Drought-induced growth decline of Aleppo and maritime pine forests in south-eastern Spain

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Abstract

Climate warming may enhance the negative effects of droughts on radial growth in areas with severe water deficit, such as Mediterranean mountains under semi-arid conditions. The impacts of drought on growth decline of Mediterranean pines have not been evaluated considering species with different vulnerability and areas with contrasting climates. Dendrochronological methods were used to assess the responses of basal area increment to drought in *Pinus pinaster* and *P. halepensis* plantations. We compared growth trends of trees with different defoliation degree in two sites in south-eastern Spain (Sierra de los Filabres and Sierra de Baza) with contrasting climatic conditions. In the more xeric area (Filabres) both pine species showed a sharp growth reduction in response to extreme droughts such as those observed in 1994-1995, 1999 and 2005. The radial growth of both species was enhanced by May and June precipitation of the year of tree-ring formation. *P. pinaster* showed higher defoliation in the xeric area (Filabres) than in the more mesic area (Baza) but needle loss was not linked to an abrupt growth reduction. Contrastingly, divergent radial growth patterns between trees showing high and low defoliation degrees were found for *P. halepensis* in the more xeric area, where a negative relationship between recent basal area increment and defoliation was found. Pine plantations in Mediterranean mountains under semi-arid conditions are highly vulnerable to warming-induced droughts. Such marginal stands constitute valuable monitoring systems to assess the negative impacts of drought on tree growth, and to test if management strategies as thinning can mitigate the negative impacts of climate warming on similar drought-stressed forests.

Key words: basal area increment; climate warming; dendroecology; drought index; Mediterranean forests; *Pinus;* tree-ring width.

Resumen

Decaimiento del crecimiento inducido por sequía en bosques de pino carrasco y pino negral del sudeste de España

El calentamiento climático puede aumentar los efectos negativos de la sequía sobre el crecimiento radial de especies arbóreas en zonas con un déficit hídrico elevado como es el caso de la montaña mediterránea semi-árida. Los impactos de la sequía sobre la disminución del crecimiento de las especies forestales mediterráneas no han sido evaluados considerando especies con distinta vulnerabilidad y zonas con diferentes condiciones climáticas. Se usaron métodos dendrocronológicos para evaluar las respuestas del incremento de área basimétrica a la sequía en repoblaciones de *Pinus pinaster* y *P. halepensis*. Se compararon las tendencias de crecimiento en árboles con diferente grado de defoliación en dos zonas cercanas del sureste de España (Sierra de los Filabres, Sierra de Baza) con climatología contrastada. En la zona más seca (Filabres) los árboles mostraron una mayor reducción del crecimiento radial en respuesta a las sequías extremas, como las observadas en 1994-1995, 1999 y 2005. El crecimiento de ambas especies respondió positivamente a la precipitación de mayo y junio del año de formación del anillo. Las poblaciones de *P. pinaster* en el área más seca (Filabres) mostraron una mayor defoliación que en la zona menos seca (Baza), pero dicha defoliación no estaba relacionada con una reducción abrupta del crecimiento. Por el contrario, encontramos una divergencia del

patrón de crecimiento entre árboles de alto y bajo grado de defoliación para *P. halepensis* en la zona más seca, donde se encontró una relación negativa entre el incremento de área basimétrica y la defoliación reciente. Las repoblaciones de pinos de las montañas mediterráneas en condiciones semiáridas son altamente vulnerables a sequías inducidas por el calentamiento climático. Estos bosques marginales constituyen un valioso sistema de seguimiento para evaluar los efectos negativos de las sequías sobre el crecimiento de los bosques y para evaluar si las estrategias de gestión como el aclareo pueden mitigar los impactos negativos del calentamiento climático sobre bosques similares sometidos a un severo déficit hídrico.

Palabras clave: incremento de área basimétrica; calentamiento climático; dendroecología; índice de sequía; bosques mediterráneos; *Pinus;* anchura del anillo de crecimiento.

Introduction

Forests are responding to climate warming through changes in growth and vigor thus acting as monitors of the effects of climate change on terrestrial ecosystems (Bonan, 2008). An increase in temperature and evapotranspiration and a greater frequency of severe droughts have been predicted for the Mediterranean Basin in the near future (IPCC, 2007). Forest dieback and growth decline are usually linked to severe droughts occurrence in areas with pronounced water deficit such as the semi-arid USA (Allen and Breshears, 1998). Thus, the negative effects of warming-induced drought might also affect negatively the performance of Mediterranean mountain forests, which are mostly drought-prone ecosystems.

Droughts can modify the hydraulic conductivity of trees reducing their vigor and causing a decline in radial growth (McDowell *et al*., 2008). Indeed, drought-induced dieback, declining radial growth and increased mortality rates have been described for drought-prone forests throughout the world (Allen *et al*., 2010). These dieback episodes usually show a great spatial variability across geographical gradients (Van Mantgem and Stephenson, 2007; Peñuelas *et al*., 2008). However, the responses of forests to warming-induced drought, including growth decline, can also vary as a function of species-specific resistance to drought and local climatic conditions (Suárez *et al*., 2004).

