

Growth response to climate and drought in *Pinus nigra* Arn. trees of different crown classes

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Abstract Tree-ring chronologies were examined to investigate the influence of climate on radial growth of *Pinus nigra* in southeastern Spain. We addressed whether drought differentially affected the ring-widths of dominant and suppressed trees and if our results supported the hypothesis that, in a Mediterranean climate, suppressed conifer trees suffer greater growth reductions than dominant trees. Climate–growth relationships were analyzed using response and correlation functions, whereas the effect of drought on trees growth was approached by superposed epoch analysis in 10 dry years. A cool, wet autumn and spring, and/or mild winter enhanced radial growth. Latewood was the most sensitive ring section in both kinds of trees and it was primarily influenced by current year precipitations. Earlywood was mostly influenced by climatic conditions previous to the growing season. In general, May was the most influential month. *Pinus nigra* was shown to be very drought sensitive tree in the study area. Tree-rings in suppressed trees showed lower growth reductions caused by drought than those of dominant trees. However, dominant trees recovered normal growth faster. Dominant trees showed a more plastic response, and suppression appeared to reduce the effect of climate on tree radial growth. Some possible causes for

these effects are discussed. Our results support the essential role of the balance between light and moisture limitations for plant development during droughts and show that it is not appropriate to generalize about the way in which suppression affects climate–growth relationship in conifers.

Keywords Black pine · Dendroecology · Tree suppression · Intraspecific competition · Southeastern Spain

Introduction

In ecosystems under Mediterranean climate, drought is the most important factor limiting tree growth and productivity (Specht 1981). Annually recurrent summer drought of variable duration, following a wet, cool season, is a characteristic trait of Mediterranean climate in the Iberian Peninsula. Climate change models for southeastern Mediterranean Spain predict a decrease in annual mean precipitation between 6 and 14% (Sumner et al. 2003). Additionally, IPCC (2007) predicts an increase in temperature for these areas in the next century. With these factors combined, the frequency of extreme droughts may increase in the future, which could lead to a reduction of forest productivity and changes in species composition. Alternate dry and wet periods (Rodrigo et al. 1999) producing cyclical droughts lasting several years, represent a distinctive character in this climatic region and might influence the response of tree growth to drought.

In forest stands, trees of different crown classes compete for light, water, and other resources and are also affected by many non-climatic variables. Dominant trees are exposed to higher direct solar radiation, vapor pressure deficit and wind velocity than suppressed trees (Kimmins

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1997). Results on how water stress affects growth of trees in different crown classes in deciduous species are not conclusive (He et al. 2005; Liu and Muller 1993; Orwig and Abrams 1997). In coniferous forests, the results are more consistent. For example, in *Pinus strobus* L. (Vose and Swank 1994), *Picea abies* L. (van den Brakel and Visser 1996), and *Pinus sylvestris* L. (Pichler and Oberhuber 2007), understory trees experience greater growth reductions during droughts than overstory trees.

Several dendroecological studies in Spain (e.g., Fernández et al. 1996; Richter et al. 1991) have focused on *Pinus nigra* Arn (black pine). In France, *P. nigra* ssp. *laricio* has been found to be a drought-sensitive species, and climate change might induce forest growth decline for the species in the future (Lebourgeois 2000). Black pine is very widely distributed and is one of the most commonly used pines in large plantations all over the Mediterranean region. This makes it very susceptible to the increase in temperature and decrease in precipitation already observed for the region (Rodrigo et al. 1999) and predicted by climate change models (Sumner et al. 2003).

Understanding how forest growth responds to drought is a key element for a deeper understanding of forest dynamics in a new environment. Increasing knowledge about the response of tree growth to climate, especially during periods of drought, is an essential step in the integration of climate variables into real sustainable management plans for forest ecosystems. Thus, our study focuses on the response of radial growth in black pine to climate in the most southeasterly part of its distribution area in Spain. For this purpose, we apply dendroecological methods commonly used to analyze climate-growth relationships and the effect of drought on tree growth (e.g., Cook and Jacoby 1977; Orwig and Abrams 1997). Instead of studying these effects on isolated trees, which would be more responsive to climate (Fritts 1976), this study is focused on black pine stands, which better represent the populations of the region. Additionally, we analyze the way in which drought affects radial growth of trees of different social status (dominant and suppressed). We hypothesize that *P. nigra* should behave in a similar way to

other coniferous species found in the literature and show greater growth reductions in suppressed trees than in the dominant trees.

Material and methods

Study sites

The study sites are located in the Cazorla Mountain Range in southeastern Spain. Forests made up of Mediterranean pines (*P. nigra*, *P. halepensis* Mill., and *P. pinaster* Ait.) cover most of the area where altitude ranges from 600 to 2,107 m a.s.l. The main soil types in the region are based on a dolomite and calcareous bedrock (Sanchez-Palomares et al. 1990). These substrates and the Mediterranean climate of distinct wet and dry seasons create leptosols (rendzinas) on higher slopes, and luvisols on flat terrain with alluvial and colluvial deposits (Sanchez-Palomares et al. 1990; FAO 2006).

In 1964, a network of permanent plots was established by INIA (Spanish National Institute of Agricultural Research) across the natural distribution area of black pine in Spain. These permanent plots have been inventoried eight times since the year of establishment. In each inventory, the diameter at breast height (DBH) of all trees was measured. The height of the 100 largest-diameter trees per hectare and of a subsample of trees in each diameter class in each plot was also measured. Stand characteristics in the last inventory are presented in Table 1. The dominant height is defined as the mean height of the 100 trees with larger DBH per hectare (Assmann 1970).

Plots were even aged and located in well-stocked stands where trees originated from natural regeneration. Altitude of the sites was 1,110–1,475 m a.s.l. and all exposures were represented. The slope in the stands ranged from flat to 30°, most of them having an intermediate to high slope. Woody understory vegetation in most cases was scarce and mainly composed of *Cistus* ssp., *Juniperus communis* L., and *Quercus faginea* Lam.

