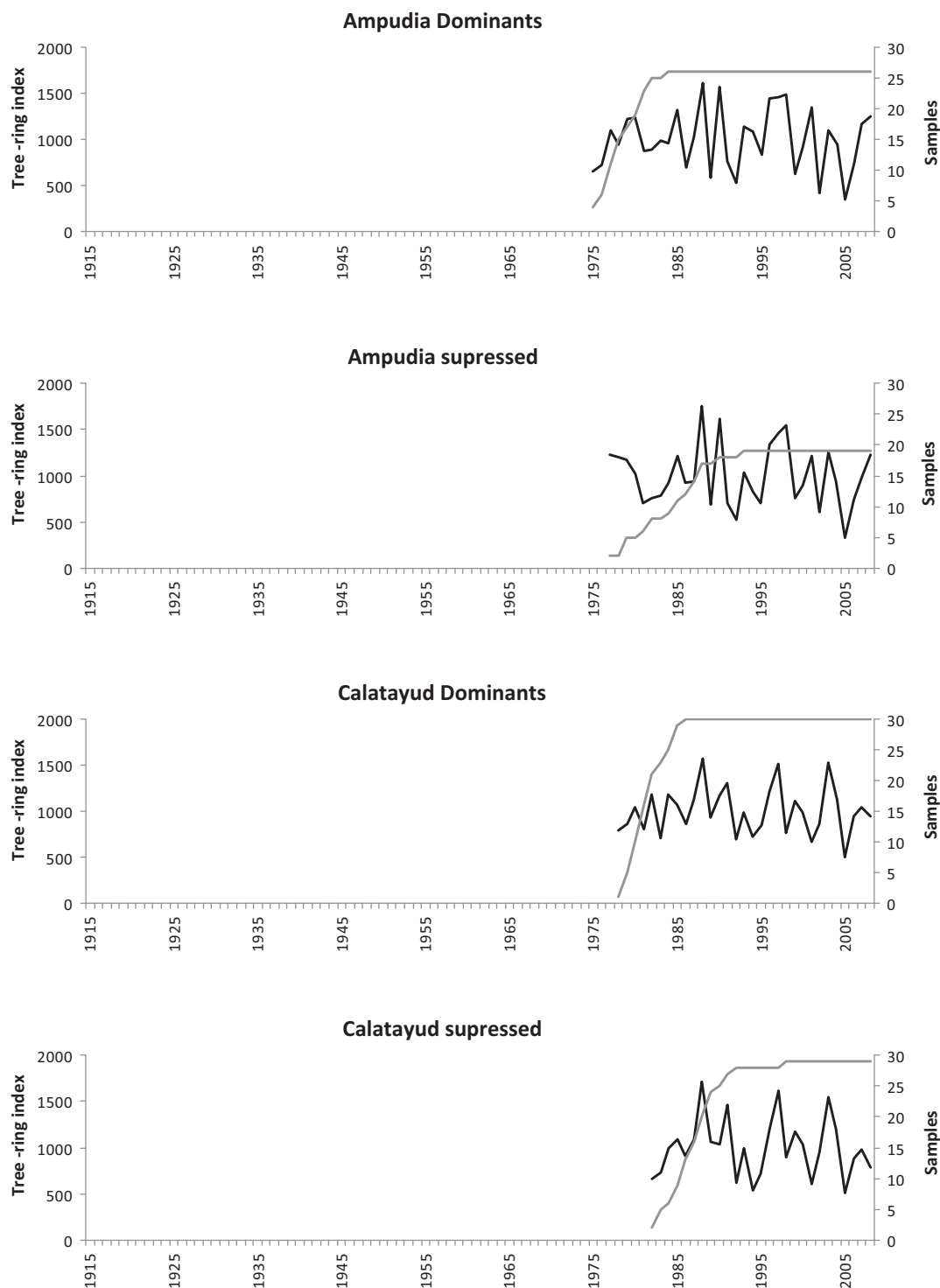


Fig. 2. Master chronologies of *Pinus halepensis* along the natural distribution in Spain. The black line shows the tree-ring index through time and the grey line shows the number of samples used in each chronology.