In Europe, several Mediterranean pine species reach their southernmost limit of distribution in the mountains from the southern Iberian Peninsula. Then, we can expect that these southernmost populations of pines growing in xeric sites may be more vulnerable to warming-induced drought stress than similar populations from growing in mesic sites (Jump *et al*., 2006; Macías *et al*., 2006; Linares *et al*., 2009). For instance, populations in xeric sites of southern Iberia may be more sensitive to drought-linked xylem embolism and can show greater growth decline than northern populations from mesic sites (Martínez-Vilalta *et al*., 2008). However, southern pine populations may also show adaptive features to withstand the negative effects of drought on growth and hydraulic conductivity (McDowell *et al*., 2008). These adaptations should depend not only on the species' resistance or vulnerability to drought but also on local conditions such as soil water holding capacity which may modulate the effects of climatic stressors (Camarero *et al*., 2004; Macias *et al*., 2006; Linares and Tíscar, 2010).

Recent episodes of growth decline associated to drought events have been reported for *Pinus sylvestris* L. in central Europe (Rebetez and Dobbertin, 2004; Bigler *et al*., 2006) and NE Spain (Martínez-Vilalta and Piñol, 2002). Moreover, mortality and growth decline of several conifers throughout the Iberian Peninsula have been the subject of considerable study and debate (Camarero *et al*., 2004). In the Iberian Peninsula, relevant episodes of forest decline were detected in response to the 1980s and 1990s droughts, mostly affecting conifer forests in xeric sites from Mediterranean mountains (Lloret and Siscart, 1995; Peñuelas *et al*., 2001; Camarero *et al*., 2004; Linares and Tíscar, 2010). These studies focused on natural forests despite recent episodes causing a sharp growth decline and leading to massive defoliation events have been also described in pine afforestations (Navarro-Cerrillo *et al*., 2007). Extensive pine afforestations are highly relevant in the Mediterranean Basin from both ecological and socioeconomic points of view. For instance, ca. 3.5 million ha were reforested with conifers since the 1940s in Spain (Allen *et al*., 2010). Nevertheless, the effects of droughts on tree dieback and growth decline have been rarely evaluated in pine reforestations despite its ecological and economic importance.

In Spain, the area occupied by maritime pine (*Pinus pinaster* Ait.) and Aleppo pine (*Pinus halepensis* Mill.)

plantations are ca. 713,000 ha and 484,000 ha, respectively (Montero, 1997; Ruiz de la Torre, 2006). Both species are Mediterranean pines dominant in xeric sites under dry to semi-arid conditions, and characterized by their high productivity and higher resistance to drought-induced embolism as compared with boreal pine species such as *P. sylvestris* (Richardson, 1998; Martínez-Vilalta *et al.*, 2004).

Climatic trends in eastern Andalusia, southern Spain, during the second half of the 20th century were characterized by a high drop of spring rain (De Luis *et al.*, 2008). Such increase in spring aridity was particularly noticeable in mountains from SE Spain (Fernández-Cancio *et al.*, 2010). Concurrently, a dieback process was detected in 2002 in Sierra de los Filabres (Andalusia, SE Spain) affecting at least 10,000 ha of *Pinus* afforestations that showed massive defoliation, spreading to the neighboring range in Sierra de Baza (Navarro-Cerrillo *et al.*, 2007; Sánchez-Salguero *et al.*, 2009). The lack of visual symptoms of forest pathogens and pests, and its coincidence with previous extreme droughts in the mid 1990s, suggested that the decline might be linked to drought stress (Fernández-Cancio *et al.*, 2010).

In this study, we used dendrochronological methods to evaluate the relationships between radial growth and drought severity in *P. pinaster* and *P. halepensis* plantations located in two mountain areas (Filabres, Baza) with contrasting climatic conditions in southern Spain. We employed dendrochronology as the best tool to quantify the severity of growth decline of trees in the context of the last 2-3 decades and its relationship with drought stress and defoliation events (Camarero *et al.*, 2004). We aimed to *(i)* quantify the changes in recent radial growth in response to severe droughts, *(ii)* determine if there are different responses to drought in the growth of both species in two study areas, and *(iii)* evaluate the correspondence between the recent defoliation degree and the growth response to drought severity, as inferred through the assessment of climate-growth relationships.

Material and methods

Study area

The study area includes afforestations of *P. pinaster* and *P. halepensis* located in the Sierra de Baza (37° 13' N, 2° 32' W, elevation range 845-2,269 m) and Sierra de los Filabres (37° 22' N, 2° 50' W, elevation range 300-2,186 m) (Fig. 1). The mean annual rainfall (1950-2009 period) ranged between 320 mm in Sierra de Filabres (from now on «Filabres») to 400 mm in Sierra de Baza (from now on «Baza») and the estimated mean annual temperature was 13.4°C at 1,000 m. These values correspond to a Mediterranean semi-arid climate. The soils had a greater water holding capacity in Baza than in Filabres, being respectively cambisols on limestone substrate and regosols on limestone substrate.

