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Contrasting vulnerability and resilience to drought-induced decline of densely planted vs. natural rear-edge *Pinus nigra* forests

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ABSTRACT

The southernmost European natural and planted pine forests are among the most vulnerable areas to warming-induced drought decline. Both drought stress and management factors (e.g., stand origin or reduced thinning) may induce decline by reducing the water available to trees but their relative importances have not been properly assessed. The role of stand origin – densely planted vs. naturally regenerated stands – as a decline driver can be assessed by comparing the growth and vigor responses to drought of similar natural vs. planted stands. Here, we compare these responses in natural and planted Black pine (*Pinus nigra*) stands located in southern Spain. We analyze how environmental factors – climatic (temperature and precipitation anomalies) and site conditions – and biotic factors – stand structure (age, tree size, density) and defoliation by the pine processionary moth – drive radial growth and crown condition at stand and tree levels. We also assess the climatic trends in the study area over the last 60 years. We use dendrochronology, linear mixed-effects models of basal area increment and structural equation models to determine how natural and planted stands respond to drought and current competition intensity. We observed that a temperature rise and a decrease in precipitation during the growing period led to increasing drought stress during the late 20th century. Trees from planted stands experienced stronger growth reductions and displayed more severe crown defoliation after severe droughts than those from natural stands. High stand density negatively drove growth and enhanced crown dieback, particularly in planted stands. Also pine processionary moth defoliation was more severe in the growth of natural than in planted stands but affected tree crown condition similarly in both stand types. In response to drought, sharp growth reduction and widespread defoliation of planted Mediterranean pine stands indicate that they are more vulnerable and less resilient to drought stress than natural stands. To mitigate forest decline of planted stands in xeric areas such as the Mediterranean Basin, less dense and more diverse stands should be created through selective thinning or by selecting species or provenances that are more drought tolerant.

1. Introduction

According to climatic models a generalized rise in temperature and related aridification trends is expected in the Circum-Mediterranean area within the current century (IPCC, 2007). Drought stress is probably among the main drivers of the current forest decline of conifer woodlands in the Mediterranean Basin, particularly in southern Europe (Linares et al., 2009; Allen et al., 2010; Sarris et al., 2010; Carnicer et al., 2011). Rear-edge tree populations located near the southernmost or dry limits of the species distribution area serve as valuable models for assessing tree sensitivity to drought stress (see Macias et al., 2006; Sánchez-Salguero et al., 2012a). Southernmost European mountain conifer forests located in southeastern Spain (Andalusia) are considered to be among the most vulnerable areas for the loss of endemic tree

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species and relict populations due to warming-induced drying trends (Bakkenes et al., 2002; Sánchez-Salguero et al., 2012a).

The processes leading to forest decline and the subsequent responses in tree vigor (vulnerability, resilience) are still poorly understood because several stress factors in addition to drought interact at different spatial and temporal scales leading to lagged cause-effect relationships (Manion, 2003; Camarero et al., 2011). According to the Manion (1981) conceptual model stress factors act successively leading to a progressive loss in tree vigor. The model starts by considering predisposing factors (e.g., site conditions), followed by inciting factors (e.g., drought) and finally ending with contributing factors (e.g., secondary insects and pathogens). However, few studies have assessed the role of past management on forest decline (but see Camarero et al., 2011; Vilà-Cabrera et al., 2013). Specifically, stand origin – planted vs. naturally regenerated stands – may act as a predisposing factor which can be incorporated into Manion (1981) conceptual framework.

Here we evaluate growth and vigor change (crown condition) in response to drought stress in both naturally regenerated stands and similar nearby plantations of the same species. Pine plantations in Spain present a series of characteristics that might make them more vulnerable and less resilient to climate change, chiefly higher density, lower biological diversity and lack of local adaptation due to unknown seed origin (e.g., Benito Garzón et al., 2011; Ruiz-Benito et al., 2012). Thus pine plantations near the rear-edge of the species distribution constitute valuable monitors of drought and past management effects on impending decline, yet the effects of drought-induced decline episodes and management on vulnerability and resilience at the stand and individual tree levels in these systems are poorly documented (Martínez-Vilalta et al., 2012). This information is however desperately needed to establish adaptation guidelines to increase the resilience of similar rear-edge forests subjected to drought-induced decline process.

The Mediterranean Basin is one of the world regions with the largest proportion of planted pine forests and a long history of planned management (FAO, 2006). For instance, the Spanish Reforestation Plan of 1939 involved planting more than 3.5 million ha of forests, mainly pine species, but reduced post-plantation thinning has often resulted in high-density stands (Montero, 1997). These dense and potentially drought-vulnerable pine plantations have shown a high vulnerabilty (elevated defoliation and mortality rates) to recent drought stress since they were often planted under favorable climatic conditions during past wet decades as the 1970s (Ruiz-Benito et al., 2012; Sánchez-Salguero et al., 2012b).

