

Climate Effect on Radial Growth of *Pinus sylvestris* at Its Southern and Western Distribution Limits

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The associations between tree-ring width and climatic variables, the tree age effect on climate-growth relationship and the drought index impact on radial growth of Scots pine (*Pinus sylvestris* L.) were studied in Mediterranean environments in the Iberian Peninsula. Dendrochronological techniques were applied to construct six tree-ring width chronologies for *P. sylvestris*. The association between tree growth and climate was analysed with correlation coefficients and bootstrapped response functions. Drought index (DRI) was used to detect the effects of aridity. Tree-ring width was positively correlated with rainfall in the growing season but this association started earlier at the lowest altitudinal sites. The effects of temperature varied according to the site. The response to climatic variables depended on the age of the trees: more of the variability was explained by climatic variables in young stands than in old stands. The significant association between radial growth and DRI suggests that drought is a determining factor in the radial growth of *P. sylvestris*. Climate forecast scenarios show an increase in rainfall irregularity in the Mediterranean region so the differential tree response to rainfall at different elevations can be used to predict tree growth for determining silvicultural treatments.

Keywords dendroclimatology, Scots pine, tree ring, pulse and interpulse

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1 Introduction

Growth-climate relationships are crucial in understanding and modelling the carbon sequestration process in forests and in developing forestry strategies to mitigate the impact of climate change. Different methodological approaches can be used to explore tree growth-climate relationships, but dendroclimatological studies are valuable tools in detecting long-term changes in radial growth in woody species in association with variable climatic responses, as a result of warmer conditions and variable precipitation (Andreu et al. 2007). Extreme sites, such as the upper tree line or dry sites, are considered the most valuable for dendroclimatological studies because there are fewer determining factors, which enables a better interpretation of growth patterns (Fritts 1976).

In arid and semi-arid ecosystems, where water is a limiting resource, water availability undergoes two different phases: pulse, when the resource is available, and interpulse, when water availability is too low for plant use (Noy-Meir 1973, Goldberg and Novoplansky 1997). Mediterranean environments in the Iberian Peninsula, which are water limited ecosystems, are characterised by summer droughts and high interannual variability in precipitation and temperature. In summer months, when temperature is favourable for growth, moisture is limiting; whereas in winter, when moisture is available, low temperature limits further growth (Mooney and Dunn 1970).

Scots pine (*Pinus sylvestris* L.) is the most widely distributed pine species throughout the world (Blanco et al. 1997) and represents one of the most important dendroecological species in Europe (Schweingruber 1996). *P. sylvestris* is one of the most important tree species in Spain in terms of both, the covered area (1 280 000 ha) and the diverse functions of stands of species (Montero et al. 2008). Forests of *P. sylvestris* in Spain occupy the southern and western limits of the worldwide distribution of the species (Barbéro et al. 1998), in assessing the impact of global warming on ecosystems, any changes in tree growth are likely to occur first in those tree stands located at the ecological boundary of the species (Tessier et al. 1997).

The forecasted impact of climate change on the diversity and distribution of European higher plants for the year 2050 indicates that Spain could be one

of the most vulnerable areas in terms of species loss, mainly because of the expected variability in climatic conditions (Bakkenes et al. 2002). Previous studies in the Iberian Peninsula concluded that, under severe dry conditions, shrub species that evolve under Mediterranean climate conditions, are more severely damaged by drought than the earlier evolved pre-Mediterranean genera, mainly trees (Peñuelas et al. 2001); furthermore among pine species, *P. sylvestris* displayed the highest mortality rate under severe droughts in the 1990s (Martínez-Vilalta and Piñol 2002).

On the other hand, age-related ecophysiological changes in trees (Bond 2000, Bond and Franklin 2002) also indicate the importance of considering tree age in climate-growth response analysis. Contradictory results have been reported for tree age and growth-climate responses, for different species analysed: for example, no differences were found between young and old specimens of *Pinus aristata* Engelm (Fritts 1976) or *Larix lyalii* Parl. (Colenutt and Luckman 1991), but climate effect was found to have a greater effect on old specimens of *Larix decidua* Mill. and *Pinus cembra* L. in the Italian Alps (Carrer and Urbinati 2004) and of *Abies lasiocarpa* (Hook.) Nutt. in North America (Peterson and Peterson 1994), than on young specimens. Previous dendroclimatological studies of *P. sylvestris* in the Iberian Peninsula concluded that this species is vulnerable to variation in rainfall during the growing season (Gutierrez 1990, Richter et al. 1991, Fernández et al. 1996), although the authors did not establish the effect of age on climate response.

Although predictions obtained with climate models are not wholly accurate, it is clear that future climate conditions may be characterised by greater extremes and perhaps more erratic fluctuations, with potentially strong effects on interannual to intraseasonal variability in rainfall (Schiwinning et al. 2004). It is therefore essential to understand how different species may be affected by temporal variations in water supply (Easterling et al. 2000). Furthermore, in arid and semiarid environments, it is essential to interpret short-term responses of individuals and populations to precipitation (Chesson et al. 2004). Different responses of species to changes in intra-season recharge have been reported for grasses and shrubs (Jobbágy and Salas 2000, Oesterheld et al. 2001) and for

annual species that grow in Mediterranean environments (Sher et al. 2004), but to our knowledge, no studies have been carried out to investigate the effects of pulse-interpulse events on the growth of woody species in Mediterranean environments in the Iberian Peninsula.

The objectives of this paper were to analyse on *P. sylvestris* a) the relationship between *P. sylvestris* tree-ring width and climatic variables (precipitation and temperature), b) the association between climate and cambial age and c) the effects of the drought and the interannual water availability (pulse and interpulse) on radial growth.

2 Material and Methods

2.1 Study Sites, Field Work and Laboratory Methods

Six sites along the natural distribution area of *Pinus sylvestris* in the Iberian Peninsula were selected (Fig. 1, Table 1). Individuals older than

100 years old were present at three sites, and individuals younger than 100 years old at the other three sites. Usually, Scots pine trees in Mediterranean environments are harvested at 120 years (maximum) so it is not easy to find trees over 140 years in the studied area.