Table 1 Stand characteristics for the study plots

	Plot	Mean age (years)	Area (m ²)	No. trees/ha	Hm (m)	Ho (m)	Dm (cm)	BA (m ² /ha)
	1	86	2,500	952	21	23	29	67
	2	173	2,500	164	29	30	54	39
	3	162	2,500	304	22	25	37	36
	4	98	2,000	535	20	23	38	64
<i>Hm</i> Mean tree height,	14	103	1,000	670	24	26	34	63
<i>Ho</i> dominant tree height, <i>Dm</i>	18	95	1,200	675	22	26	31	58
mean diameter at breast height,	20	99	2,000	380	23	25	41	51
<i>BA</i> basal area								

Climate data

Daily maximum and minimum temperatures (°C) and precipitation (mm) were collected from the meteorological station at Santiago de la Espada (Jaén) (38°06'N, 02°33'W, 1,340 m a.s.l.) located approximately 25 km from sampling sites. The climate of the area is Mediterranean subnemoral with Atlantic influence, particularly favorable for sclerophyllous forests (Allué-Andrade 1990). For the period considered, between 1940 and 2005, mean annual temperature was 12.9°C, with possible frost from November to April. Absolute maximum and minimum temperatures were 40 and −22°C. Precipitation (annual mean of 730 mm) showed a winter maximum and summer drought that in the area lasted an average of 3–4 months, between June and September (Fig. 1).

Dendroecological analyses

In June 2006, 15–16 trees from each social status, i.e. crown class (dominant and suppressed), were sampled from each plot. In plot J02, only dominant trees were sampled since no suppressed trees were present. Dominant trees were defined as those within each plot that had the largest DBH during the eight inventories (1964–2006), and suppressed trees as those with the smallest DBH in the last inventory. For each tree, two cores were taken from the upper slope side at a 120° angle from each other, to avoid reaction wood.

Applying a standard procedure, cores were mounted to grooved boards and sanded with three different grits. Widths of three tree-ring sections (i.e. total ring (TR), earlywood (EW) and latewood (LW)) were measured to the

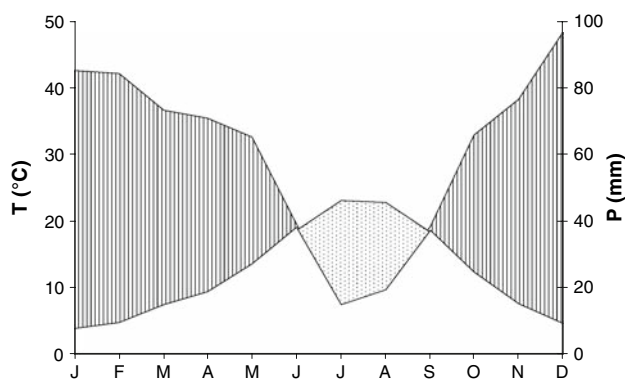


Fig. 1 Climate diagram for the Santiago de la Espada meteorological station (38°06'N, 2°33'W, 1,340 m a.s.l.) for the period 1940–2005. Mean temperature = 12.9°C, mean annual precipitation = 730 mm. The diagram describes the arid season (precipitation $< 2 \times$ temperature, dotted area), and humid season (precipitation $> 2 \times$ temperature, area with vertical lines)

nearest 0.01 mm with a measuring table and registered in a computer using TSAP (Rinn 1996). Qualitative visual aspects (darkening and tracheid size) were used to define transition from EW to LW.

After plotting the single curves, raw ring-width series were visually cross-dated. They were later statistically cross-dated with TSAP by the *Gleichläufigkeit* (sum of equal slopes intervals in percentage), *t*-values (determines the correlation between the curves) and the cross-date index (CDI), which is a combination of both. Those cores in which correct cross-dating was not possible were removed from further analysis.

Several statistics commonly used in dendrochronology were calculated from the raw ring-width data (before standardization) for each tree using ARSTAN (Cook and Holmes 1984), and later averaged per plot. Mean sensitivity (MS) measures the relative difference from one tree-ring to the next and thus the year to year variation, whereas first order autocorrelation coefficients (AC) reflect the way in which the previous years growth influences current year growth (Fritts 1976), and mean interseries correlation (\bar{R}) as a measure of the between-tree signal (Briffa and Jones 1990). In addition, expressed population signal (EPS) was calculated to assure that chronologies, especially those of suppressed trees, correctly portrayed the hypothetical perfect chronology (Wigley et al. 1984).

To remove age-related growth trends, individual series were detrended with ARSTAN using a spline function with a 50% frequency response of 32 years (Fritts 1976). Such a flexible spline was necessary to detrend the suppressed trees, which in many cases showed competition as well as abrupt release events (Blasing et al. 1983). Dimensionless ring width indices (RWI) were computed by dividing the observed raw ring-width value by the value of the fitted spline. To obtain residual chronologies, autocorrelation was removed using autoregressive (AR) models of specific order for each individual series. A robust estimation of the mean was used to compute chronologies for each plot. Social status residual chronologies were later averaged with a robust estimation of the mean since the high cross-correlation among cores and mean inter-series correlation supported it. These crown class chronologies were used for further dendroclimatic analysis.

Mean monthly temperature and total monthly precipitation (predictor variables) were regressed against ring-width indices to assess climate-growth relationships (Fritts 1976). Correlation and response function were calculated with DENDROCLIM2002 (Biondi and Waikul 2004), which uses bootstrapped error estimates (Guiot 1991). The first function computes simple Pearson correlation coefficients. In the second one, coefficients are estimates obtained by multivariate technique of principal components that allows the use of correlated independent

variables (multicollinearity) and produces reliable regression coefficients (Fritts 1976; Briffa and Cook 1990).

The nonparametric technique of superposed epoch analysis (SEA) can be used to assess the relationship between extreme climatic events (key events) and a strength of the response in the corresponding year (key response) (Haurwitz and Brier 1981). In this case, drought years were defined as key events and tree growth indices as key responses. Centered in the year of the drought, 5 years before and 5 years after were taken as background years for comparison. In this paper, drought is defined as an extraordinary departure from mean cool season (October to May) precipitation, lower than the mean by one standard deviation for the period 1940–2005, as opposed to summer drought, considered as the absence of precipitation during the warmer months of the year. The selected key years (drought) were 1942, 1943, 1945, 1950, 1953, 1967, 1968, 1981, 1995, and 1999 (Fig. 2). Although the year 2005 was the driest for the period, it was not considered for the SEA because there were not five post-drought years to compare with.

The differences between the ring-width index (RWI) of the three tree-ring sections of each core and their means were calculated and later averaged for event years and background years (Orwig and Abrams 1997). The *T* statistic as described by Haurwitz and Brier (1981) and modified by Prager and Hoening (1989) was used to test whether the RWI of the drought years differed significantly from pre- and post-drought years. These departures from the mean did not meet the general assumptions for normality so Monte Carlo randomizations were run in SAS (SAS Institute Inc. 2004) to select 10,000 sets of 11 years to compute confidence intervals for the *T*.