Field sampling

The trees were classified into two vigor classes according to their current defoliation degree: «healthy» trees with low to moderate defoliation (hereafter abbreviated as H trees) lower than 25% of the crown, and defoliated trees (hereafter abbreviated as D trees) with crown defoliation higher than 25% (Ferretti, 1994). Stratified sampling was done for each species, study site and vigor class, with the sampled trees randomly selected from each canopy stratum. Selected trees represent every vigor class and they were located at a distance greater than 100 m from the closest stand edge. The diameter at breast height (dbh, cm), total height (m) and vigor class (H or D) were registered for each tree (Table 1). The selected trees were felled and a transversal disk of the bole at 1.3 m height was obtained.

Dendrochronological methods

The disks were dried and polished with sandpapers of successively fine grain until its growth rings were

Table 1. Description of the trees sampled in the Baza (B) and Filabres (F) study areas

Species (code)	No. trees		Dbh (cm)		Height (m)		Defoliation (%)	
	B	**F**	**B**	**F**	**B**	**F**	**B**	**F**
P. halepensis (Ph)	38	16	16.1 ± 0.8	16.2 ± 0.9	6.5 ± 0.3	6.6 ± 0.4	25.0 ± 2.6	27.3 ± 3.9
P. pinaster (Pp)	45	19	17.5 ± 0.5	17.7 ± 0.6	6.2 ± 0.2	6.2 ± 0.2	24.0 ± 2.2[a]	47.5 ± 5.0[b]

Values are means ± SE. Different letters indicate significant (*P* < 0.05) differences between study areas (Mann-Whitney *U* test).
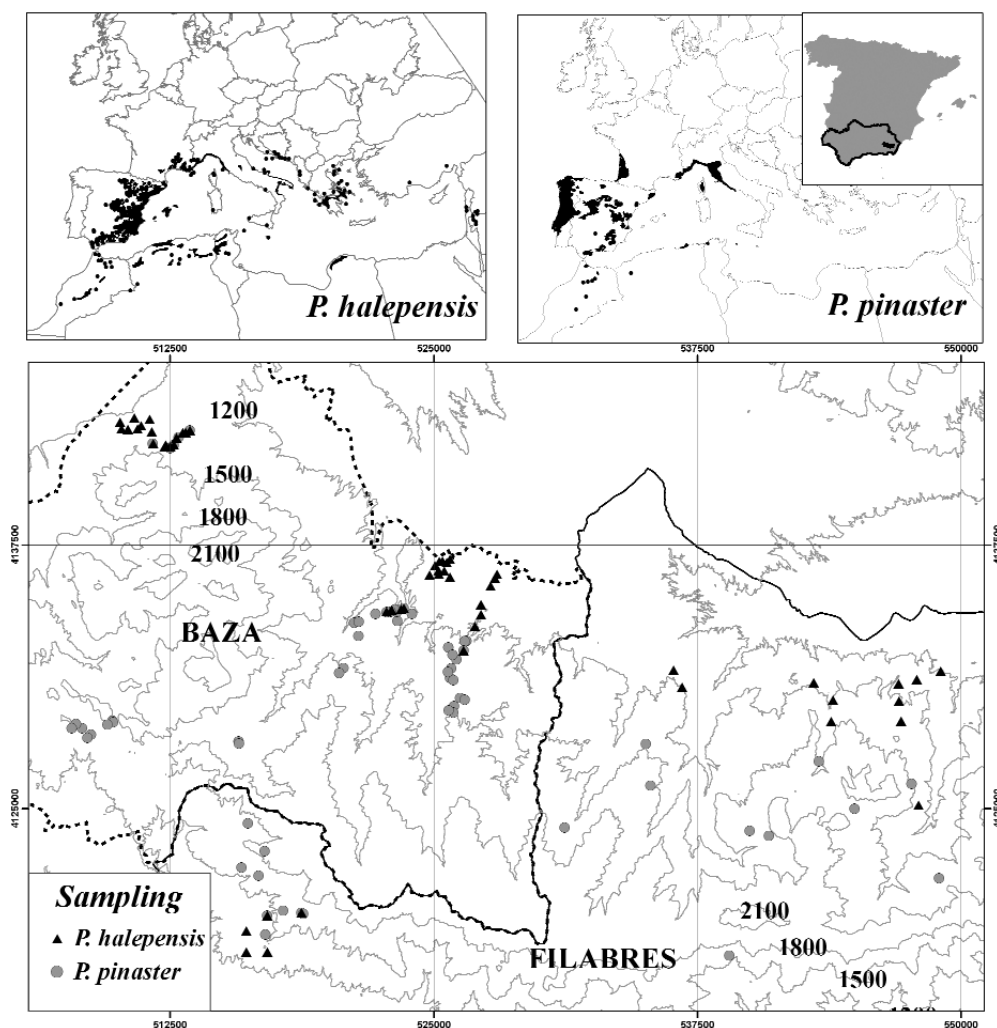
Figure 1. Study area and sampling sites (different symbols or lines correspond to the two study species and areas, respectively). The upper inset maps show the distribution of both species and the location of the study area in SE Spain (Andalusia). The distribution maps are based on information provided by Alia and Martin (2002) and Fady *et al.* (2003).

clearly visible. Two opposite radii per section perpendicular to the maximum slope were selected to avoid reaction wood. The ring series along these radii were visually cross-dated based on characteristic rings (Yamaguchi, 1991). The polished surfaces of the disks were subsequently scanned to a resolution of 300 ppp. The annual growth rings in the synchronized tree-ring series were measured with a resolution of 0.01 mm using the semi-automatic measurement system WinDendro™ (Regents Co., Canada). Cross-dating of the tree-ring series was evaluated using the COFECHA program (Holmes, 1983).