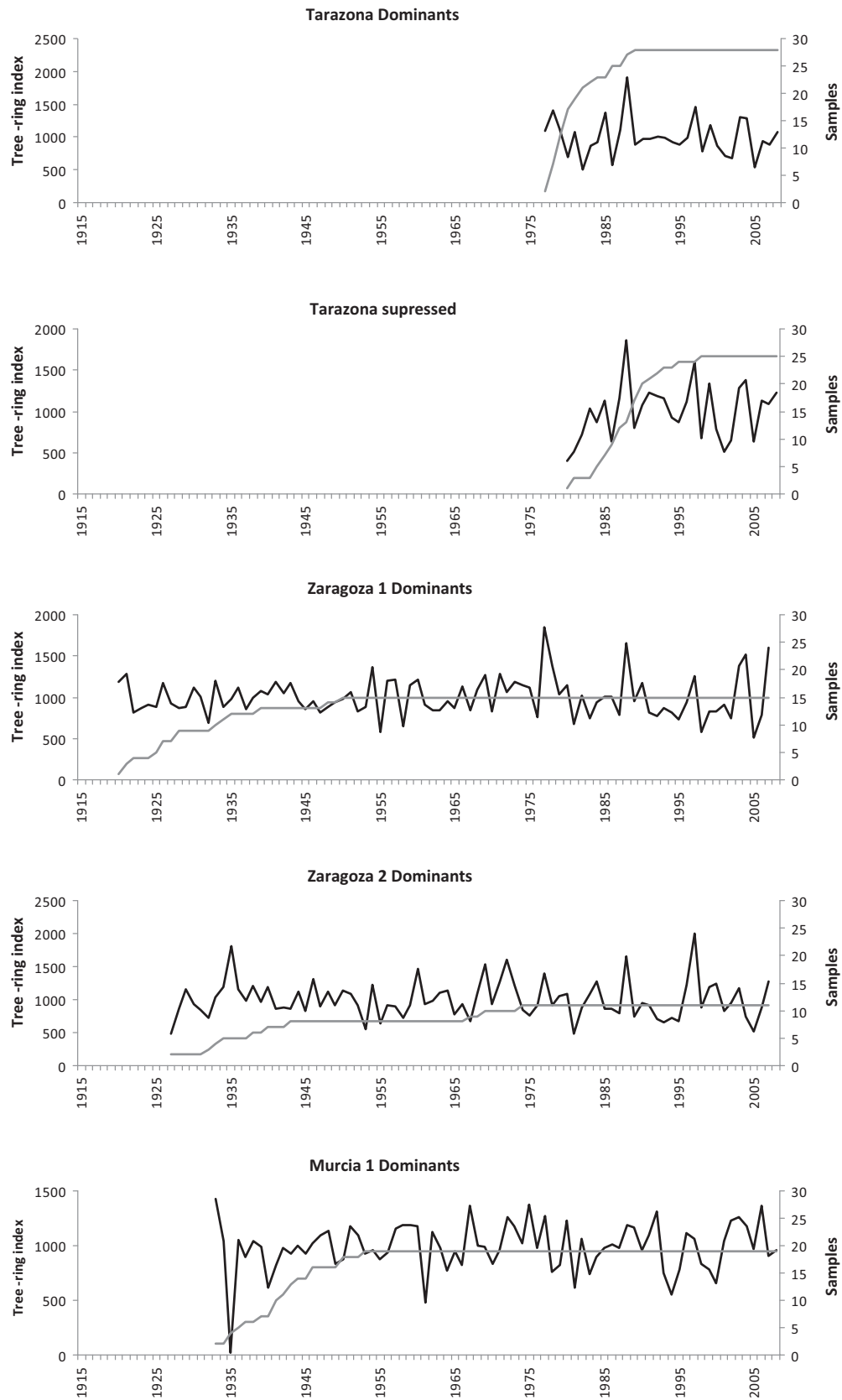


Fig. 2. (Continued).