In the summer of 2006, two cores were extracted at 1.30 m above ground level from fifteen dominant and co-dominant trees at each sampling site. Cores were glued onto channelled wood, dried for two weeks and polished with progressively finer grade sandpaper. Tree rings were dated, in order to establish the calendar year in which a tree ring was formed, by analysis of samples under a binocular microscope by standard dendrochronological techniques (Stokes and Smiley 1968, Fritts 1976, Cook and Kairiukstis 1990). The transverse sections (cores) were scanned at high resolution (2000 dpi) with an Epson Expression 1640 XL scanner (precision, 0.01 mm) and rings were measured with WinDENDRO software (Regent Instrument Inc. 2002). The v6.06P COFECHA program (Holmes 2001, Grissino-Mayer 2001, available at www.ltrr.arizona.edu) was applied to

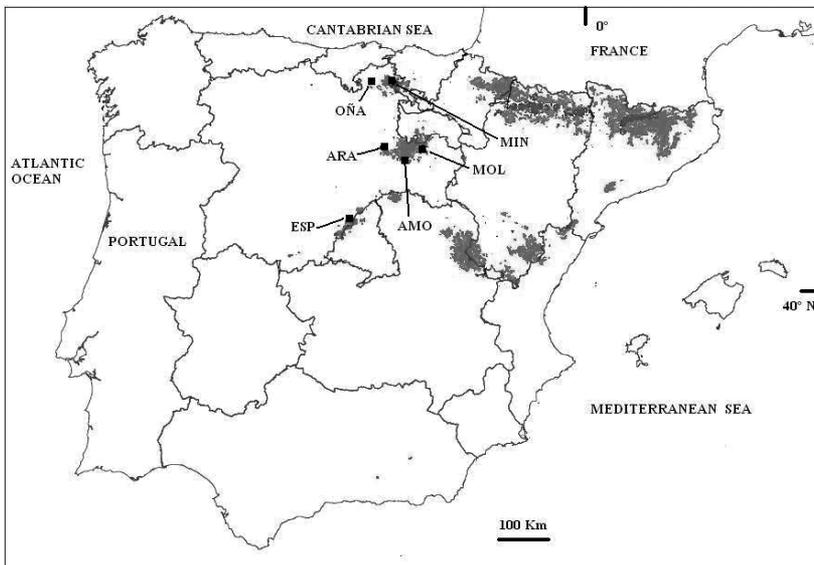


Fig. 1. Sampling sites set up across the natural distribution area of *Pinus sylvestris* woodlands in Spain [Shaded area (Catalán 1991)]. Site codes: MIN: *Miñón*; OÑA: *Oña*; ESP: *El Espinar*; MOL: *Molinos Piqueras*; AMO: *Amogable*; ARA: *Arauzo*.

Table 1. Geographical position of six sampling sites of *Pinus sylvestris* in the Iberian Peninsula.

Site name	Code	Latitude N	Longitude W	Altitude (m.a.s.l.)
<i>Miñón</i>	MIN	42°54'46"	03°21'27"	860
<i>Oña</i>	OÑA	42°58'22"	03°18'12"	760
<i>El Espinar</i>	ESP	40°38'58"	04°12'07"	1426
<i>Molino Piqueras</i>	MOL	42°04'36"	02°30'18"	1676
<i>El Amogable</i>	AMO	41°50'44"	02°55'48"	1134
<i>Arauzo de Miel</i>	ARA	41°53'04"	03°21'32"	1081

assess the accuracy of measurement and dating. This program calculates the Pearson's correlation indices between the indexed tree-ring series and a master reference chronology in a series of consecutive, partially overlapping segments of a length specified by the user.

The v6.05P ARSTAN program (Cook and Holmes 1984, Holmes 2001; available at www.ltrr.arizona.edu) was used to eliminate biological trends in tree-ring series and to minimize variations in growth that are not shared by most trees (Fritts 1976). Standardisation removes geometrical and ecological trends while preserving inter-annual high-frequency variations that are presumably related to climate. Each tree-ring chronology was standardised in two-steps by fitting first, to a negative exponential or straight line, and then to a cubic smoothing spline with a 50% frequency response of 64 years, which was flexible enough to reduce considerably any non-climatic variance (Cook and Peters 1981). The standardised series were averaged to obtain a master chronology for each study site by applying a biweight robust estimation of the mean value function (Cook et al. 1990). Finally, the chronologies were prewhitened by autoregressive modelling. Raw chronology conversion to a ring-width indices expressed the annual variations in radial growth of *P. sylvestris* at the population level in each sampling site. The quality of the chronology was evaluated by mean sensitivity (MS), signal-to-noise ratio (SNR), and expressed population signal (EPS), (Wigley et al. 1984, Fritts and Swetnam 1989, Briffa 1995, Schweingruber 1996). The tree-ring index was used to be compared with climatic variables.

2.2 Climatic Data

Monthly precipitation and mean monthly temperature, provided by the Agencia Estatal de Meteorología (National Meteorological Agency, Spain) were selected to assess the climate-growth relationship. Recorded meteorological data, that varied from 61 to 71 years, pertain to four meteorological stations placed at less than 30 km from the sampling sites: Miranda del Ebro (Burgos), Villafraja (Burgos), Observatorio (Soria) and Aldea del Rey Niño (Avila) (Table 2, Fig. 2). Climatic series were considered homogeneous after applying the HOM (Homogeneity of Meteorological Data) routine of the DPL [Dendrochronology Programme Library (Holmes 1983; available at www.ltrr.arizona.edu)].

2.3 Growth-Climate Relationship Analysis

To determine the climatic variables that control the radial growth of *P. sylvestris*, mean monthly temperature and monthly rainfall were compared with the local chronologies for each sampling site. The local chronologies were compared with the meteorological station closest to the analysed site. The period explored was from June prior to the current growth year to September of the current growth year. The v 5.17 PRECON program (Fritts 1999; available at www.ltrr.arizona.edu) was used to compute the response of tree growth to climate, by means of a multiple stepwise regression. Coefficients were considered significant at * $p < 0.05$ and ** $p < 0.01$. A bootstrap analysis, that estimates the error of the dataset by repeated random

Table 2. Meteorological data used in this study. Rainfall: annual precipitation; Temp.: mean annual temperature; Site: code of the sampling sites related to the meteorological station; Period: time with data available (Agencia Estatal de Meteorología, Spain).