Raw ring width values during drought years were compared to the years before and after the drought to quantitatively analyze growth decreases and recoveries (Fekedulegn et al. 2003). Percent growth changes were calculated as follows:

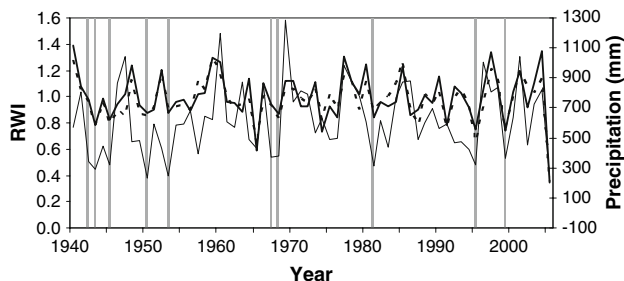


Fig. 2 Ring width index (RWI) of total ring width of dominant (solid thick line) and suppressed (dotted thick line) and Autumn to Spring precipitation (October of previous year to May of the current year; solid thin line) plotted against calendar year. Vertical bars indicate the ten drought years considered for superposed epoch analysis (SEA; see text for details)

- drought versus prior year: $[(D_0 - D_{-1})/D_{-1}] \times 100$,
- post-drought year versus pre-drought year: $[(D_{+1} - D_{-1})/D_{-1}] \times 100$,
- drought year versus 5 years pre-drought: $[(D_0 - D_{-5})/D_{-5}] \times 100$,
- 5 years post-drought versus drought year: $[(D_{+5} - D_0)/D_0] \times 100$, and
- 5 years post-drought versus 5 years pre-drought: $[(D_{+5} - D_{-5})/D_{-5}] \times 100$,

where D_0 is the raw ring width (RW) for any of the tree-ring sections the year of drought, D_{-1} is RW for the year prior to drought, D_{+1} is RW for the year after drought, D_{-5} is the average of RW for the 5 years prior to drought, and D_{+5} is the average of RW for the 5 years after drought. Analysis of variance for multiple comparisons was carried out using proc GLM in SAS (SAS Institute Inc 2004).

Results

The time span of the chronologies varied from 78 years for the suppressed trees in plot J01 to 233 years in dominant trees of plot J14 (Table 2). The high values of the mean interseries correlation (*Rbar*) suggested a good agreement between the individual series in a site chronology (Table 2). Thus, series from dominant trees and from suppressed trees were averaged into two separate general chronologies and used for further dendroclimatological analysis. The values for expressed population signal (EPS) were in all cases and for all years higher than 0.85 (data not shown). First order autocorrelation coefficients (AC) were lowest for LW (dominant mean = 0.56; suppressed mean = 0.61). Mean sensitivity (MS) in LW was higher (dominant mean = 0.41; suppressed mean = 0.39) than in EW (dominant mean = 0.29; suppressed mean = 0.34). TR and EW series of dominant trees were less sensitive (lower MS) than suppressed trees while the opposite was true for LW (Table 2).

Climatic influence on tree ring growth

Dominant and suppressed trees had a similar pattern in their TR growth response to climatic variables. In both cases, temperature had a fluctuating significant influence on TR growth, changing from negative to positive in different seasons (Fig. 3). Growth was negatively influenced by high temperatures in late-summer and early autumn of the previous year. Afterward, in late-fall and winter, higher temperatures promoted growth. High temperatures in the current spring and September again had a negative influence on growth, which was more pronounced in suppressed trees. However, current May temperature only had

Table 2 Chronology statistics in (a) dominant trees and (b) suppressed trees for each ring section (*TRW* total ring, *EW* earlywood, *LW* latewood) calculated in raw ring-width data before detrending

Plot	Altitude (m)	No. of trees	Chronology time-span (years)	TRW			EW			LW		
				Rbar	MS	AC	Rbar	MS	AC	Rbar	MS	AC
(a) Dominant trees												
J01	1,240	15	1919–2005 (87)	0.66	0.29	0.73	0.67	0.31	0.73	0.47	0.42	0.46
J02	1,100	15	1830–2005 (176)	0.47	0.27	0.80	0.50	0.28	0.79	0.33	0.38	0.63
J03	1,440	15	1806–2005 (200)	0.64	0.28	0.76	0.66	0.28	0.77	0.44	0.42	0.54
J04	1,475	16	1910–2005 (96)	0.60	0.31	0.70	0.59	0.33	0.68	0.47	0.46	0.49
J14	1,450	15	1773–2005 (233)	0.49	0.30	0.70	0.48	0.31	0.70	0.43	0.44	0.54
J18	1,295	15	1910–2005 (96)	0.41	0.24	0.71	0.54	0.27	0.69	0.24	0.32	0.59
J20	1,330	15	1906–2005 (100)	0.78	0.29	0.83	0.81	0.27	0.83	0.59	0.45	0.64
Mean	1,333	106	1773–2005 (233)	0.58	0.28	0.75	0.61	0.29	0.74	0.42	0.41	0.56
(b) Suppressed trees												
J01	1,240	16	1919–2005 (87)	0.61	0.29	0.77	0.67	0.32	0.77	0.29	0.36	0.54
J03	1,440	12	1842–2005 (164)	0.33	0.32	0.73	0.35	0.36	0.72	0.20	0.42	0.55
J04	1,475	15	1913–2005 (93)	0.61	0.31	0.81	0.59	0.35	0.77	0.41	0.40	0.66
J14	1,450	11	1897–2005 (109)	0.64	0.32	0.79	0.67	0.35	0.79	0.45	0.43	0.64
J18	1,295	12	1911–2005 (95)	0.78	0.28	0.81	0.82	0.34	0.79	0.49	0.35	0.68
J20	1,330	16	1907–2005 (99)	0.72	0.29	0.80	0.73	0.30	0.79	0.52	0.41	0.58
Mean	1,372	82	1842–2005 (164)	0.61	0.30	0.78	0.64	0.34	0.77	0.39	0.39	0.61

Rbar mean interseries autocorrelation, *MS* mean sensitivity, *AC* first-order serial autocorrelation coefficient

significant effects on suppressed trees. In both crown classes, growth was positively correlated with precipitation during the late autumn and winter of the previous year (Fig. 3) and precipitation in the current spring, with suppressed trees showing higher correlations.

The influence of temperatures in EW growth followed a fluctuating pattern for the seasons similar to that observed for TR growth. For this tree-ring section, temperatures of previous autumn months correlated negatively with tree growth. High winter temperatures produced a positive influence on the growth of trees in both social statuses. However, current spring temperatures were only significant for suppressed trees (Fig. 3). EW of dominant trees showed higher positive correlations with precipitation of previous autumn than suppressed trees, but both were influenced by the current May temperatures.