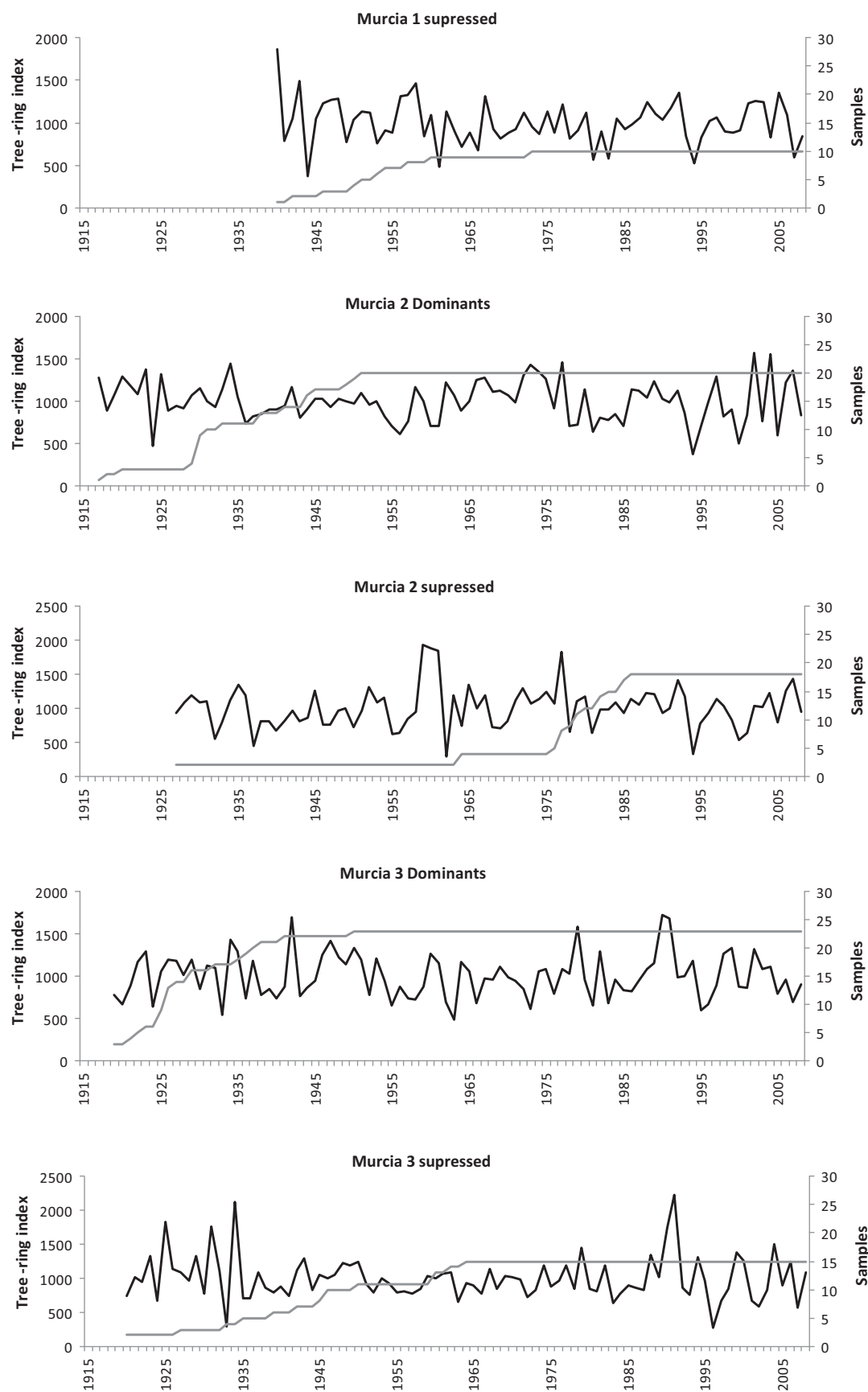


Fig. 2. (Continued).

Table 2

Descriptive statistics of the master chronologies of *Pinus halepensis*. SD: standard deviation; MS: mean sensitivity; SNR: signal to noise ratio; EPS: expressed population signal; Var: variance in first eigenvector; mean corr.: mean correlation among trees.

Code	Crown class	Location	Time span	SD	MS	SNR	EPS	Var.	Mean corr.
AmD	Dom.	Palencia	1974–2008	0.32	0.40	66.08	0.98	74.82%	0.861
Ams	Suppr.	Palencia	1976–2008	0.32	0.37	14.30	0.93	57.34%	0.722
CaD	Dom.	Aragón	1977–2008	0.25	0.33	28.70	0.96	70.28%	0.819
Cas	Suppr.	Aragón	1981–2008	0.31	0.36	15.57	0.94	63.16%	0.755
TaD	Dom.	Aragón	1976–2008	0.29	0.33	39.87	0.97	71.00%	0.831
Tas	Suppr.	Aragón	1979–2008	0.34	0.35	20.33	0.95	64.38%	0.784
Z1	Dom.	Aragón	1919–2007	0.24	0.25	8.94	0.90	48.40%	0.679
Z2	Dom.	Aragón	1926–2007	0.28	0.30	8.31	0.89	55.18%	0.724
MD1	Dom.	Murcia	1932–2008	0.20	0.21	12.86	0.93	44.45%	0.656
Ms1	Suppr.	Murcia	1939–2008	0.25	0.28	3.94	0.98	39.90%	0.596
MD2	Dom.	Murcia	1915–2008	0.24	0.25	18.20	0.95	51.00%	0.707
Ms2	Suppr.	Murcia	1921–2008	0.33	0.31	8.10	0.96	57.25%	0.751
MD3	Dom.	Murcia	1915–2008	0.30	0.32	30.20	0.97	62.68%	0.778
Ms3	Suppr.	Murcia	1917–2008	0.34	0.32	14.35	0.94	55.35%	0.731

Table 3

Descriptive statistics of the mean dominant and suppressed chronologies. SD: standard deviation; MS: mean sensitivity; SNR: signal to noise ratio; EPS: expressed population signal; Var: variance in first eigenvector; mean corr.: mean correlation among trees.

Social class	Time span	Av. core num.	Av. ring num.	Age range	SD	MS	SNR	EPS	Var.	Mean corr.
Dom.	1915–2008	22	1139	95–27	0.27	0.30	26.64	0.94	0.60	0.70
Suppr.	1917–2008	19	732	92–20	0.32	0.33	12.77	0.95	0.56	0.63