To analyze changes in growth patterns, we calculated annual basal area increment (BAI) for both pine spe-

cies and study areas, considering both health classes separately, using the following formula:

$$BAI = \pi \left(R^2_t - R^2_{t-1} \right) \qquad [1]$$

where R is the radius of the tree and t is the year of tree-ring formation.

We also obtained the residual chronologies of ring-width indices by eliminating the long-term growth trends related to increasing tree size and age and reducing the first-order autocorrelation. Detrending of the tree-ring series was done by fitting a negative exponential curve to each series. Dendrochronological statistics were used to compare growth of less or more defoliated trees. We calculated the mean sensitivity

(MSx), a measure of the relative difference of growth between consecutive rings, and the first-order auto-correlation (AR1), a measure of similarity in width between consecutive rings (Fritts, 1976). Dimension-less Residual indices of tree growth were produced by dividing the raw ring width values by the values of the fitted curve and performing autoregressive modeling of the results with the program ARSTAN (Cook, 1985).

Climate data

We used two sources of climate data for different purposes. First, to assess climate-growth relationships we used data from thirty local meteorological stations with long and continuous records located near both study areas (source AEMET). Second, to quantify changes in climatic trends of both study areas during the 20th century we obtained data interpolated data from the period 1900-2006 for the of 0.5°-grid (coordinates 37° 00'-37° 30' N and 2° 30'-3° 00' W) from the database CRU TS 2.1 (Mitchell *et al*., 2001). Missing data of the local series were reconstructed by linear regressions based on local interpolation considering the nearest and most complete stations (Fernández Cancio and Manrique Menéndez, 1997).

A regional series of monthly climate variables (mean temperature, total rainfall) for each study area (Filabres, Baza) was obtained using the subroutine MET of the *Dendrochronology Program Library* package (Holmes, 2001). The homogeneity of the climatic series was assessed using the subroutine HOM of the same package. Finally, we calculated an index of annual water deficit or drought index (DRI, in mm) since this may be a better indicator of the effects of water availability on tree growth than temperature or precipitation itself. The DRI was calculated since 1950 using mean values of the two regional climate series derived from local data. The DRI is defined as the difference between the accumulated precipitation (P) and the potential evapotranspiration (PET) since August of the previous year up to July of the year of tree-ring formation, *i.e.* DRI = P − PET (Thornthwaite, 1948, Bigler *et al*., 2006). Thus, lower (higher) DRI values indicate higher (lower) water deficit.

Growth response to climate

The relationships between radial growth and climate were evaluated for each species, study area and vigor class using the residual chronologies and the regional climate series of mean monthly temperature and monthly precipitation. Growth-climate relationships were quantified using Pearson correlation coefficients. Growth indices and monthly climatic series were compared from August of the previous year to September of the year of tree-ring growth because this is the most influential period for radial growth of both studied pines (Richter and Eckstein, 1991; De Luis *et al*., 2007; Camarero *et al*., 2010). Correlation analyses were performed using the program DENDROCLIM 2002 (Biondi and Waikul, 2004).

Results

Mean maximum temperatures in the study area have significantly increased since 1950, whereas spring rainfall has decreased in the same period (Fig. 2). The lowest DRI values were observed in 1994, 1995, 1999 and 2005, and corresponded to years characterized by severe droughts.

BAIs of both species showed similar trends and sharp reductions in both study areas corresponding to years with low DRI values, *i.e.* 1995, 1999 and 2005 (Fig. 3). We also noted a greater divergence in BAI patterns between *P. halepensis* with different defoliation degree in Filabres and, to a lower degree, in Baza. Contrastingly, no BAI divergence was noted for *P. pinaster* according to the trees' defoliation, despite this species showed the highest defoliation degree in the xeric area (Filabres).

Mean tree-ring widths in the period 1980-2006 significantly ($P < 0.05$) differed between vigour classes for *P. halepensis* in both study areas, being higher for trees with low defoliation degree (Table 2). In the xeric Filabres area, more defoliated *P. halepensis* trees had a higher mean sensitivity and first-order autocorrelation than less defoliated trees (Table 2).

We found significant positive (negative) relationships between growth and precipitations (temperatures) of May and June for both pine species (Fig. 4). In Filabres, the growth of both pines was also related positively to the rainfall of January and March, whereas precipitation in the previous September also favored growth.