Meteorological station	Latitude	Longitude	Altitude (m)	Rainfall (mm)	Temp. (°C)	Site	Period
Miranda del Ebro (Burgos)	42°40'42"	02°57'20"	520	529.97	12.08	MIN-OÑA	1936–2005
Villafría (Burgos)	42°21'22"	03°37'57"	890	564.67	10.15	ARA	1943–2005
Observatorio (Soria)	41°46'00"	02°28'00"	1082	529.85	10.59	MOL-AMO	1944–2005
Aldea del rey Niño (Avila)	41°34'35"	04°42'02"	1160	522.24	9.17	ESP	1935–2005

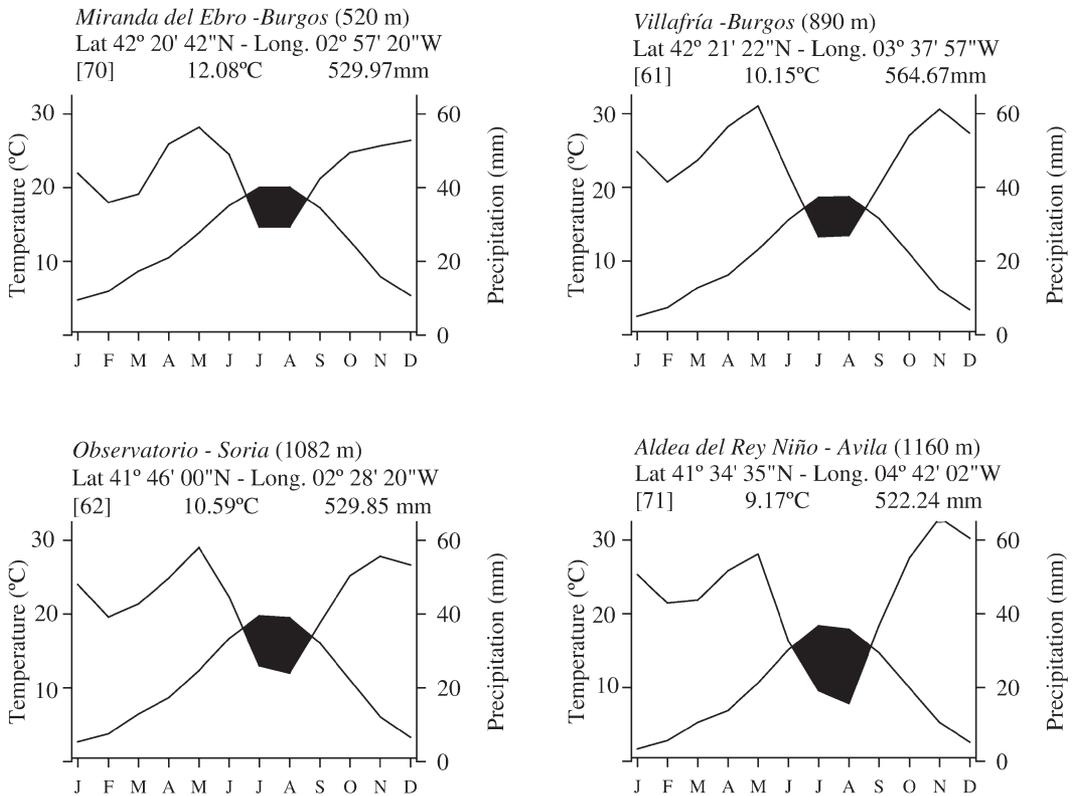


Fig. 2. Climate diagrams of Miranda del Ebro (Burgos), Villafría (Burgos), Observatorio (Soria) and Aldea del Rey Niño (Avila) meteorological stations.

sampling of the data as to increase the sample size artificially, was also applied to improve the robustness of the correlation coefficients. A total of 1000 bootstrap interactions were considered in the analysis (Mooney and Duval 1993).

2.4 Drought Index Effect and Pulse and Interpulse Analysis

The drought index (DRI) of Thornthwaite (1948) was applied to detect the pulse-interpulse effect on

radial growth of *Pinus sylvestris*. The DRI at each sampling site was calculated from the months where the response function analysis showed a significant association between precipitation and radial growth (May and June at *Miñon*, *Oña* and *Arauzo de Miel* sites; June and July at *El Espinal* site; July at *Amogable* site and July and August at *Molino Piqueras* site).

The monthly DRI was calculated by the formula (Eq. 1):

$$\text{DRI} = \text{P} - \text{PET} \quad (1)$$

Where DRI is the drought index, P=monthly precipitation and PET=the potential evapotranspiration estimated from the monthly mean temperature and the geographical position of the meteorological station. The Pearson's correlation

coefficient was calculated for DRI and tree-ring width (Sokal and Rohlf 1995).

3 Results

All six chronologies analysed (Fig. 3) displayed high SNR (10.67–24.74) and EPS values (0.91–0.96), while the variance accounted for the first eigenvector was over 35 % (Table 3). The mean sensitivity varied from 0.15 to 0.26 and the standard deviation from 0.18 to 0.35, depending on the sampling site.

The association between radial growth and climatic variables (mean monthly temperature and monthly precipitation) at the *Miñon* and *Oña* sites showed that rainfall in the growing season (May

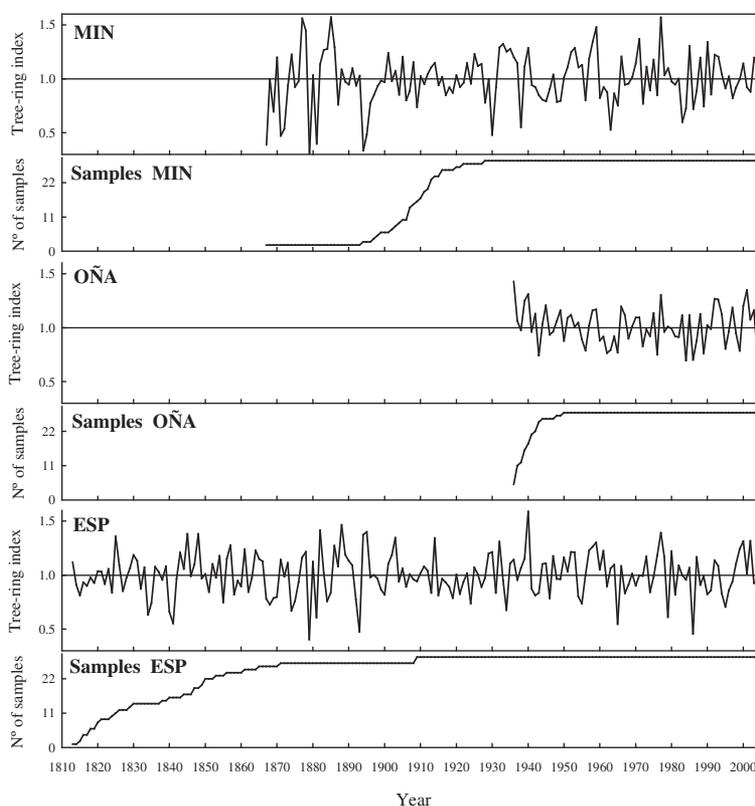


Fig. 3. Standardised chronologies of *Pinus sylvestris* along the natural distribution area in Central Spain. The upper part of each figure show the tree-ring indexes through time and the bottom part the number of samples used in each chronology.

Table 3. Descriptive statistic of the six chronologies of *Pinus sylvestris* in Spain. SD: standard deviation; MS: mean sensitivity; SNR: signal to noise ratio; EPS: expressed population signals. Var.: variance in first eigenvector and Mean. Corr.: mean correlation among trees.