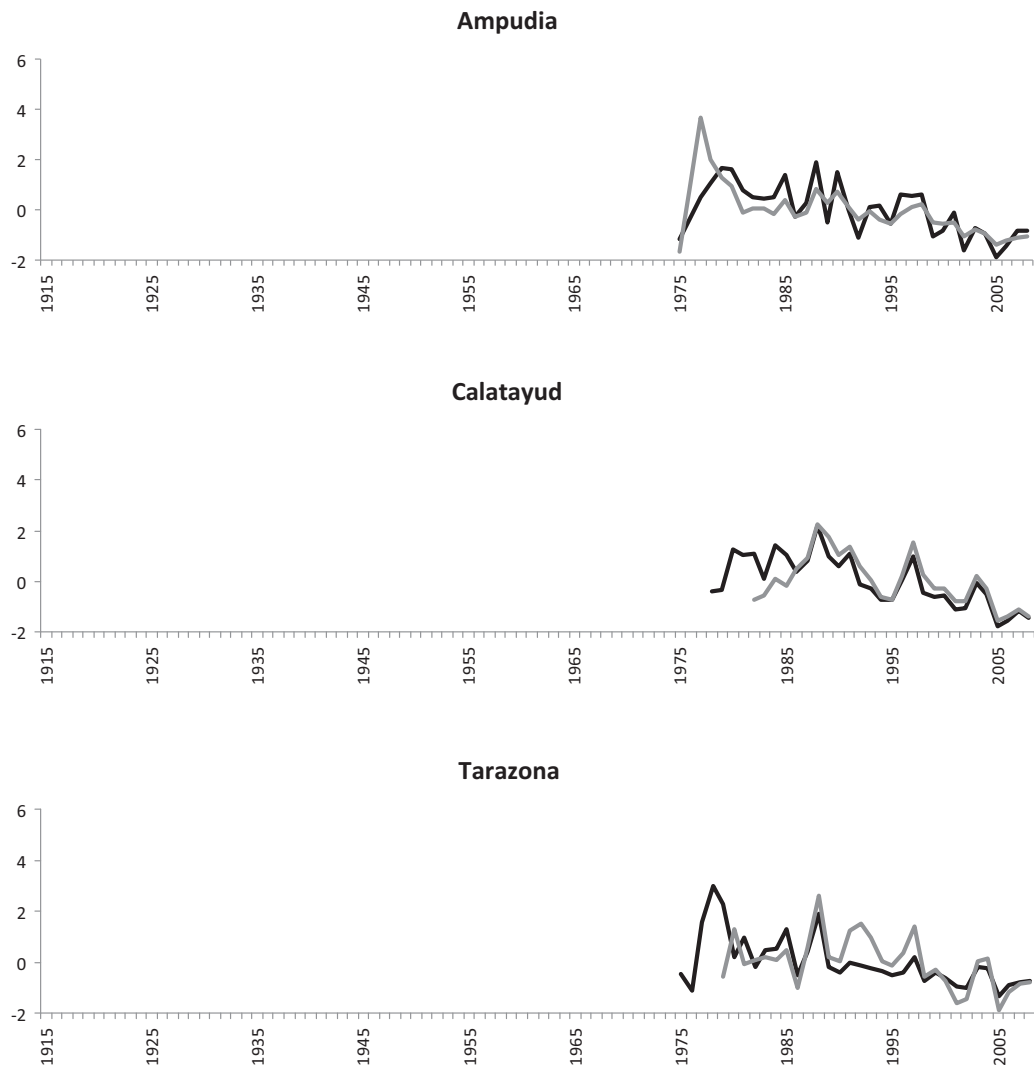


Fig. 3. Normalized chronologies of *Pinus halepensis*. The black line shows the mean dominant series and the grey line shows the mean suppressed series.