LW was the tree-ring section, where growth response to temperature differed most between different crown classes. Suppressed trees showed negative correlations with temperatures in spring–summer while dominant trees were influenced by July alone. Precipitation in winter and current spring had a significant positive influence on growth in dominant and suppressed trees alike (Fig. 3).

When the response function coefficients were used, the climatic variables of fewer months appeared to have a significant influence on growth. Only May precipitation had a significant effect on all tree-ring sections of trees in both crown classes (Fig. 3). In addition, TR growth in

dominant trees was positively affected by March temperature. A warm December in the previous year enhanced growth of EW in both kinds of trees. Development of LW in both crown classes was positively influenced by autumn precipitation, whereas March temperature positively affected dominant trees only (Fig. 3).

Effect of drought on tree-ring growth

Response of radial growth to drought was clearly depicted by the SEA (Fig. 4). Significant reductions in growth were observed in TR and LW in trees of both competition classes. The reductions in radial growth were greater in dominant trees than in suppressed trees for all tree-ring sections (Table 3). However, both crown classes followed a similar pattern in the evolution of growth associated with drought and post-drought years. Among ring sections, radial increments in EW were significantly less affected than in the LW during drought years (Table 3). The magnitude of TR reductions was intermediate between those experienced by EW and LW, but significantly different from them (Fig. 4; Table 3). All tree-ring sections showed a recovery after the growth depression caused by drought (Table 3). One year after drought, LW had almost recovered normal growth (no significant reduction) while reductions in EW were similar to the previous year (Fig. 4). In fact, LW showed greater growth 1 year after

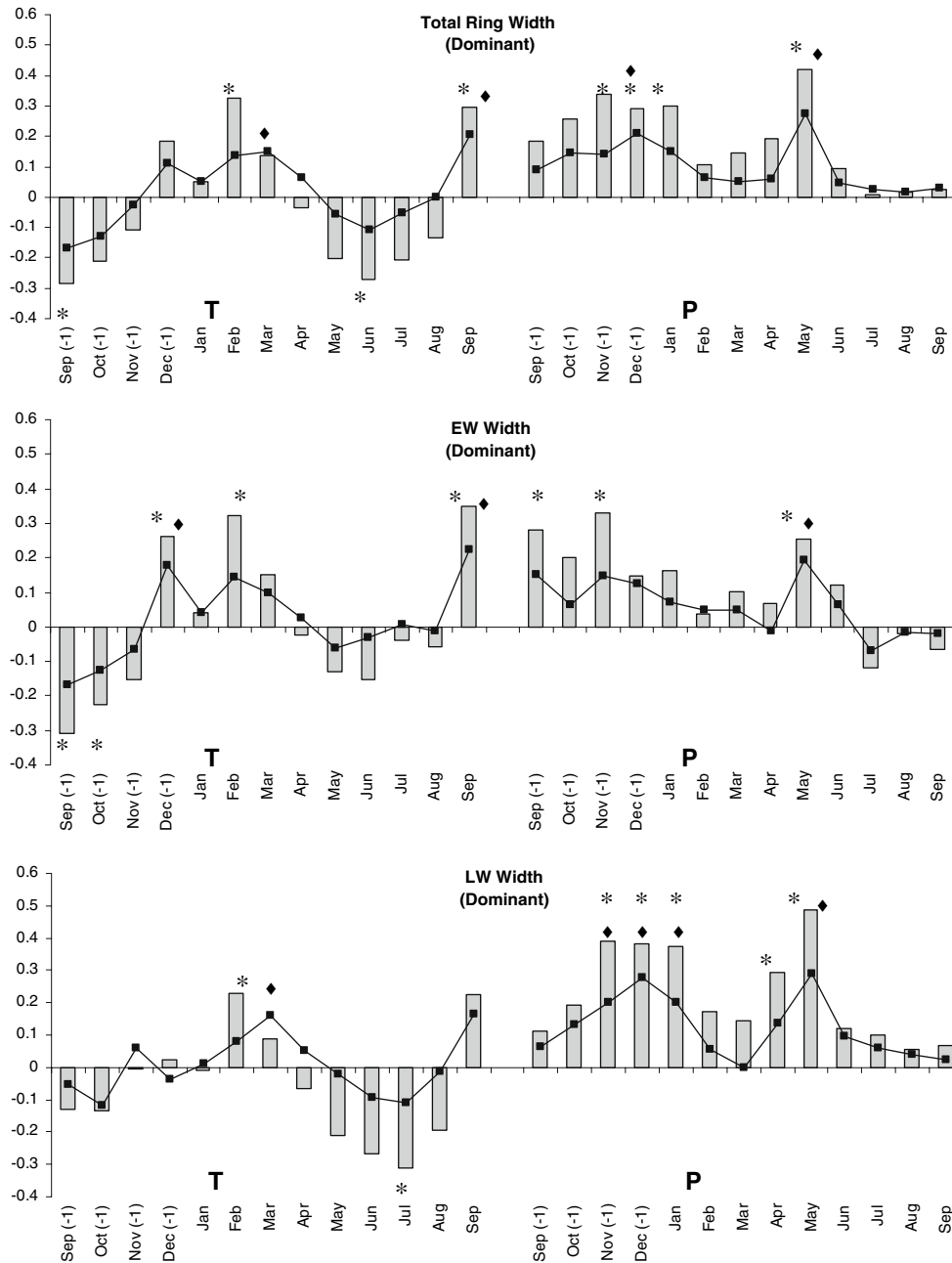


Fig. 3 Correlation (bars) and response (lines) functions for monthly temperatures (T) and precipitations (P) from previous September to September of the current year. Climate instrumental data and data for

each ring compartment are from the period 1940 to 2005; total of 66 years. Asterisks and diamonds denote significance ($P < 0.05$) of correlation and response functions, respectively

the drought than 1 year before, while EW still experienced radial growth reductions (Table 3).

Two years after the drought event, radial growth in all tree-ring sections had recovered to the level of pre-drought years (Fig. 4). This second year, LW even achieved a higher increase than in pre-drought years. When the 5 post-drought years were compared to the drought years, LW exhibited the greatest positive change growing 80 and 60%

faster in dominant and suppressed trees, respectively, and differences being significant between ring sections (Table 3). After the second post-drought year, growth departures fluctuated between positive and negative compared to the mean (Fig. 4). Nonetheless, growth in the 5 post-drought years was slightly but significantly higher (different from zero) than in pre-drought years except in the case of LW (Table 3).