Overall, in the xeric area (Filabres), the more defoliated trees of both species showed a stronger negative (positive) association with monthly maximum temperatures in summer (precipitation in winter and spring)
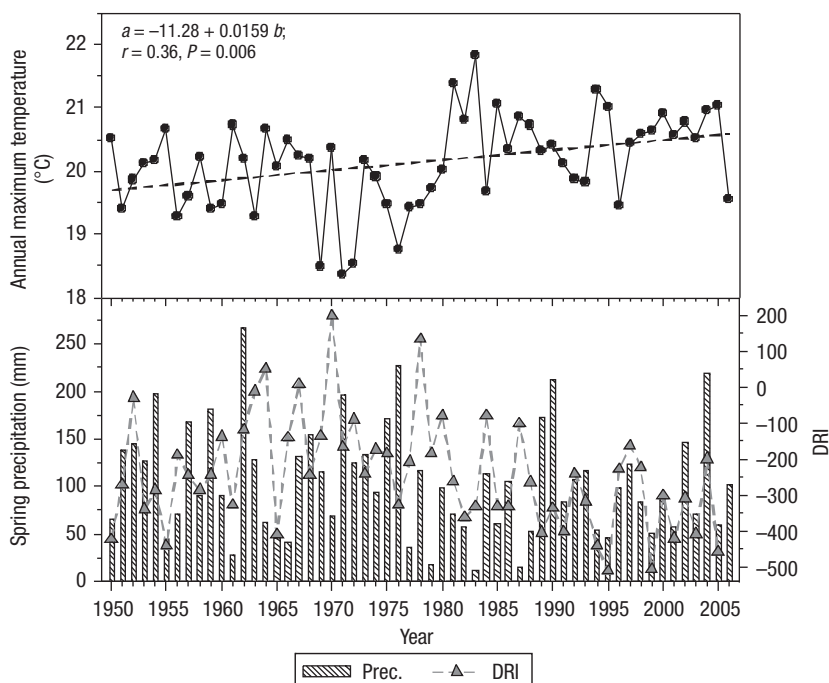
Figure 2. Regional trends of mean annual maximum temperature, spring precipitation and annual drought index (DRI) during the 1950-2006 period. Lower (higher) DRI values correspond to higher (lower) water deficit. The linear regression shows the significant warming trend in the study area. Negative (positive) values of the drought index indicate higher (lower) water deficit. The regional climatic data are based on a regional mean calculated using data from 30 local stations.

than less defoliated individuals, In this area, the temperatures of June and July showed negative relationships with growth of *P. halepensis* trees with low or high defoliation levels, respectively (Fig. 4). Despite the stronger negative growth-temperature associations of defoliated trees in the xeric area, the mean relationship with annual maximum temperature was more

negative for less defoliated than for more defoliated *P. halepensis* trees (Table 3). Finally, the basal area increment of *P. halepensis* after 1995 was consistently and negatively related to current defoliation in the xeric area (Filabres) but not in the mesic area (Baza) [This was analyzed in SPSS v.15 software (SPSS Inc., Chicago IL)] (Fig. 5).

Table 2. Dendrochronological statistics of the radial growth series for trees with low (H, healthy trees; defoliation < 25%) or high defoliation (D, declining trees; defoliation > 25%) (H, < 25%) considering the two pine species (*Ph, P. halepensis; Pp, P. pinaster*) in the Baza (B) and Filabres (F) study areas

Study area species	Tree-ring width[1] (mm)		MSx[2]		AR1	
	H	**D**	**H**	**D**	**H**	**D**
F-*Ph*	2.5 ± 0.3[a]	1.8 ± 0.2[b]	0.35 ± 0.02[a]	0.44 ± 0.01[b]	0.50 ± 0.07[a]	0.70 ± 0.04[b]
B-*Ph*	1.9 ± 0.2[a]	1.6 ± 0.2[b]	0.40 ± 0.02	0.41 ± 0.02	0.44 ± 0.04	0.47 ± 0.06
F-*Pp*	2.4 ± 0.3	2.0 ± 0.3	0.35 ± 0.02	0.38 ± 0.01	0.73 ± 0.03	0.75 ± 0.05
B-*Pp*	2.2 ± 0.2	2.1 ± 0.2	0.42 ± 0.01	0.44 ± 0.02	0.47 ± 0.04	0.54 ± 0.03