	MIN	OÑA	ESP	MOL	AMO	ARA
Time span	1867–2005	1932–2005	1811–2005	1945–2005	1949–2005	1846–2005
Core number	29	28	29	30	30	24
Ring number	2956	1845	4803	1528	1538	4490
Age range	81–140	55–74	99–195	40–61	46–57	127–160
SD	0.28	0.18	0.24	0.35	0.19	0.30
MS	0.26	0.20	0.19	0.25	0.15	0.18
SNR	18.82	20.13	19.89	24.74	15.30	10.67
EPS	0.95	0.95	0.95	0.96	0.93	0.91
Var.	43.17	46.41	45.95	54.99	38.23	35.88
Cor.	0.40	0.43	0.43	0.51	0.34	0.30

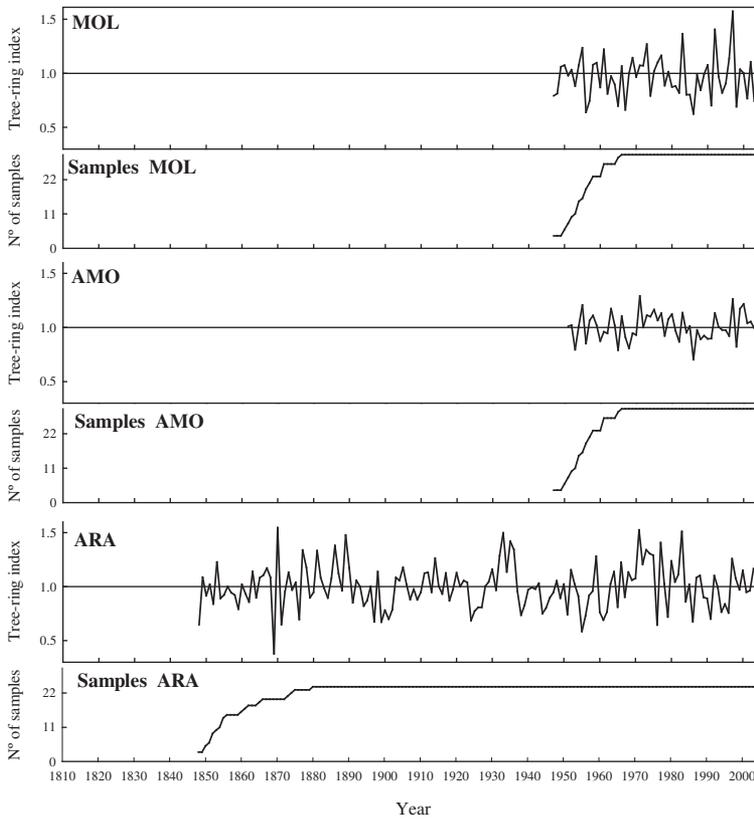


Fig. 3 continued.

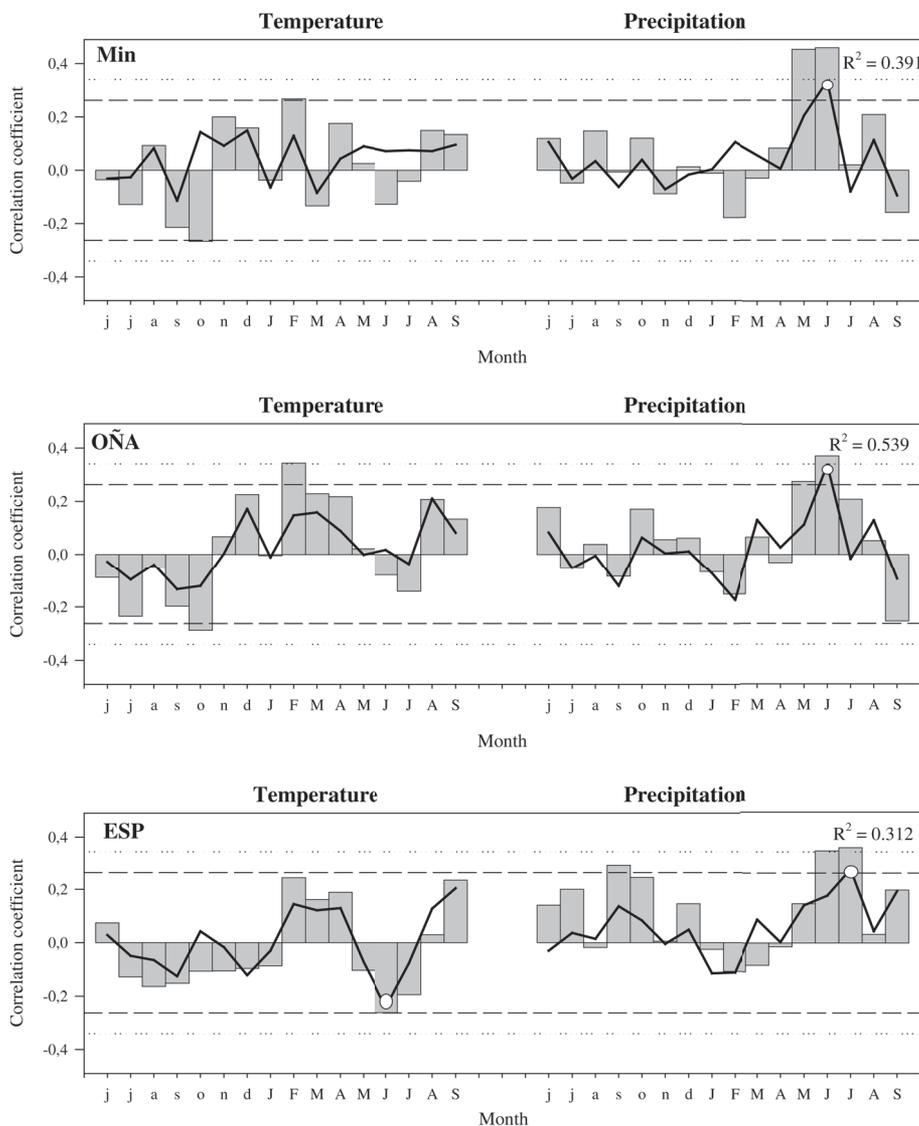


Fig. 4. Correlation coefficients (bars) and bootstrapped response function (lines) that relate the effect of regional climatic variables (mean monthly temperature – monthly precipitation) and growth of *Pinus sylvestris* during the 1950–2005 period at *Miñon*, *Oña*; *El Espinar*, *Molino Piqueras* and *Arauzo de Miel* sites. *Amogable* site was analysed from 1960–2005. The analysed period is from June of the previous growing season to September of the current growing season. Bars higher than the dashed lines show a significant coefficient at $p < 0.05$. Bars higher than the dotted lines show a significant coefficient at $p < 0.01$. White circles indicate the months where the bootstrapped response function coefficients are significant at $p < 0.05$. R^2 values show the total variance explained by both variables. Lower case letters indicate the months prior to the growing season. Upper case letters indicate the growing season months.