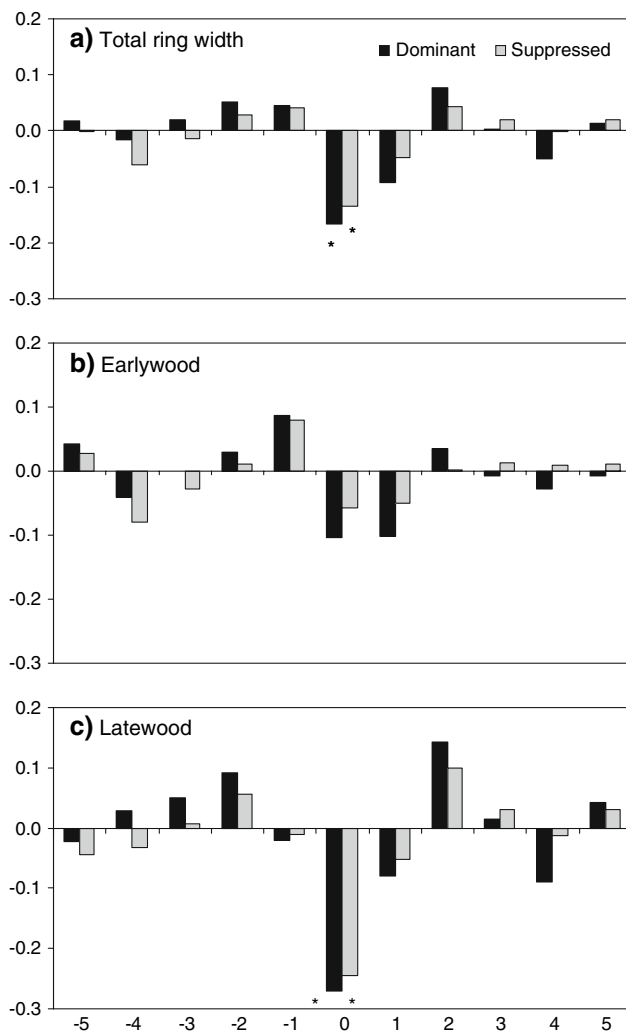


Fig. 4 Tree growth departures shown in the superposed epoch analysis for the drought years and 5 years before and after drought. Values were averaged for the ten drought events considered. Asterisks denote a departure greater than expected to occur by chance from 10,000 random simulations ($P < 0.005$)

Discussion

Dendroclimatological studies have indicated that black pine tree-ring growth at low elevations in France (Lebourgeois 2000), in some Alpine sites (Strumia et al. 1997), and in central mountain range of Spain (Fernández et al. 1996) is predominantly affected by summer temperature and precipitation. Our study showed a similar temperature–growth relationship, but a lack of correlation between precipitation in summer months and black pine radial growth (Fig. 3). These results indicate that whilst summer drought (absence of precipitation in the warmest months of the year) is very likely to affect radial growth, as in most Mediterranean species (Cherubini et al. 2003), it does not affect inter-annual variations of black-pine growth in the study area, except indirectly, by the influence of high temperatures on evapotranspiration. One reason could be that almost every year summer months are dry and there is little variation between the years. Furthermore, when summer precipitation occurs it is most often as erratic, brief storm events that might only affect a small part of the region and might not significantly influence soil water content (Cowling et al. 2005).

Chronologies of dominant and suppressed trees showed expressed population signals (EPS) above 0.85 (Wigley et al. 1984) and high values of mean sensitivity (MS; Table 2), which suggests that trees are responding to regional limitation factors such as climate and chronologies are useful for the study of climate–growth relationships (Fritts 1976). Radial growth of black pine in the study area was positively influenced by warm and wet autumn–winter, and cool rainy spring (Fig. 3). The timing of this influence, however, showed some variation depending on the tree-ring section analyzed. Wet and cool previous-year autumns and warm winters promoted growth of EW more significantly than precipitation in any month of the current year.

Table 3 Means \pm SE and relative changes ($\% \pm$ SE) in raw ring width in dominant (D) and suppressed (S) trees for each ring section

Ring section		Mean (mm)	Drought vs. prior year (%)	Post- vs. pre-drought (%)	Drought vs. 5 year pre-drought (%)	5 year post-drought vs. drought (%)	5 year post- vs. 5 year pre-drought (%)
TRW	D	1.69 \pm 0.01 a	−12.57 \pm 1.25 ab	−2.46 \pm 1.56 a	−20.10 \pm 0.70 a	28.49 \pm 1.28 a	4.80 \pm 0.84 a
	S	0.48 \pm 0.00 b	−9.65 \pm 1.59 ab	−0.53 \pm 1.88 a	−15.43 \pm 1.00 b	26.72 \pm 1.68 a	2.84 \pm 1.13 ab
EW	D	1.12 \pm 0.01 c	−7.49 \pm 1.38 bc	−6.19 \pm 1.65 a	−13.22 \pm 1.80 b	16.02 \pm 1.14 b	6.62 \pm 0.83 a
	S	0.32 \pm 0.00 d	−3.07 \pm 1.96 c	−2.27 \pm 2.20 a	−8.34 \pm 1.17 c	16.53 \pm 1.78 b	4.43 \pm 1.19 a
LW	D	0.56 \pm 0.00 e	−14.46 \pm 1.67 b	17.61 \pm 2.50 b	−30.32 \pm 1.87 d	80.43 \pm 2.98 c	−0.56 \pm 1.07 b
	S	0.16 \pm 0.00 f	−11.06 \pm 1.95 ab	14.49 \pm 2.59 b	−23.98 \pm 1.76 a	63.71 \pm 2.86 d	−0.95 \pm 1.46 b

TRW Total-ring, EW earlywood, LW latewood

Departures are pooled from the ten drought episodes considered. Means in a column with the same letter are not significantly different at $P < 0.005$. See text for relative changes calculations

Nonetheless, autumn-to-spring precipitation as well as low summer temperatures positively influenced LW increment (Fig. 3).

In both competition classes, MS and AC followed the same trend as shown by Lebourgeois (2000) for dominant black pines: MS increased and AC decreased from total-ring to EW to LW (Table 2). These results suggested that radial increments of this later tree-ring section were less affected by previous year growth (Levitt 1972; Fritts 1976) than by climate and its year-to-year variations. The soil water storage is recharged during the wet cold period (Fig. 1) starting from the upper soil horizons. During most years, the soil in spring is likely to have enough water to support tree growth. However, the soil water content later in the summer can vary greatly between wet and dry years. Black pine (Peñuelas and Filella 2003) and other Mediterranean species (Rambal 1984) display a gradual water uptake from upper to deeper soil layers as the soil dries out during the growing season. Thus, the variable water accumulation and the depth of the soil from which trees take the water in different seasons could reduce sensitivity to precipitation in EW and increase it in LW.