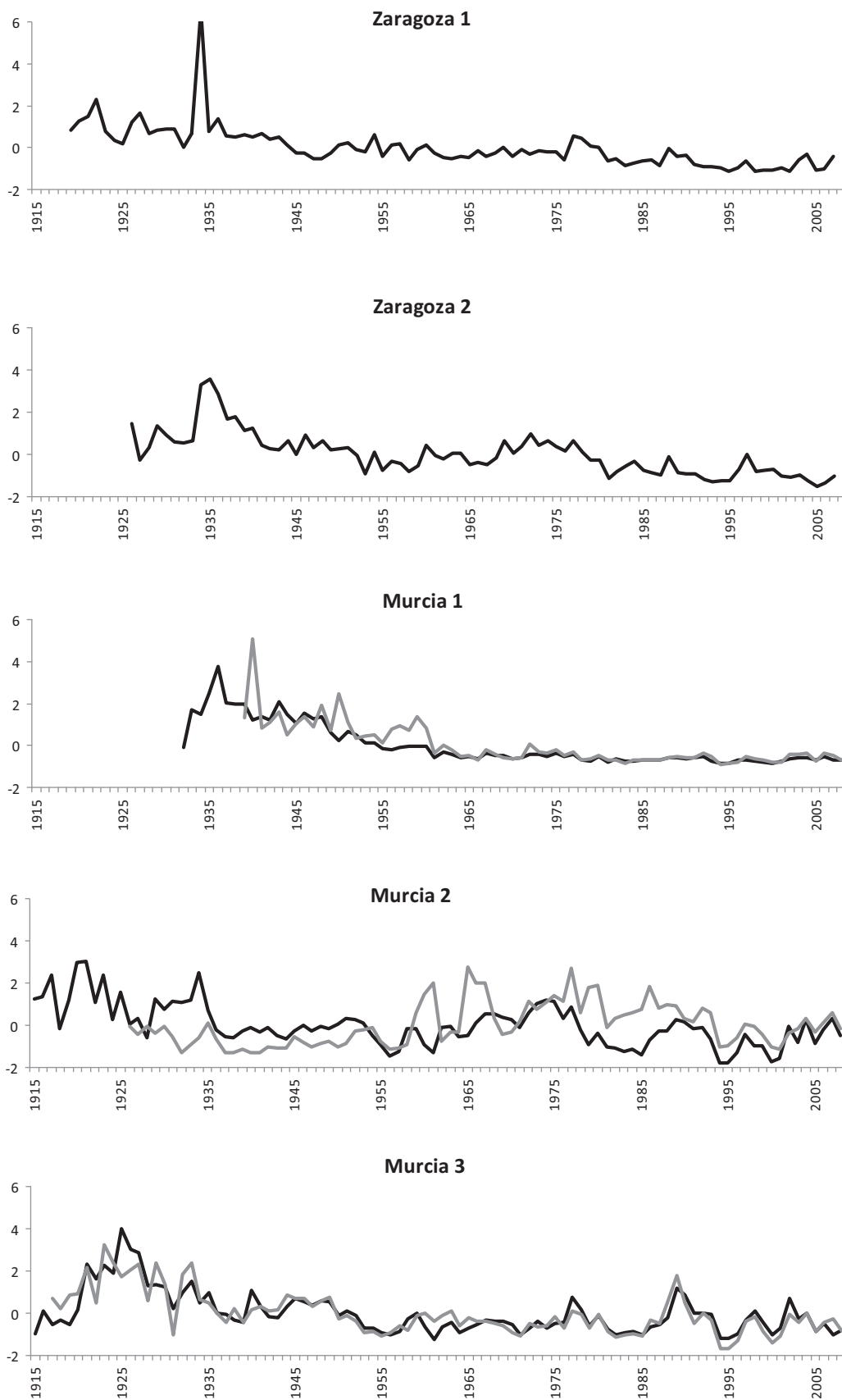


Fig. 3. (Continued).

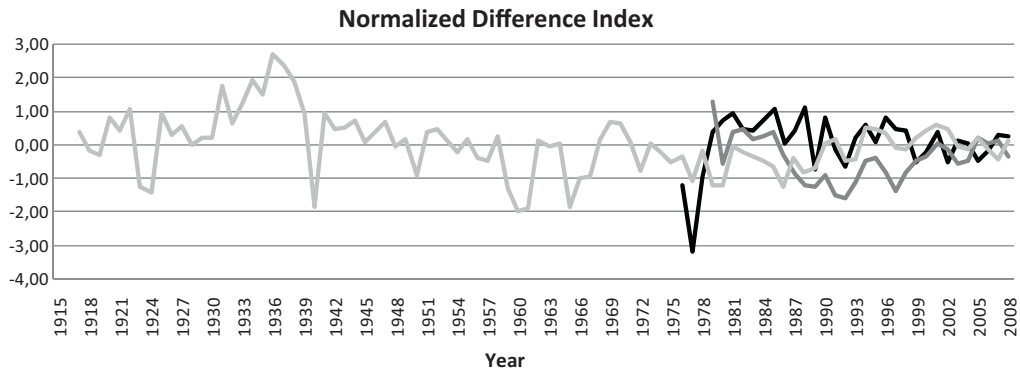


Fig. 4. Normalized Difference Index of Palencia (black line), Aragón (dark grey line) and Murcia (light grey line).

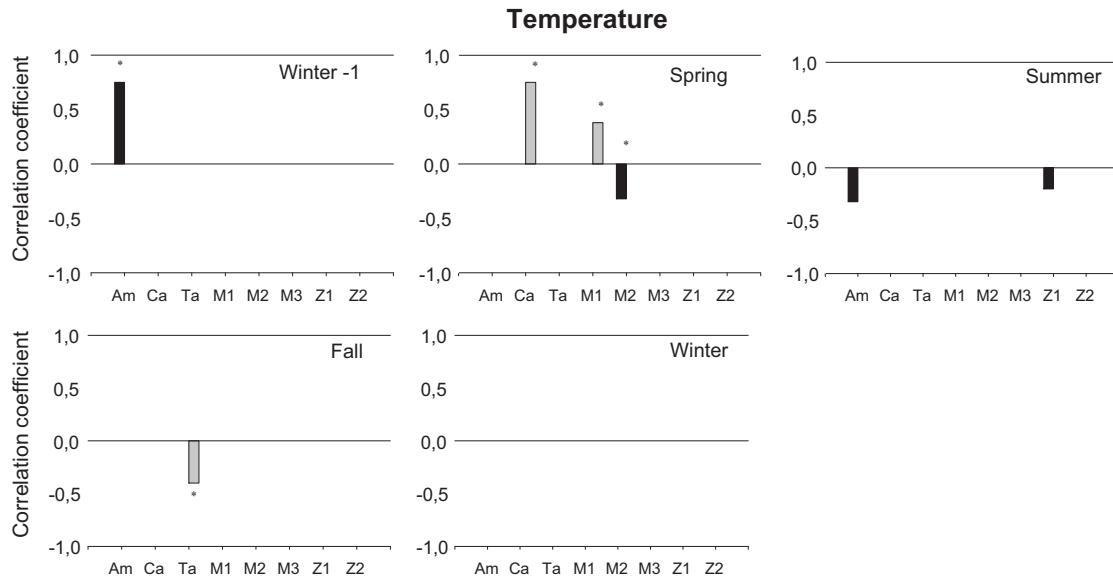


Fig. 5. Correlation coefficients between tree-ring width and temperature. Black bars represent dominant trees and grey bars represent suppressed trees (* $p < 0.05$).