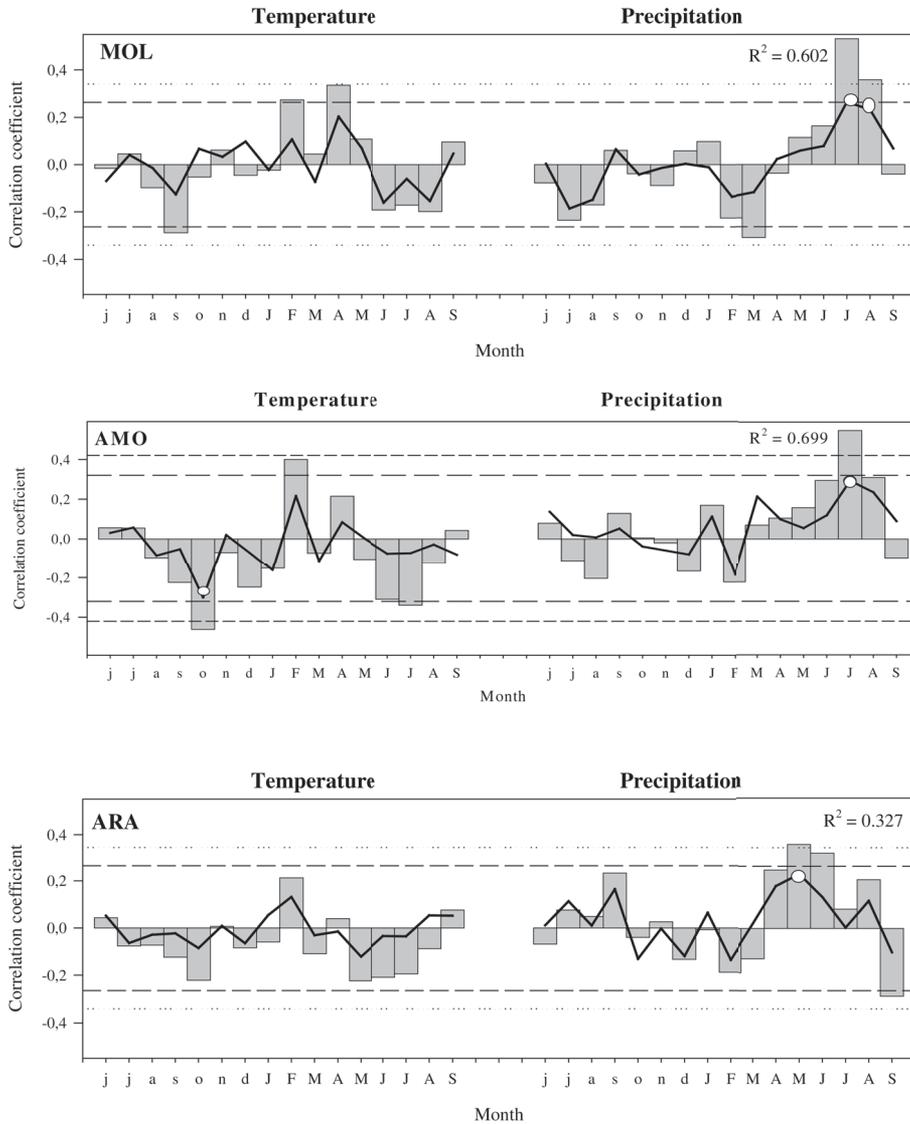


Fig. 4 continued.

and June) had a positive effect on growth of this species. On the other hand, temperature was positively correlated with radial growth in February and negatively in the October prior to the growing season (Fig. 4). The association between radial growth and climatic variables at the *El Espinar* site showed that rainfall during the growing season (June and July) had a positive effect on growth of this species. High temperatures during the growing season limited growth (Fig. 4). At

the *Molino Piqueras* site, a positive relationship between growth and rainfall during the growing season (July and August) was observed; temperature was significantly, negatively related to growth in September, and positively in February and April prior to the growing season (Fig. 4). At the *Amogable* site there was also a positive relationship between growth and rainfall in the growing season (July), and between growth and mean temperature in February. Temperature lim-

ited growth in October prior to the growing season (Fig. 4). Finally, rainfall in May and June had a significant effect on growth at the *Arauzo de Miel* site (Fig. 4). The total variance explained by both variables ranged from 31.2% to 60.2%, according to the sampling site and the tree age (Fig. 4). The variance for the *Amogable* site was higher compare to the other sites analysed, although the study period was shorter than at the other sites [from 1960 to 2005 (Fig. 4)].

The age-dependent response to climate in the response function analysis indicated that young stands have higher variability explained by climatic variables (from 53 to 69%) than old stands [from 31 to 39% (Table 3, Fig. 4)]. The Pearson's correlation coefficient between tree-ring index and DRI revealed a significant association for all sampling sites [* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$ (Table 4)]. By mean of an example, two chronologies from an old stand (*Miñon* site) and