Enhancement of EW growth after cool rainy autumns suggests that carbohydrate accumulation and the size of the dormant cambial zone (formed during autumn) are important for following-years growth (e.g., Vaganov et al. 2006). Positive correlation with warm winters reflects the limiting effect of cold winter temperatures on photosynthesis of Mediterranean pines (Rathgeber et al. 2005). Contrastingly, current summer temperatures primarily influenced LW increments, as a more immediate reflection of its time of formation (Camarero et al. 1998). We found no clear reason for the significant influence of current-year September on the development of EW (formed in spring) suggesting the effect of statistical artifacts. Growth–climate relationships in this study are 1 month ahead of those of black pine in western France (Lebourgeois 2000), where TRW is primarily influenced by July temperature and June precipitation, whereas in southeastern Spain it appears to be June temperature and May precipitation that are most influential (Fig. 3).

Our results have shown that tree-ring growth shows a greater negative correlation with spring temperatures in suppressed than dominant trees (Fig. 3), which could be caused by the faster desiccation produced by high temperatures of the upper soil layers. Suppressed trees usually have less developed root systems and less moisture is available to them (e.g., Van Lear and Kapeluck 1995). In addition, trees under high competitive stress have a lower autotrophic-to-heterotrophic-tissue ratio than dominant trees (Naidu et al. 1998), and therefore respiration might almost exceed photosynthesis during periods with high temperature.

Suppression seemed to affect the MS of trees. Suppressed trees showed higher MS than dominant trees in TR and EW, and lower values in LW (Table 2). One explanation could be that dominant trees have a deeper root system and start to suffer water stress later in summer, when LW is formed. Our results of first-order autocorrelation (AC) indicated that the effect of prior growth on current growth was higher in suppressed trees than in dominant trees (Table 2). Growth-limiting factors for suppressed trees in a stand are not only climate or soil, but also root and crown competition (Kimmins 1997). These later factors remain fairly constant from one year to the next (except when thinning or cuts are applied) therefore similarly affecting radial growth in several consecutive years. In addition, longer longevity of the foliage of plants shaded (Nilsen et al. 1987) or under unfavorable conditions (Eckstein et al. 1999) could account for this effect on AC, but not in MS.

During very dry years, radial growth of all tree ring sections was significantly reduced in dominant and suppressed trees (Fig. 4) as previously observed in other conifers (e.g., Oberhuber 2001; Eilmann et al. 2006; Pichler and Oberhuber 2007). Periods of water stress alter the partitioning of newly fixed carbon in such a way that production of soluble leaf carbohydrates and starch breakdown are favored for osmotic adjustment (e.g., Chaves et al. 2003) and less carbon is diverted for growth. Also carbon allocation is modified to maintain root growth and improve water acquisition (Chaves et al. 2003). In addition, a greater proportion of the fixed carbon is lost through photorespiration during water stress (Wingler et al. 1999).

Growth regulators and hormones play an important role in drought-induced growth reductions. Water stressed plants show greater production of abscisic acid (ABA) (e.g., Xiong et al. 2002), which alters the plant morphology to reduce the loss of water. ABA is crucial in drought resistance of trees by, for example, triggering stomatal closing, which reduces photosynthetic activity (e.g., Lebourgeois et al. 1998) but increases the water use efficiency (Mansfield et al. 1990). ABA is also involved in reducing the size of conducting elements in the xylem by blocking the action of indole-3-acetic acid (IAA), which is responsible for tracheid expansion (Little and Savidge 1987). IAA production is in part related with the size of the crown in pines (Funada et al. 2001), which is in accordance with lower radial-growth in small crown trees. Higher ABA concentrations in the more stressed or suppressed plants (Aasamaa et al. 2004) might have rendered them drought hardened (Chandler and Robertson 1994), which could in part explain the lower response to drought observed in suppressed trees (Table 3). These smaller reductions are in accordance with earlier findings in several deciduous species (Liu and Muller 1993). However, our results are opposite to greater growth reductions found in understory

P. strobus (Vose and Swank 1994), *Picea abies* (van den Brakel and Visser 1996), and suppressed *P. sylvestris* (Pichler and Oberhuber 2007).

There is evidence that suppressed trees suffer greater drought stress because of greater root competition for soil moisture (Kloppel et al. 1993). However, it is also true that trees under the influence of neighboring crowns experience an environment that reduces transpiration (Bréda et al. 2006) such as lower direct solar radiation and wind velocity, and higher water vapor pressure (Kimmins 1997) so that effects of droughts and climate in general are buffered and climate sensitivity of understory trees reduced (Phipps 1982). Therefore, differences between our results and those of other studies in conifers (Vose and Swank 1994; van den Brakel and Visser 1996; Pichler and Oberhuber 2007) could be explained by assuming (1) a species-specific response to competition and drought because of different evolutionary history (Peñuelas et al. 2001), or (2) a differential plant–plant interactions to drought because of different environments (Pugnaire and Luque 2001; Pichler and Oberhuber 2007) where some canopy protection reduces water stress during drought in dry sites (Holmgren et al. 1997) but not in more humid ones. Such interactions between crown class and site (dry-mesic vs xeric) have previously been observed by Orwig and Abrams (1997), who also found that understory trees experienced greater growth reductions than dominant trees only in mesic sites. It remains essential to study the interactions of site type and crown class on the growth of black pine.

Despite the observed differential effects of drought between crown classes, the SEA depicted a common pattern of growth decrease during drought and higher post-drought growth compared to pre-drought growth (Fig. 4). A similar growth recovery trend in SEA for TRW of *Pinus virginiana* (Mill.) has been shown in dry sites, whereas in mesic sites trees exhibited prolonged post-drought reductions (Orwig and Abrams 1997). Therefore, our results add further evidence that conifers in xeric sites might be better adapted to water scarcity and stand drought episodes than those at mesic sites. Adaptations to drought may include: developing deeper roots or increasing the root to shoot ratio (e.g., Lloret et al. 1999), modifying the diameter of tracheids (e.g., Linton et al. 1998) or developing anatomic features in needles to reduce water loss (e.g., Grill et al. 2004).