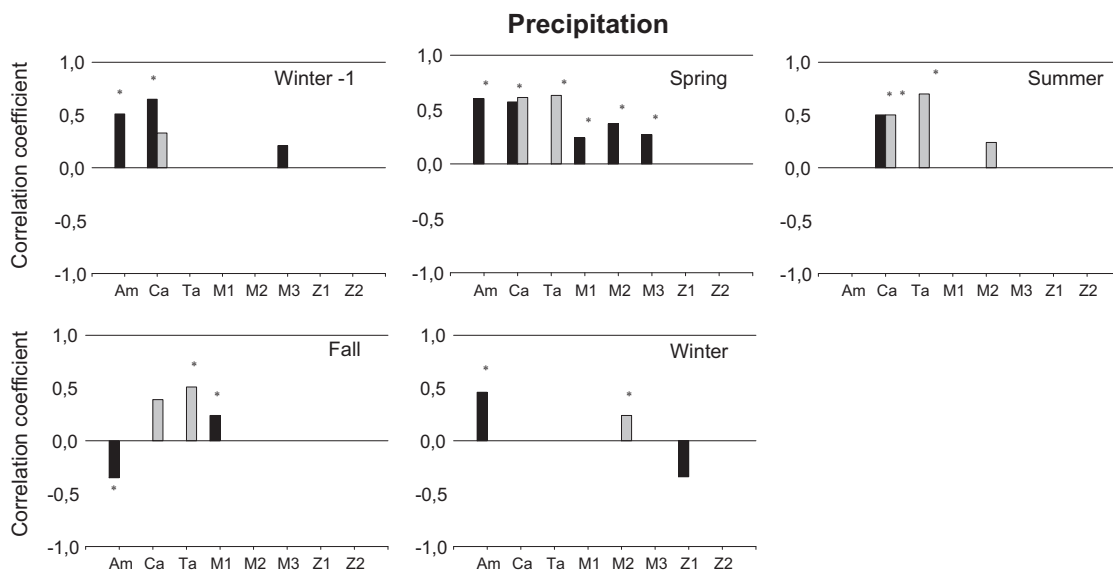


Fig. 6. Correlation coefficients between tree-ring width and precipitation. Black bars represent dominant trees and grey bars represent suppressed trees (* $p < 0.05$).

Table 4Descriptive statistics of the IADFs in *Pinus halepensis* according to age (younger than 80 years and older than 80 years) and crown class (dominant and suppressed).

	Age		Crown class	
	<80	>80	Dom	Suppr.
Number of trees	79	66	87	58
Period	1974–2008	1915–2008	1915–2008	1917–2008
Trees with IADF	28	33	32	30
Trees with IADF (%)	41.77	43.94	36.78	51.72
Tree rings in total	4183	9319	9112	4390
Tree rings with IADFs	67	40	64	43
Percentage of IADF	0.016	0.004	0.007	0.010
Mean stabilized IADF	0.65	0.55	0.61	0.61

Table 5

Stepwise selection (pp: monthly precipitation; tt: mean monthly temperature; AIC: Akaike's Information Criterion; L: likelihood).

Variables included in the model	AIC	–2log L
pp-October	519.728	515.728
pp-July, pp-October	505.353	499.353
pp-June, pp-July, pp-October	491.281	483.281
tt-May, pp-June, pp-July, pp-October	478.292	468.292
tt-September, tt-May, pp-June, pp-July, pp-October	460.197	448.197
pp-May, tt-September, tt-May, pp-June, pp-July, pp-October	453.722	439.722
pp-August, pp-May, tt-September, tt-May, pp-June, pp-July, pp-October	450.977	434.977
pp-October, pp-August, pp-May, tt-September, tt-May, pp-June, pp-July, pp-October	445.196	427.196
pp-October, pp-August, tt-September, tt-May, pp-June, pp-July, pp-October	445.241	429.241
pp-November, pp-October, pp-August, tt-September, tt-May, pp-June, pp-July, pp-October	440.880	422.880
tt-July, pp-November, tt-October, tt-July, pp-October t, pp-August, tt-September, tt-May, pp-June, pp-July, pp-October	433.910	413.910
pp-March, tt-July, pp-November, tt-October, tt-July, pp-October, pp-August, tt-September, tt-May, pp-June, pp-July, pp-October	426.127	404.127

were grouped according to site location (Table 4), age (Table 5) and crown class (Table 6). The percentage of trees with IADFs was rather similar for young and old stands. However, the percentage of IADFs and the mean stabilized IADF was higher for young stands than for old stands. The percentage of trees with IADFs and the percentage of IADFs were both higher for suppressed than dominant trees. Mean stabilized IADF was the same for both crown classes.

The nonlinear logistic equation form was chosen to model the probability of occurrence of IADFs with monthly precipitation and mean monthly temperature as variables (Table 5). The logistic function estimated that 10 monthly climatic variables out of 24 had a significant effect on predicting future IADFs (Tables 6 and 7). The model showed that, without considering crown classes, precipita-

tions in October, December, March, April, June and mean monthly temperatures in June and September had a positive impact on the formation of IADFs, while precipitations in November and July and mean monthly temperatures in May had a negative impact on the formation of IADFs. Precipitations in December and April had a positive impact on the formation of IADFs in both dominant and suppressed trees, while precipitations in July had a negative impact. The area underneath ROC curve was 0.918 for all trees, 0.917 for dominant trees and 0.943 for suppressed trees. The accuracy of the model is also sufficient to use it to predict occurrence of IADFs. IADF frequency in relation to calendar year (Fig. 7) showed an increase in IADFs from the 1980s to the present. 1983, 1989, 1995 and 1999 were the years with more IADFs, with a stabilized frequency higher than 0.2.