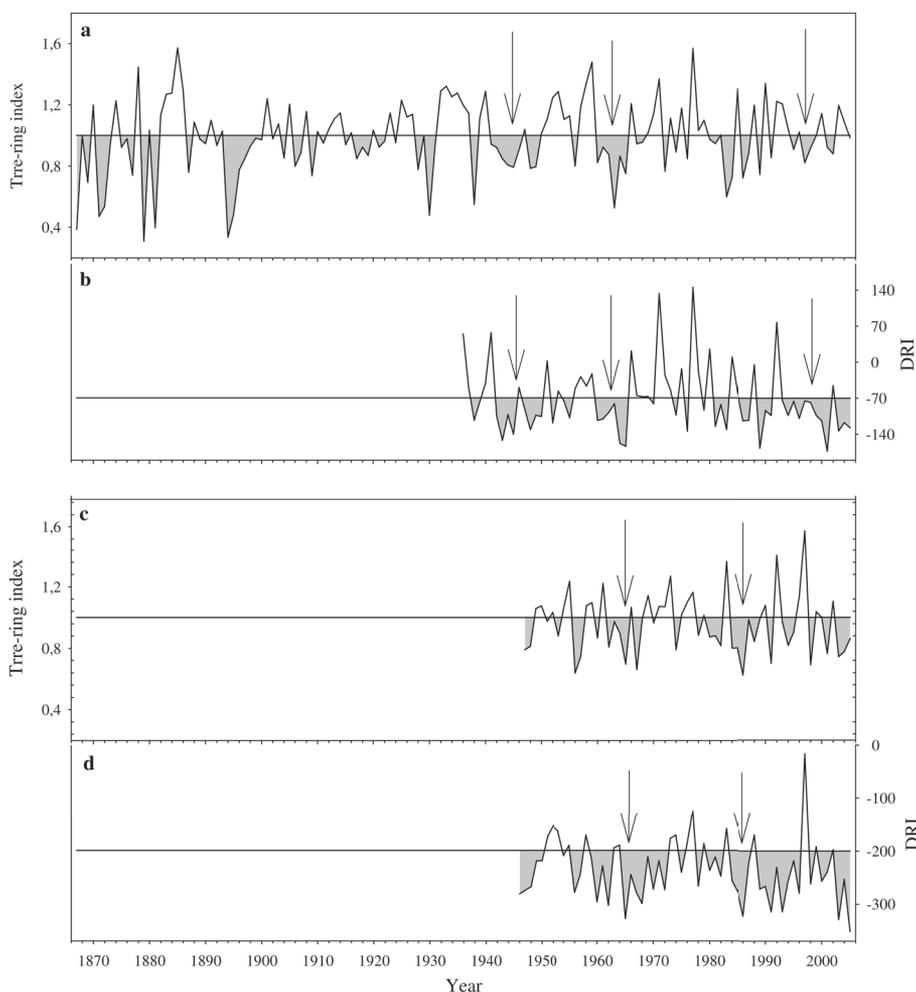


Fig. 5. Radial growth index of *Pinus sylvestris* at the *Miñon* site (a); May and June DRI from the Miranda del Ebro meteorological station (b) and radial growth index at the *Molino Piqueras* site (c); and July and August DRI from Observatorio, Soria meteorological station (d). Arrows indicates low tree-ring growth that coincides with low DRI values.

Table 4. Pearson's correlation coefficient between tree-ring index of *Pinus sylvestris* and DRI (May and June at *Miñon*, *Oña* and *Arauzo de Miel* sites; June and July at *El Espinar* site and July and August at *Molino Piqueras* and *Amogable* sites) (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$).

	Period	Correlation
MIN	1936–2005	0.47***
OÑA	1936–2005	0.31**
ESP	1944–2005	0.31*
MOL	1944–2005	0.56***
AMO	1935–2005	0.46**
ARA	1935–2005	0.43***

a young stand (*Molino Piqueras* site) are represented (Fig. 5), illustrating how small tree-ring width coincided with negative DRI values.

4 Discussion

Pinus sylvestris is a useful species in dendro-chronological studies since accurate statistical values are obtained indicating clear responses to environmental causal factors. In the present study, the relationship between climatic variables and radial growth was identified in *P. sylvestris* stands in Spain by dendrochronological methods. The six studied chronologies showed high mean sensitivity (MS), signal-to-noise-ratio (SNR), expressed population signal (EPS) and percentage of the variance accounted by the first eigenvector, suggesting a strong common signal for related-climatic environmental factors. The mean sensitivity values are comparable with the range (0.16 to 0.34) observed for four different pine species growing in the Iberian peninsula (Richter et al. 1991) and for two stands of *P. sylvestris* growing on the Central Mountains System in Spain (MS from 0.13 to 0.20; Fernández et al. 1996).

Expressed population signal (EPS) values were higher than 0.85, which suggests that the chronologies describe well enough the infinite, hypothetical population of *P. sylvestris* at each sampling site (Wigley et al. 1984). High signal-to-noise ratio (SNR) values suggest that the proportion

of explainable variation due to climate or other causal factors is high enough for all the sampling sites. The first eigenvector variance indicated good homogeneity within each site, which is comparable to the 35 to 64% values calculated for four pines species in Spain (Richter et al. 1991).

The association between growth and climate shows that rainfall in the growing season had a significant positive effect on radial growth at all sites, no matter of the altitudinal location, geographical position or cambial age. Rainfall had different effects on growth within the growing season: at sites located at the lowest altitudinal positions (*Miñon*, *Oña* and *Arauzo de Miel*), a positive effect was observed in spring (May and June), in contrast with sites located at a higher altitudinal positions where the positive association occurred in late spring and early summer [June and July (*El Espinar* site)] and in summer [July and August (*Molino Piqueras* and *Amogable* sites)]. These differences may be due to temperature. Sites located at the lowest altitudinal positions are warmer, the growing season starts early, and thus spring rainfall is a driving factor that affects growth. However, sites located at the highest altitudinal position are colder, the growing season starts later and growth depends on summer rainfall. These results indicated the importance of the within-season precipitation dynamics, which may be as or more important than the seasonal or annual total for plant growth (Fay et al. 2000, Knapp et al. 2002).

These results also complement those of previous studies that highlighted the essential effect of precipitation on radial growth of different pine species growing in the Iberian Peninsula under Mediterranean climatic conditions, such as, for example, *Pinus nigra* Arnold, *P. halepensis* Mill. and *P. pinaster* Ait. (Génova 1994, Fernández et al. 1996, Raventós et al. 2001, Martín-Benito et al. 2008, Bogino and Bravo 2008).

Previous studies in Spain suggest that both, the decrease in rainfall and the increase in mean temperature must be considered as the most important factors that affect growth of the Scots pine (Gutiérrez 1989); previous studies on four pine species, including *P. sylvestris*, analysed together also showed the positive impact of winter temperatures (December and February) on radial growth (Richter et al. 1991). Moreover, a study in the Central

Pyrenees corresponding to the period 1952–1993 also indicated the positive impact of temperatures (in November and in May) on radial growth of *P. sylvestris* (Tardif et al. 2002). In this study, rainfall was found to be important at all sites analysed, but the effect of temperature varied depending on the site considered: from positive in the winter prior to the growing season (*Miñón, Oña, Molino Piqueras* and *Amogable* sites) to negative in the autumn prior to the growing season (*Miñón, Oña, Molino Piqueras* and *Amogable* sites) as well as in the summer in the growing season (*El Espinar* and *Amogable* sites). It was thus concluded that the local growth pattern of this species is the result of a changing association with mean temperature, which varies according to the site analysed. Previous studies suggest that species growing in temperate areas (Tessier et al. 1994, Dittmar et al. 2003, Pederson et al. 2004) do not show a common response to climatic variables, and that the response of *P. sylvestris* in Spain to climatic variables varies depending on the sampling site (Gutierrez 1989).