Values are means ± SE. Different letters indicate significant ($P<0.05$) differences between defoliation classes within areas (Mann-Whitney *U* test). [1] The tree-ring width was calculated for the period 1980-2006. [2] Variables' abbreviations: MSx: mean sensitivity of residual chronologies; AR1, first-order autocorrelation of standard chronologies. The annual MSx measures the relative difference of indexed tree-ring width from one year to the next, and it is calculated by dividing the absolute value of the differences between each pair of ring-width indices by the mean of the paired index (Fritts, 1976).
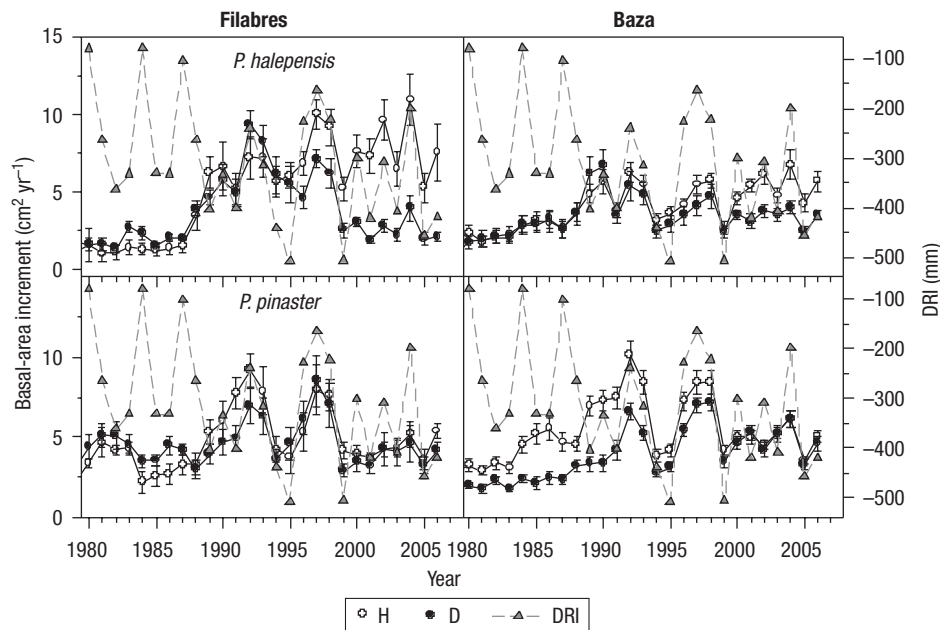
Figure 3. Recent trends in basal area increment (BAI) of the two pine species studied in the Filabres and Baza study areas according to the crown defoliation of trees. Trees were classified as healthy with low defoliation (H, white symbols, defoliation < 25%) or declining with high defoliation (D, black symbols, defoliation > 25%). The grey line corresponds to the annual drought index (DRI) with negative (positive) values indicating highest (lower) water deficit. Note the severe droughts in 1994-1995 and 1999 (low DRI values). Bars correspond to the standard error.

Discussion

On the whole, the climate-growth associations found for *P. pinaster* and *P. halepensis* were similar to those found in other Iberian forests under Mediterranean climatic conditions (Bogino and Bravo, 2008; De Luis *et al.* 2009; Vieira *et al.*, 2009). Nevertheless, pine plantations of both Mediterranean pine species (*P. pinaster*, *P. halepensis*) in south-eastern Spanish

Table 3. Comparisons of climate-growth relationships (*r*, Pearson correlations) between radial growth (ring-width index) and the mean annual maximum temperature for the two studied pine species in the xeric Filabres study area. The correlations (means ± SE) were compared between trees with low (H, healthy trees; defoliation < 25%) or high defoliation (D, declining trees; defoliation > 25%) of each species using one-way ANOVAs

Species	Defoliation	*r*	*F*	*P*
P. halepensis	H	−0.13 ± 0.03	4.2	0.05
	D	−0.09 ± 0.01		
P. pinaster	H	−0.07 ± 0.04	4.5	0.04
	D	−0.20 ± 0.04		

mountains are undergoing acute processes of growth decline and forest dieback, despite they are theoretically better adapted to withstand drought than boreal species as *P. sylvestris* (Richardson, 1998). This apparently drought-induced decline is characterized by a sharp reduction in basal area increment and high levels of needle loss. The high sensitivity of growth of defoliated trees to precipitation and maximum temperatures suggest that their growth decline and subsequent needle loss were caused by warming-incited drought stress. Specifically, warming-induced water deficit in spring seems to be the main climatic trigger for similar drought-induced growth declines in other Iberian forests (Martínez-Vilalta and Piñol, 2002; Camarero *et al.*, 2004). The fact that growth of *P. halepensis* trees with low and high defoliation levels responded negatively to June and July temperatures, respectively, suggests that individuals with different vulnerability to drought stress could have different radial-growth phenology. Further studies should evaluate xylogenesis in co-occurring individuals of the same species with different defoliation degree to test this hypothesis.