Table 6Climatic variables with a significant effect on the probability of IADFs in *Pinus halepensis* (pp: monthly precipitation; tt: mean monthly temperature).

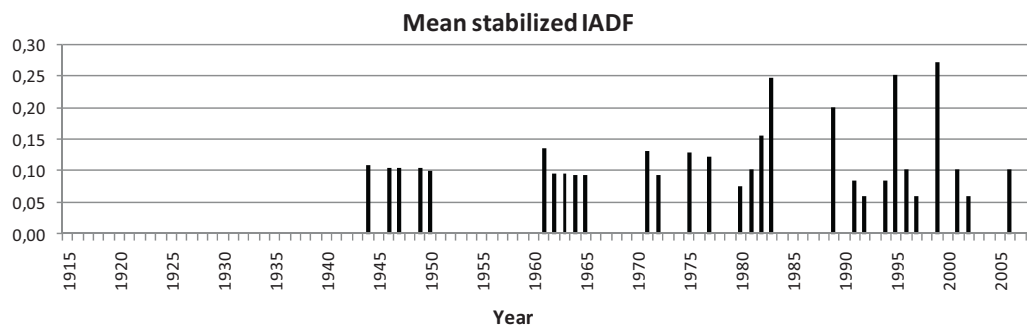
Parameter	AmD	Ams	CaD	Cas	TaD	Tas	Z1	Z2	M1D	M1s	M2D	M2s	M3D	M3s
pp-October												**		
pp-January		* –	*** +									***		
pp-March												***		
pp-April									*	–				
pp-May			*** +		*** +									
pp-July	* –		** –	*** –										
pp-August			*** +											
pp-September			* –											
tt-October				** +										
tt-February			** +											
tt-March												**	–	
tt-May					*** –				*	–				
tt-June											*	+		
tt-July				** –							*	+		
tt-August											*	–		
tt-September				* +										

The absence of an asterisk shows that there was no significant association.

* $p < 0.05$.** $p < 0.01$.*** $p < 0.001$.

Table 7Climatic variables with a significant effect on the probability of IADFs in *Pinus halepensis* (pp: monthly precipitation; tt: mean monthly temperature).

Parameter	All				Dominant				Suppressed			
	Estim.	St. error	Wald χ^2	Pr > χ^2	Estim.	St. error	Wald χ^2	Pr > χ^2	Estim.	St. error	Wald χ^2	Pr > χ^2
Intercept	8.05	3.22	6.25	0.01	8.98	3.55	6.41	0.01	5.98	3.82	2.45	0.12
pp-October	−0.03	0.01	17.26	<.0001								
pp-November	0.04	0.01	14.67	0.00								
pp-December	−0.07	0.01	38.20	<.0001	−0.08	0.01	29.14	<.0001	−0.09	0.02	21.90	<.0001
pp-January									0.12	0.04	9.53	0.00
pp-March	−0.02	0.01	9.01	0.00								
pp-April	−0.02	0.01	8.64	0.00	−0.02	0.01	8.08	0.00	−0.07	0.03	6.08	0.01
pp-May					−0.03	0.01	7.11	0.01				
pp-June	−0.06	0.01	22.72	<.0001	−0.06	0.02	17.27	<.0001				
pp-July	0.03	0.01	23.08	<.001	0.02	0.01	4.69	0.03	0.07	0.02	14.13	0.00
tt-November									1.75	0.53	10.88	0.00
tt-December									−1.40	0.45	9.48	0.00
tt-May	0.72	0.15	23.20	<.0001					0.67	0.29	5.35	0.02
tt-June	−0.50	0.15	10.66	0.00	−0.40	0.16	6.50	0.01				
tt-September	−0.51	0.14	12.94	0.00					−1.69	0.52	10.39	0.00

**Fig. 7.** Mean stabilized IADF in relation to calendar year.

Discussion

P. halepensis appears as a reliable species for dendrochronological studies, showing good correlations between trees growing at the same site, high expressed population signals and accurate statistical values which suggest a clear response to environmental factors. In addition, it confirms the tendency of Mediterranean species to develop special anatomical structures (Schweingruber, 1993). We found common radial growth patterns among dominant and suppressed series in the same site. These results agree with previous studies in the Iberian Peninsula suggesting that pine species growing in the southern dendroecological section could have a common growth response to environmental factors (Richter et al., 1991; Bogino and Bravo, 2008).

The descriptive statistics of the chronologies suggest that the tree-ring series reflects one or more associated factors (including climate), and a strong response of radial growth dynamics to changes in climatic conditions shown by the mean sensitivity values (MS) from 0.21 to 0.40 that are higher than the 0.16 to 0.34 values found in previous studies on pine species (*P. sylvestris* L., *P. nigra* Arnold, *P. pinaster* Ait. and *Pinus mugo* ssp. *uncinata* Turra.) in the Iberian Peninsula (Richter et al., 1991; Bogino and Bravo, 2008, 2009; Martin-Benito et al., 2008; Bogino et al., 2009; Vieira et al., 2009).