The age-dependent response to climate indicate that young stands have higher variability explained by climatic variables than old stands. Ecophysiological changes related to tree age indicated a reduction in photosynthesis and in stomatal conductance, changes in leaf structure and in canopy structure (Bond 2002, Bond and Franklin 2002), which may imply a variable association between radial growth and climate according to age. A study of *Pinus ponderosa* Douglas ex. C. Lawson in Oregon showed that as trees become older, the water storage capacity in the stems increases, which provides a buffer against short-term water stress (Anthoni et al. 2002) and may imply, as in the present study, a lower vulnerability to climatic conditions in old trees.

The significant association between radial growth and DRI in the growing season suggests that this index is an accurate tool for predicting restrictions in radial growth of *P. sylvestris*. The DRI provides accurate estimates of growth restrictions and mortality of *P. sylvestris* and has been applied in Switzerland, with a similar correlation coefficient as in the present sampling sites (Bigler et al. 2006).

Estimation of the impact of drought events on growth of *P. sylvestris* becomes important consid-

ering that previous studies in Spain demonstrated that among all pine species, *P. sylvestris* displays the highest mortality rate under severe droughts (Martínez-Vilalta and Piñol 2002), and that in Switzerland drought processes are considered as a major factor in death of *P. sylvestris* (Eilmann et al. 2006). Considering the predicted higher variability in precipitation in the future and that the mean annual temperature has increased by 1.6 °C in the last century in the Iberian Peninsula (IPCC 2007), the applications of these results in models to predict future growth may be essential to corroborate the forecast of climate change, which suggest that Spain could be one of the areas most vulnerable to species loss due to climatic variability (Bakkenes et al. 2002).

5 Conclusion

The relationship between climate and radial growth of *Pinus sylvestris* varied depending on the climatic variable analysed: rainfall in the growing season was the main climatic variable that determined growth at all the sites analysed, while the association with temperature varied depending on the site, and was positive or negative. The relationship between cambial age and climate suggests the importance of considering this variable during analysis of the relationship between growth and climate. Drought was found to be a determining factor for tree growth and should be considered in models that forecast the impact of climate change in Mediterranean environments.

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References

- Andreu, L., Gutiérrez, E., Macías, M., Ribas, M., Bosch, O. & Camarero, J. 2007. Climate increases regional tree-growth variability in Iberian pine forest. *Global Change Biology* 13: 804–815.
- Bakkenes, M., Alkemade, J.R.M., Ihle, F., Leemans, R. & Latour, J.B. 2002. Assessing effects of forecasted climate change on the diversity and distribution of European higher plants for 2050. *Global Change Biology* 8: 390–407.
- Barbéro, M., Loisel, R. & Quezel, P. 1998. Pines of the Mediterranean Basin. In: Richardson D.M. (ed.). *Ecology and biogeography of Pinus*. Cambridge University Press, Cambridge, UK. p. 153–170.
- Bigler, C., Ulrich Bräker, O., Bugmann, H., Dobbertin, M. & Rigling, A. 2006. Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. *Ecosystems* 9: 330–343.
- Blanco, E., Casado, M., Costa, M., Escribano, R., García Antón, M., Génova, M., Gómez Manzanque, G., Gómez Manzanque, F., Moreno, J., Morla, C., Regato, P. & Sainz Ollero, H. 1997. *Los bosques ibéricos*. Editorial Planeta, Barcelona, España.
- Box, G.E.P. & Jenkins, G.M. 1976. *Time series analysis, forecasting and control*. Revised edn. Holden-Day, San Francisco, CA.
- Bogino, S. & Bravo, F. 2008. Growth response of *Pinus pinaster* Ait. to climatic variables in central Spanish forests. *Annals of Forest Sciences* 65: 506–518.
- Bond, B. 2000. Age-related changes in photosynthesis of woody plants. *Trends in Plant Science* 5: 349–353.
- & Franklin, J. 2002. Aging in Pacific Northwest forests: a selection of recent research. *Tree Physiology* 22: 73–76.
- Briffa, K.R. 1995. Interpreting high-resolution proxy climate data—the example of dendroclimatology. In: von Storch, H. & Navarra, A. (eds.). *Analysis of climate data variability, application of statistical techniques*. New York, Springer. p.77–94.
- Carrer, M. & Urbinatti, C. 2004. Age-dependent tree-ring growth responses to climate in *Larix decidua* and *Pinus cembra*. *Ecology* 85: 730–740.
- Catalán, G. 1991. Las regiones de procedencia de *Pinus sylvestris* L. y *Pinus nigra* Arn. Subsp. *Salzmannii* (Dunal) Franco en España. ICONA, Madrid.
- Chesson, P., Gebauer, R., Schwinning, S., Huntly, N., Wiegand, K., Ernest, M., Sher, A., Novoplansky, A. & Weltzin, J. 2004. Resource pulses, species interactions and diversity maintenance in arid and semi-arid environments. *Oecologia* 141: 236–253.
- Colenutt, M. & Luckman, B. 1991. The dendrochronological characteristics of alpine larch. *Canadian Journal of Forest Research* 25: 777–789.
- Cook, E.R. & Holmes, R.L. 1984. Program ARSTAN users manual. Laboratory of Tree Ring Research, University of Arizona, Tucson, Arizona, USA.
- & Kairiukstis, L.A. 1990. *Methods of dendrochronology: applications in the environmental sciences*. Kluwer, Dordrecht.
- & Peters, K. 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring Bulletin* 41: 45–53.
- Cook, E., Briffa, K., Shiyatov, S. & Mazepa, V. 1990. Tree-ring standardization and growth-trend estimation. In: Cook E., Kairiukstis L. (eds.). *Methods of dendrochronology: applications in the environmental sciences*. Kluwer Academic Publishers, Dordrecht. p. 104–132.
- Di Rienzo, J., Balzarini, M., Casanoves, F., González, L., Tablada, E. & Robledo, C. 2002. Infostat software estadístico versión 2. Grupo infoStat, FCA, Universidad Nacional de Córdoba, Argentina.
- Dittmar, C., Zech, W. & Elling, W. 2003. Growth variations of common beech (*Fagus sylvatica* L.) under different climatic and environmental conditions in Europe – a dendroecological study. *Forest Ecology and Management* 173: 63–78.
- Easterling, D.R., Meehl, G.A., Parmesan, C., Changnon, S.A., Karl, T.R. & Mearns, L.O. 2000. Climate extremes: observation, modelling, and impact. *Science* 289: 2068–2074.
- Fay, P.A., Carlisle, J.D., Knapp, A.K., Blair, J.M. & Collins, S.L. 2000. Altering rainfall timing and quantity in a mesic grassland ecosystem: design and performance of rainfall manipulation shelters.