Conclusions

Our results demonstrate that black pine individuals experience great growth reductions during severe drought episodes. Dominant trees showed a more plastic response,

reducing growth during the drought more than suppressed trees but also recovering faster afterward. In this same sense, growth in dominant trees was less affected by previous year growth experiencing lower growth inertia, and thus these trees were more sensitive to climate. All these facts suggest that it is not appropriate to draw a general conclusion on how competition modulates the effect of drought on the growth of coniferous trees of different social status (Pichler and Oberhuber 2007). All results point toward the essential role of the balance between light and moisture limitations for plant development during droughts (for a review see Callaway and Walker 1997).

If, as climate change models predict, rainfall concentrates more during autumn months (Sumner et al. 2001), it may lead to increased growth as has been shown in France for the species (Lebourgeois et al. 2000), since previous autumn precipitation was found to be critical for black pine growth. However, some models predict higher summer temperatures (IPCC 2007), which, as we have shown, reduce radial growth in *P. nigra*. The results of this study and those found in the literature (Orwig and Abrams 1997) suggest that conifers at xeric sites might be more adapted to water scarcity and withstand drought episodes better. Although whilst this may be true at the current frequency of drought events, it may not be the case if this frequency increases as a result of global changes in temperature and precipitation trends. Therefore, the balance of these two effects is likely to influence growth trends and species composition (Walther et al. 2002) in the light of climate change uncertainties.

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References

- Aasamaa K, Sober A, Hartung W, Niinemets Ü (2004) Drought acclimation of two deciduous tree species of different layers in a temperate forest canopy. *Trees* 18:93–101
- Allué-Andrade JL (1990) Atlas fitoclimatológico de España: taxonomías. MAPA-INIA. Madrid, Spain
- Assmann E (1970) The principles of forest yield study. Pergamon Press Ltd., Oxford, 506 pp
- Biondi F, Waikul K (2004) DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. *Comput Geosci* 30:303–311
- Blasing TJ, Duveck DN, Cook ER (1983) Filtering the effects of competition from ring-width series. *Tree Ring Bull* 43:19–30

- van den Brakel JA, Visser H (1996) The influence of environmental conditions on tree-ring series of Norway spruce for different canopy and vitality classes. *For Sci* 42:206–219
- Bréda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Ann For Sci* 63:625–644
- Briffa KR, Cook ER (1990) Methods of response function analysis. In: Cook ER, Kairiukstis LA (eds) *Methods of dendrochronology; applications in the environmental sciences*. Kluwer, Dordrecht, pp 240–247
- Briffa KR, Jones PD (1990) Basic Chronology Statistic and Assessment. In: Cook ER, Kairiukstis LA (eds) *Methods of dendrochronology; applications in the environmental sciences*. Kluwer, Dordrecht, pp 137–152
- Callaway RM, Walker LR (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* 78: 1958–1965
- Camarero JJ, Guerrero-Campo J, Gutiérrez E (1998) Tree ring growth and structure of *Pinus uncinata* and *Pinus sylvestris* in the central Spanish Pyrenees. *Artic Alpine Res* 30:1–10
- Chandler PM, Robertson M (1994) Gene expression regulated by abscisic acid and its relation to stress tolerance. *Annu Rev Plant Physiol Plant Mol Biol* 45:113–141
- Chaves MM, Maroco JP, Pereira JS (2003) Understanding plant responses to drought: from genes to the whole plant. *Funct Plant Biol* 30:239–264
- Cherubini P, Gartner BL, Tognetti R, Bräker OU, Schoch W, Innes JL (2003) Identification, measurement and interpretation of tree rings in woody species from mediterranean climates. *Biol Rev* 78:119–148
- Cook ER, Jacoby GC Jr (1977) Tree ring drought relationships in the Hudson Valley, NY. *Science* 198:399–401
- Cook ER, Holmes RL (1984) Users manual for program ARSTAN. Laboratory of Tree-Ring Research, Tucson
- Cowling RM, Ojeda F, Lamont BB, Rundel PW, Lechmere-Oertel R (2005) Rainfall reliability, a neglected factor in explaining convergence and divergence of plant traits in fire-prone mediterranean-climate ecosystems. *Global Ecol Biogeogr* 14:509–519
- Eckstein RL, Karlsson PS, Weih M (1999) Leaf life span and nutrient resorption as determinants of plant nutrient conservation in temperate-arctic regions. *New Phytol* 143:177–189
- Eilmann B, Weber P, Rigling A, Eckstein D (2006) Growth reactions of *Pinus sylvestris* L. and *Quercus pubescens* Willd. to drought years at a xeric site in Valais, Switzerland. *Dendrochronologia* 23:121–132
- FAO (2006) World reference base for soil resources (2006) Food and Agriculture Organization of the United Nations, Rome
- Fekedulegn D, Hicks RR Jr, Colbert JJ (2003) Influence of topographic aspect, precipitation and drought on radial growth of four major tree species in an Appalachian watershed. *For Ecol Manage* 177:409–425
- Fernández A, Génova M, Creus J, Gutiérrez E (1996) Dendroclimatology investigation covering the last 300 years in central Spain. In: Dean JS, Meko DM, Swetman TW (eds) *Tree rings, environment and humanity*. Radiocarbon. U. of Arizona, Tucson, pp 181–190
- Fritts HC (1976) *Tree rings and climate*. Academic Press, London
- Funada R, Kubo T, Tabuchi M, Sugiyama T, Fushitani M (2001) Seasonal variations in endogenous indole-3-acetic acid and abscisic acid in the cambial region of *Pinus densiflora* Sieb, et Zucc. stems in relation to earlywood-latewood transition and cessation of tracheid production. *Holzforschung* 55:128–134
- Grill D, Tausz M, Pöllinger U, Jiménez MS, Morales D (2004) Effects of drought on needle anatomy of *Pinus canariensis*. *Flora* 199:85–89
- Guiot J (1991) The bootstrapped response method. *Tree Ring Bull* 51:39–41
- Haurwitz MW, Brier GW (1981) A critique of the superposed epoch analysis method: its application to solar-weather relations. *Mon Weather Rev* 109:2074–2079
- He JS, Zhang QB, Bazzaz FA (2005) Differential drought responses between saplings and adult trees in four co-occurring species of New England. *Trees* 19:442–450
- Holmgren M, Scheffer M, Huston M (1997) The interplay of facilitation and competition in plant communities. *Ecology* 78:1966–1975
- IPCC (2007) *Climate change, fourth assessment report*. Cambridge University Press, London, UK (in press)
- Kimmins JP (1997) *Forest ecology*. Prentice Hall Inc, NJ, pp 596
- Kloeppel BD, Abrams MD, Kubiske ME (1993) Seasonal ecophysiology and leaf morphology of four successional Pennsylvania barrens species in open versus understory environments. *Can J For Res* 23: 181–189
- Lebourgeois F (2000) Climatic signals in earlywood, latewood and total ring width of Corsican pine from western France. *Ann For Sci* 57:155–164
- Lebourgeois F, Levy G, Aussenac G, Clerc B, Willm F (1998) Influence of soil drying on leaf water potential, photosynthesis, stomatal conductance and growth in two black pine varieties. *Ann For Sci* 55:287–299
- Lebourgeois F, Becker M, Chevalier R, Dupouey JL, Gilbert JM (2000) Height and radial growth trends of Corsican pine in western France. *Can J For Res* 30: 712–724
- Levitt L (1972) *Responses of plants to environmental stresses*. Academic Press, NY
- Linton MJ, Sperry JS, Williams DG (1998) Limits to water transport in *Juniperus osteosperma* and *Pinus edulis*: implications for drought tolerance and regulation of transpiration. *Funct Ecol* 12:906–911
- Little CHA, Savidge RA (1987) The role of plant growth regulators in forest tree cambial growth. *Plant Growth Regul* 6: 137–169
- Liu Y, Muller RN (1993) Effect of drought and frost on radial growth of overstory and understory stems in a deciduous forest. *Am Midl Nat* 129:19–25
- Lloret F, Casanovas C, Peñuelas J (1999) Seedling survival of Mediterranean shrubland species in relation to root:shoot ratio, seed size and water and nitrogen use. *Funct Ecol* 13:210–216
- Mansfield TA, Hetherington AM, Atkinson CJ (1990) Some current aspects of stomatal physiology. *Annu Rev Plant Physiol Plant Mol Biol* 41:55–75
- Naidu SL, Lucia EHD, Thomas RB (1998) Contrasting patterns of biomass allocation in dominant and suppressed loblolly pine. *Can J For Res* 28:1116–1124
- Nilsen ET, Sharifi MR, Rundel PW (1987) Leaf dynamics in an evergreen and a deciduous species with even-aged leaf cohorts, from different environments. *Am Midl Nat* 118:46–55
- Oberhuber W (2001) The role of climate in the mortality of Scots pine (*Pinus sylvestris* L.) exposed to soil dryness. *Dendrochronologia* 19:45–55
- Orwig DA, Abrams MD (1997) Variation in radial growth responses to drought among species, site, and canopy strata. *Trees* 11:474–484
- Peñuelas J, Filella I (2003) Deuterium labelling of roots provides evidence of deep water access and hydraulic lift by *Pinus nigra* in a Mediterranean forest of NE Spain. *Environ Exp Bot* 49:201–208
- Peñuelas J, Lloret F, Montoya R (2001) Severe drought effects on Mediterranean woody flora in Spain. *For Sci* 47:214–218
- Phipps RL (1982) Comments on interpretation of climatic information from tree rings, eastern North America. *Tree Ring Bull* 42:11–22