P. pinaster showed higher defoliation degree in the xeric than in the mesic area, which reflects its greater
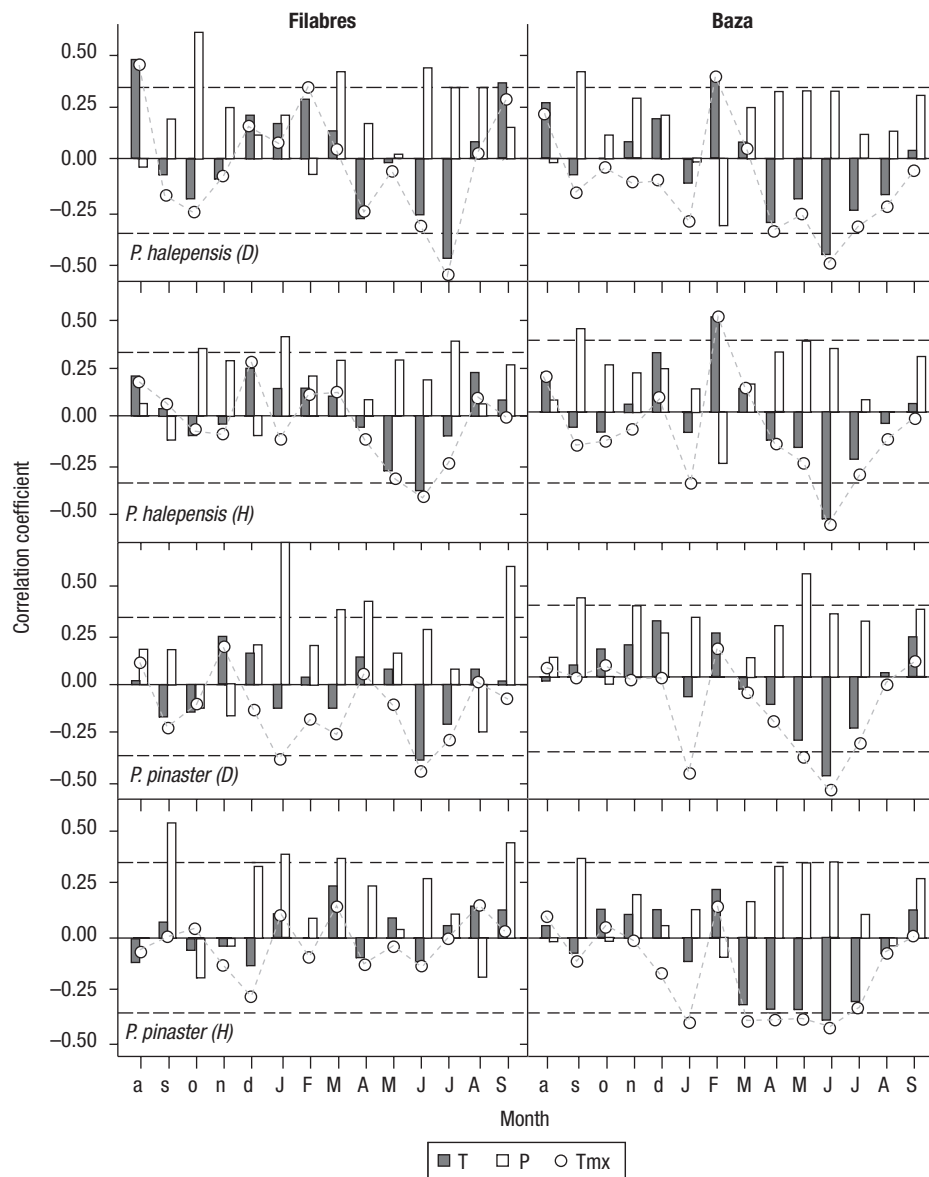
Figure 4. Relationships between radial growth (ring-width indices) and monthly climatic variables (T, mean temperature –black bars; P, total precipitation –white bars; Tmx, mean maximum temperature –grey dashed lines) for the two studied pine species in the Filabres and Baza study areas considering separately trees with low (H, healthy trees; defoliation <25%) or high defoliation (D, declining trees; defoliation >25%). Growth is related with climate data from the previous (months abbreviated by lowercase letters) and current (months abbreviated by uppercase letters) years, being the current year that of tree-ring formation. The significance levels ($P < 0.05$) are indicated by dashed horizontal lines.

vulnerability to episodes of drought-induced xylem embolism and needle loss in comparison with *P. halepensis* (Martínez-Vilalta *et al*., 2004). Although *P. pinaster* is regarded as being native to Sierra de los Filabres (García Latorre and Garcia Latorre, 2007), afforestations were mostly performed in low quality sites, suggesting that growth responses to climatic