- Ecosystems 3: 308–319.
- Fernández, A., Génova, M., Creus, J. & Gutiérrez, E. 1996. Dendroclimatological investigation covering the last 300 years in Central Spain. Tree rings, environments and humanity. Dean J., Meko, D. & Swetnam, T. (eds.). *Radiocarbon*. p 181–190.
- Fritts, H.C. 1976. *Tree ring and climate*. Academic Press Inc, London.
- 1999. PRECON version 5.17. [Online document]. Available at: <http://www.ltr.arizona.edu/webhome/hal/dlprecon.html>.
- & Swetnam, T. 1989. Dendroecology: a tool for evaluating variations in past and present forest environments. *Advances in Ecological Research* 19: 111–188.
- Génova, M. 1994. Dendroecología de *Pinus nigra* Arnold subsp. *salzmannii* (Dunal) Franco y *Pinus sylvestris* L. en el Sistema Central y en la serranía de Cuenca (España). Tesis doctoral. Departamento de Biología, Universidad Autónoma de Madrid.
- Goldberg, D. & Novoplansky, A. 1997. On the relative importance of competition in unproductive environments. *Journal of Ecology* 85: 409–418.
- Grissino-Mayer, H.D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Research* 57: 205–221.
- Gutiérrez, E. 1989. Dendroclimatological study of *Pinus sylvestris* L. in southern Catalonia (Spain). *Tree-ring Bulletin* 49: 1–9.
- 1990. Dendroecología de *Pinus sylvestris* L. en Catalonia. *Orsis* 5: 23–41.
- Holmes, R.L. 1983. Computer-assisted quality control in tree-ring dating and measurement. *Tree-ring Bulletin* 43: 69–78.
- 2001. Dendrochronology program library. Available from the Laboratory of Tree-ring Research, University of Arizona, Tucson, USA.
- IPCC. 2007. Fourth assessment report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Jobbágy, E. & Sala, O. 2000. Controls of grass and shrub aboveground production in the Patagonian steppe. *Ecological Applications* 10: 541–549.
- Knapp, A.K., Fay, P.A., Blair, J.M., Collins, S.L., Smith, M.D., Carlisle, J.D., Harper, C.W., Danner, B.T., Lett, M.S. & Mc Carron, J.K. 2002. Rainfall variability, carbon cycling, and plant species diversity in a mesic grassland. *Science* 298: 2202–2205.
- Martín Benito, D., Cherubini, P., del Río, M. & Cañellas, I. 2008. Growth response to climate and drought in *Pinus nigra* Arn. trees of different crown classes. *Trees* 22: 263–273.
- Martínez-Vilalta, J. & Piñol, J. 2002. Drought-induced mortality and hydraulic architecture in pine populations of the NE Iberian Peninsula. *Forest Ecology and Management* 161: 247–256.
- Montero, G., del Río, M., Roig, S. & Rojo, A. 2008. Silvicultura de *Pinus sylvestris* L. In: Serrada, R., Montero, G. & Reque, J. (eds.). *Compendio de Silvicultura Aplicada en España*. INIA, Ministerio de Educación y Ciencia, España. p. 503–534.
- Mooney, H. & Dunn, L. 1970. Convergent Evolution of Mediterranean-Climate evergreen sclerophyll shrubs. *Evolution* 2: 292–303.
- Mooney, C.Z. & Duval, R.D. 1993. Bootstrapping: a nonparametric approach to statistical inference. Sage University Paper Series on Quantitative Applications in the Social Sciences, 07-095. Sage, Newbury Park.
- Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annual Review in Ecology and Systematics* 4: 25–41.
- Oesterheld, M., Loreti, J., Semmartin, M. & Sala, O. 2001. Inter-annual variation in primary production of a semi-arid grassland related to previous-year production. *Journal of Vegetation Science* 12: 137–141.
- Pederson, N., Cook, E., Jacoby, G., Peteet, D. & Griffin, K. 2004. The influence of winter temperature on the annual radial growth of six northern range margin tree species. *Dendrochronologia* 22: 7–29.
- Peterson, D.W. & Peterson, D.L. 1994. Effects of climate on radial growth of subalpine conifers in the North Cascade Mountains. *Canadian Journal of Forest Research* 24: 1921–1932.
- Peñuelas, J., Lloret, F. & Montoya, R. 2001. Severe drought effects on Mediterranean Woody Flora in Spain. *Forest Science* 47: 214–218.
- Raventós, J., De Luís, M., Gras, M., Cufar, K., González-Hidalgo, J., Bonet, A. & Sánchez, J. 2001. Growth of *Pinus pinea* and *Pinus halepensis* as affected by dryness, marine spray and land use changes in a Mediterranean semiarid ecosystem. *Dendrochronologia* 19: 211–220.
- Regent Instrument Inc. 2002. Windendro™ v.2002a. Québec, Qc.
- Richter, K., Eckstein, D. & Holmes, R.L. 1991. The dendrochronological signal of pine trees (*Pinus*

- spp.) in Spain. *Tree-Ring Bulletin* 51: 1–13.
- Schweingruber, F. 1996. *Tree rings and environment: dendroecology*. Haupt, Berne.
- Schwinning, S., Sala, O., Loik, M. & Ehleringer, J. 2004. Thresholds, memory, and seasonality: understanding pulse dynamics in arid/semi-arid ecosystems. *Oecologia* 141: 191–193.
- Sher, A., Goldberg, D. & Novoplansky, A. 2004. The effect of mean and variance in resource supply on survival of annuals from Mediterranean and desert environments. *Oecologia* 141: 353–362.
- Sokal, R.R. & Rohlf, F.J. 1995. *Biometry: the principles and practice of statistics in biological research*. 3rd ed. WH Freeman and Co., New York, UEA.
- Stokes, M. & Smiley, T. 1968. *An introduction to tree-ring dating*. University of Arizona Press, Tucson, UEA.
- Tardif, J., Camarero, J., Ribas, M. & Gutiérrez, E. 2002. Spatiotemporal variability in tree growth in the central Pyrenees: climatic and site influences. *Ecological Monographs* 73: 241–257.
- Tessier, L., Nola, P. & Serre-Bachet, F. 1994. Deciduous *Quercus* in the Mediterranean region: tree ring/climate relationship. *New Phytologist* 126: 355–357.
- , Guibal, F. & Schweingruber, F. 1997. Research strategies in dendroecology and dendroclimatology in mountain environments. *Climate Change* 36: 499–517.
- Thornthwaite, C.W. 1948. An approach toward a rational classification of climate. *Geographical Review* 38: 55–94.
- Wigley, T.M.L., Briffa, K.R. & Jones, P.D. 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology* 23: 201–213.

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