- Pichler P, Oberhuber W (2007) Radial growth response of coniferous forest trees in an inner Alpine environment to heat-wave in 2003. *For Ecol Manage* 242: 688–699
- Prager MH, Hoenig JM (1989) Superposed epoch analysis: a randomization test of environmental effects on recruitment with application to chub mackerel. *Trans Am Fish Soc* 118: 608–618
- Pugnaire FI, Luque MT (2001) Changes in plant interactions along a gradient of environmental stress. *Oikos* 93: 42–49
- Rambal S (1984) Water balance and pattern of root water uptake by a *Quercus coccifera* L. evergreen scrub. *Oecologia* 62: 18–25
- Rathgeber CBK, Misson L, Nicault A, Guiot J (2005) Bioclimatic model of tree radial growth: application to the French Mediterranean Aleppo pine forests. *Trees* 19:162–176
- Richter K, Eckstein D, Holmes RL (1991) The dendrochronological signal of pine trees (*Pinus* spp.) in Spain. *Tree Ring Bull* 51: 1–13
- Rinn F (1996) TSAP-reference manual. Frank Rinn, Heidelberg, Germany
- Rodrigo FS, Esteban-Parra MJ, Pozo-Vázquez D, Castro-Díez Y (1999) A 500-year precipitation record in Southern Spain. *Int J Climatol* 19:1233–1253
- Sánchez-Palomares O, Elena-Roselló R, Carretero-Carrero MP (1990) Caracterización de edáfica de los pinares autóctonos españoles de *Pinus nigra* Arn. Comunicaciones INIA. Serie: Recursos Naturales No 55. INIA, Madrid, Spain
- SAS Institute Inc (2004) SAS/STAT 9.1 user's guide. SAS Institute Inc. Cary, USA
- Specht RL (1981) Primary production in Mediterranean climate ecosystems regenerating after fire. In: Di Castri F, Goodall DW, Specht RL (eds) Mediterranean-type shrublands. Elsevier, Amsterdam, pp 257–267
- Strumia G, Wimmer R, Grabner M (1997) Dendroclimatic sensitivity of *Pinus nigra* Arnold in Austria. *Dendrochronologia* 15: 129–137
- Sumner GN, Homar V, Ramis C (2001) Precipitation seasonality in eastern and southern coastal Spain. *Int J Climatol* 21:219–247
- Sumner GN, Romero R, Homar V, Ramis C, Alonso S, Zorita E (2003) An estimate of the effects of climate change on the rainfall of Mediterranean Spain by the late twenty first century. *Clim Dyn* 20:789–805
- Vaganov EA, Hughes MK, Shaskin AV (2006) Growth dynamics of conifer tree rings- images of past and futures environments. Springer, Heidelberg
- Van Lear DH, Kapeluck PR (1995) Above- and below-stump biomass and nutrient content of a mature loblolly pine plantation. *Can J For Res* 25:361–367
- Vose JM, Swank WT (1994) Effects of long-term drought on the hydrology and growth of a white-pine plantation in the southern Appalachians. *For Ecol Manage* 64:25–39
- Walther GR, Post E, Convery P, Menzel A, Parmesan C, Beebee TJC, Fromentin JM, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. *Nature* 416:389–395
- Wigley TML, Briffa KR, Jones PD (1984) On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *J Appl Meteorol* 23:201–213
- Wingler A, Quick W, Bungard R, Bailey K, Lea P, Leegood R (1999) The role of photorespiration during drought stress: an analysis utilizing barley mutants with reduced activities of photorespiratory enzymes. *Plant Cell Environ* 22:361–373
- Xiong L, Schumaker KS, Zhu J-K (2002) Cell signaling during cold, drought, and salt stress. *Plant Cell* 14:S165–S183