stress can be tightly conditioned by local site conditions (Tardif *et al*., 2003; Bogino and Bravo, 2008). Indeed, the negative effects of drought stress on tree growth are greatly modulated by local factors as topography (Linares and Tíscar, 2010). On the other hand, *P. halepensis* seems to be better adapted to the semi-arid conditions of this area, as the moderate defoliation
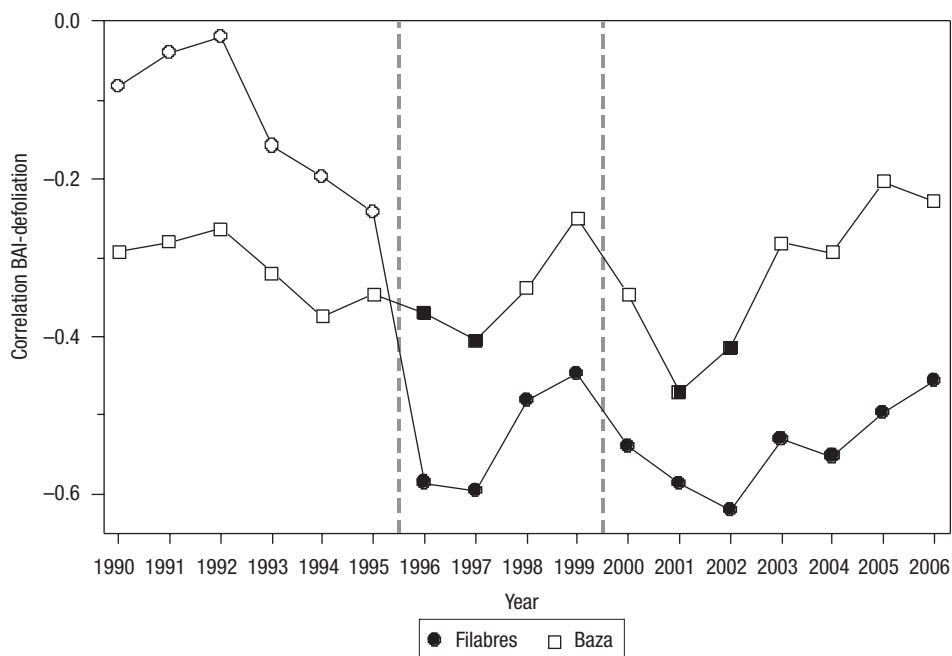
Figure 5. Relationships between annual basal area increment (BAI) values and current defoliation degree for *P. halepensis* in each study area. Filled symbols are significant correlation coefficients (*P* < 0.05). The dashed vertical lines indicate sharp changes in the BAI-defoliation associations after the severe droughts in 1994-1995 and 1999.

levels and the sustained growth patterns of healthy trees indicated. The responses of growth to climate in *P. pinaster* and *P. halepensis* are age- and size-dependent (De Luis *et al.*, 2009; Vieira *et al.*, 2009), but these factors were not relevant in our case since all trees were of similar age and size. Therefore, neither age nor size seems to be among the main causes of the differential response of growth and defoliation to drought stress in our study case.

The divergence of radial growth after extreme droughts was observed in *P. halepensis*, being more evident in the xeric than in the mesic site, but this was not noted in *P. pinaster*. Although a high degree of defoliation and mortality were observed since 2001 in Filabres (Navarro-Cerrillo *et al.*, 2007), growth divergence and a negative association between basal-area increment and the degree of defoliation was evident in *P. halepensis* since the severe droughts of 1994-1995. Such findings suggest a lagged response of needle loss to drought stress and growth decline, which in our study may have lasted from 1995 (first sharp reduction in basal-area increment) to 2002 (defoliation), *i.e.* 7 years. The lagged responses to climatic stress of growth decline and defoliation greatly complicate the disentangling of the cause-effect relationships in episodes of forest dieback (Pedersen, 1999; Dobbertin, 2005).

The increased climate variability associated with the current climate change (Manrique and Fernández Cancio, 2000) could lead to growth decline in Iberian pine species (Andreu *et al.*, 2007). Such decline may be linked to the described dieback episodes in marginal plantations under severe drought stress and with a high year-to-year variability in precipitation. Rainfall variability was responsible of the sharp growth declines in 1994-1995 and 1999, but also caused high basal-area increment in wet years (*e.g.* 1992, 1997) when radial growth of *P. pinaster* was similar in both study sites. Furthermore, more research is required to unravel the relative contributions of long- (*e.g.,* temperature rise) and short-term (*e.g.,* droughts) climatic stressors on growth decline.

Precipitation in April-June influenced positively radial growth, whereas mean temperature in March-July had a negative effect on wood formation. In the xeric area (Filabres), water availability in late spring and early summer seems to be a major driver for tree growth since maximum radial growth rates of both pines occur in this time (De Luis *et al.*, 2007; Bogino and Bravo, 2008; Camarero *et al.*, 2010). Specifically, *P. halepensis* trees with low defoliation increased growth after the 1999 drought meanwhile *P. pinaster* maintained low growth rates after this drought regard-

less of their defoliation degree. This could be explained by a lower adaptation to drought resistance of *P. pinaster*, in particular in the xeric area. A difference between both study areas is the greater positive influence of February temperatures on *P. halepensis* growth in Baza than in Filabres, which suggests a greater thermal limitation to growth in Baza than in Filabres.

The observed defoliation and decline in radial growth of *P. halepensis* and *P. pinaster* plantations was strongly linked to drought stress in spring. Even if *P. pinaster* is less tolerant to drought stress than the co-occurring *P. halepensis*, we suggest that the specific responses of growth were conditioned by contrasting climatic conditions and local variability in soil water holding capacity. Therefore, xeric areas and sites with low water holding capacity, such as south-facing slopes on limestone substrate, may predispose pines to drought-induced decline, as was the case of declining *P. pinaster* stands.

The severe droughts of 1994-1995 and 1999 induced a decline in radial growth and the selective defoliation of Aleppo and maritime pine plantations through a reduction in spring water availability. We found a divergence of radial growth between trees currently showing different defoliation levels for *P. halepensis* in the more xeric area (Filabres) where basal-area increment and recent defoliation were negatively related. Contrastingly, *P. pinaster* showed a growth reduction irrespective of the trees' defoliation level which suggests that this species is less adapted to the increasingly arid conditions of the study areas than *P. halepensis*.

Acknowledgements

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