The expressed population signal (EPS) ranging from 0.89 to 0.98 is in all cases higher than the critical level of 0.85 suggested by Wigley et al. (1984), which implies that the chronologies are representative of tree growth in the stands. First eigenvector variance ranges from 39.90 to 74.82%, indicating good homogeneity within the same site. It can be concluded that the fourteen mean chronologies have high MS, SNR, EPS and percentage of the

variance accounted for by the first eigenvector, suggesting a strong common signal to related-climatic environmental factors. Ampudia showed higher values of MS, SNR and EPS than the other two locations, especially the dominant trees. However, in the regions of Aragón and Murcia the mean suppressed series showed a higher sensitivity than the mean dominant series. There is evidence that suppressed trees suffer greater drought stress because of greater root competition for soil. However, understory trees receive lower solar radiation and higher wind protection by the influence of neighbouring crowns reducing transpiration rates. Therefore, climatic sensitivity may be reduced (Bréda et al., 2006; Martin-Benito et al., 2008). In Mediterranean forests tree density is low and the protection effect from the dominant to the suppressed trees gets reduced.

The results show that *P. halepensis* growth is mainly controlled by precipitation. Previous studies reported that growth of Aleppo pine is controlled by soil water availability (Rathgeber et al., 2005) and precipitation is the main factor influencing tree growth of pine species in semiarid Mediterranean conditions (Raventós et al., 2001). Winter previous to the growing season and spring precipitation are related positively with tree-ring growth. The same results were found in the Attica basin (Greece) (Papadopoulos et al., 2009). Other Mediterranean pine species showed similar results: growth of *P. pinea* in a dry Mediterranean area in Portugal, *P. pinaster* in central Spain and *P. sylvestris* at its southern distribution limits were positively correlated with rainfall (Campelo et al., 2006; Bogino and Bravo, 2008; Bogino et al., 2009). Growth of *P. nigra* in central Spain and *P. pinaster* in Portugal were mainly influenced by May precipitation (Martin-Benito et al., 2008; Vieira et al., 2009).

We found a higher tendency in young stands for developing IADFs. These results corroborate previous dendroecological

studies which suggested that IADFs were more frequent in younger tree rings (Rigling et al., 2001; Villalba and Veblen, 1994; Vieira et al., 2009; Bogino and Bravo, 2009). This could be due to a faster response of young trees to changing factors (Villalba and Veblen, 1994) and/or to a longer growing season of young trees (Rossi et al., 2008). Since young trees have a different response to environmental factors than old trees, the incorporation of age-dependent differences on the appearance of special ring features such as IADFs and its association to climatic variables in any dendrochronological study provides a useful proxy for complementing and enhancing the dendroclimatological data. In addition, it can give important clues to predict differences on how young and old trees react to climate change.

The occurrence of IADFs in *P. halepensis* was positively correlated with precipitation in December and April and negatively correlated with precipitation in July. These results are consistent with those of previous studies in *P. pinaster* in central Spain, where IADFs were mainly correlated with rainfall pulses in late winter and spring (Bogino and Bravo, 2009). IADFs correlated positively with precipitation events early in summer following a water deficit early in the growing season in *P. pinea* in southern Portugal (Campelo et al., 2006), which is consistent with the present results that showed precipitation in July to have a negative effect on IADFs. Favourable climatic conditions in winter and spring as well as water deficits early in the growing season followed by rainfall indicate an increase in the probability of the occurrence of IADFs. This corroborates that growth may temporarily stop, but is always ready to resume activity as soon as climatic conditions become favourable.

Winter precipitation that precedes the formation phase of the tree-rings as well as the spring rainfall at the beginning of the tree-growth play a prevailing role to the development of wider tree rings in *P. halepensis* (Papadopoulos et al., 2009). These climatic conditions coincide with the favourable conditions for the formation of IADFs in our study. Therefore we can agree with previous studies that have shown that IADFs are more frequent in wider tree rings (Vieira et al., 2009; Rigling et al., 2001; Villalba and Veblen, 1994). As it was previously reported (Bogino and Bravo, 2009) a higher frequency in IADFs occurred in the last 50 years. The increase in drought events in the Iberian Peninsula (IPCC, 2007) may explain the higher IADF frequency during this period.

Conclusions

Pinus halepensis is an accurate species for tree-ring analysis with good correlations between trees growing at the same site and a clear response to environmental factors. Suppressed trees showed higher sensitivity than dominant trees, with greater growth rates during favourable years except for Ampudia, where dominant trees showed higher sensitivity than suppressed trees. Precipitation was the main factor influencing tree-ring growth. IADFs were more frequent in young than in old stands with no clear differences according to crown classes. The probability model used, showed that high precipitation in spring and winter indicates an increase in the probability of the occurrence of IADFs, while high precipitation in July indicates a decrease in the probability of the occurrence of IADFs. A higher frequency in IADFs occurred in the last 50 years, which coincides with the increase in drought events in the Iberian Peninsula.

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