Black pine (*Pinus nigra* Arn.) is widely distributed in southern Europe, where it covers a wide latitudinal and longitudinal gradient from Austria to Algeria and from Turkey to Spain (Barbero et al., 1998). The subspecies *P. nigra* subsp. *salzmannii* (Dunal) Franco covers an area over 350,000 ha in Spain (Fig. 1a). The Iberian *P. nigra* forests represent the southwestern limit of distribution of the species and some stands in SE Spain include some of the driest sites where *P. nigra* grows. Dendrochronological studies have revealed that recurrent and severe droughts have negatively affected Iberian *P. nigra* radial growth during the second half of the 20th century (Andreu et al., 2007; Linares and Tíscar, 2010; Martín-Benito et al., 2010a; Camarero et al., 2013). Further, these declining growth patterns have been observed in natural stands and also in planted populations (Sánchez-Salguero et al., 2012a,b).

Many decline studies are based on the assumption of established relationships between growth, vigor status (defoliation, mortality) and the stress factor (Wunder et al., 2006). Yet, establishing these relationships is difficult because of the highly variable nature of decline over space and time (Hawkes, 2000). Thus, long-term permanent monitoring plots represent valuable tools to accurately assess climate–growth–vigor associations and changes in vulnerability and resilience in response to drought. Here, we analyze how environmental, structural and climatic variables modulate the effects of warming-induced drought stress and management on vigor and growth in natural vs. planted *P. nigra* stands and trees. We use a retrospective approach based on assessments of crown condition, here considered as a surrogate of tree vigor, measured in long-term monitoring plots of the regional Andalusian Forest Monitoring Network (hereafter abbreviated as AFMN). Previous studies suggest that crown condition is an accurate descriptor of tree vigor and well correlated with tree growth (Dobbertin, 2005). The intensity of defoliation by *Thaumetopoea pytiocampa* Schiff., the pine processionary moth (hereafter abbreviated as PPM), was also considered since this is the major defoliator of Mediterranean pine stands and reduces tree growth (Hódar et al., 2003). We define vulnerability as relative loss in growth after a drought, whereas resilience is defined as the capacity of trees to recover levels similar to those previous to the drought (Lloret et al., 2011).

Our specific aims are: (1) to examine if naturally regenerated and planted *P. nigra* stands exhibit contrasting growth responses to drought, (2) to investigate the relationships among growth patterns and sensitivity to drought as predictors of recent crown condition at the tree level, and (3) to determine if stand and tree variables (age, size, competition), biotic factors (PPM outbreaks) and drought stress act synergistically causing differential forest decline in natural vs. planted stands. We hypothesize that planted *P. nigra* stands would show a higher vulnerability and less resilience in response to drought than natural stands.

2. Materials and methods

The study area is located in eastern Andalusia, southeastern Spain (Fig. 1), and includes the southern limit of distribution of *P. nigra* subsp. *salzmanii* which comprises declining forests (Linares and Tíscar, 2010; Sánchez-Salguero et al., 2012a). In this area 44,000 km^2 are currently forested (REDIAM, 2009). Mountain systems surround the region and lie on both sides of the Guadalquivir River Basin, with palaeozoic and siliceous materials dominant in the north, and limestone and sandstone substrates prevailing in the south. The climate is Mediterranean, with mean annual precipitation varying between 140 and 2153 mm. Dry and warm summers (average July temperature is within the range 15–31 °C; precipitation varies from 0 to 39 mm) are followed by cold winters (average January temperature varies from −2 to 12 °C). The natural *P. nigra* forests in eastern Andalusia are dominant in north-oriented and high-elevation sites (1500–2270 m a.s.l) and occupy ca. 107,000 ha. Plantations cover ca. 40,000 ha and they were mostly planted in mid to high-elevation sites (1200–2150 m) between the 1960s and 1970s using seeds mostly collected in southern Spain (Alía et al., 2005).

The data used in this study are from the Andalusia adaptation (AFMN) of the “Pan-European Programme for Intensive and Continuous Monitoring of Forest Ecosystems” within the context of the International Cooperative Programme (ICP) on Assessment and Monitoring of Air Pollution Effects on Forests (Dobbertin, 2004). These intensive monitoring plots have been established since 1985 based on a 16-km grid covering Europe. In addition, the Andalusian government established in 2000 a regional forest monitoring network (AFMN) with the same harmonized criteria, but based on a 8-km grid covering the forested surface of Andalusia (2,106,252 ha) (for more details see Appendix A). The AFMN comprised data from 408 circular plots distributed systematically and each plot had a variable radius but always included 24 trees (Fig. 1b).

2.1. Climate data

We used monthly climatic data (mean temperature, total precipitation) for the period from 1950 to 2010 provided by the

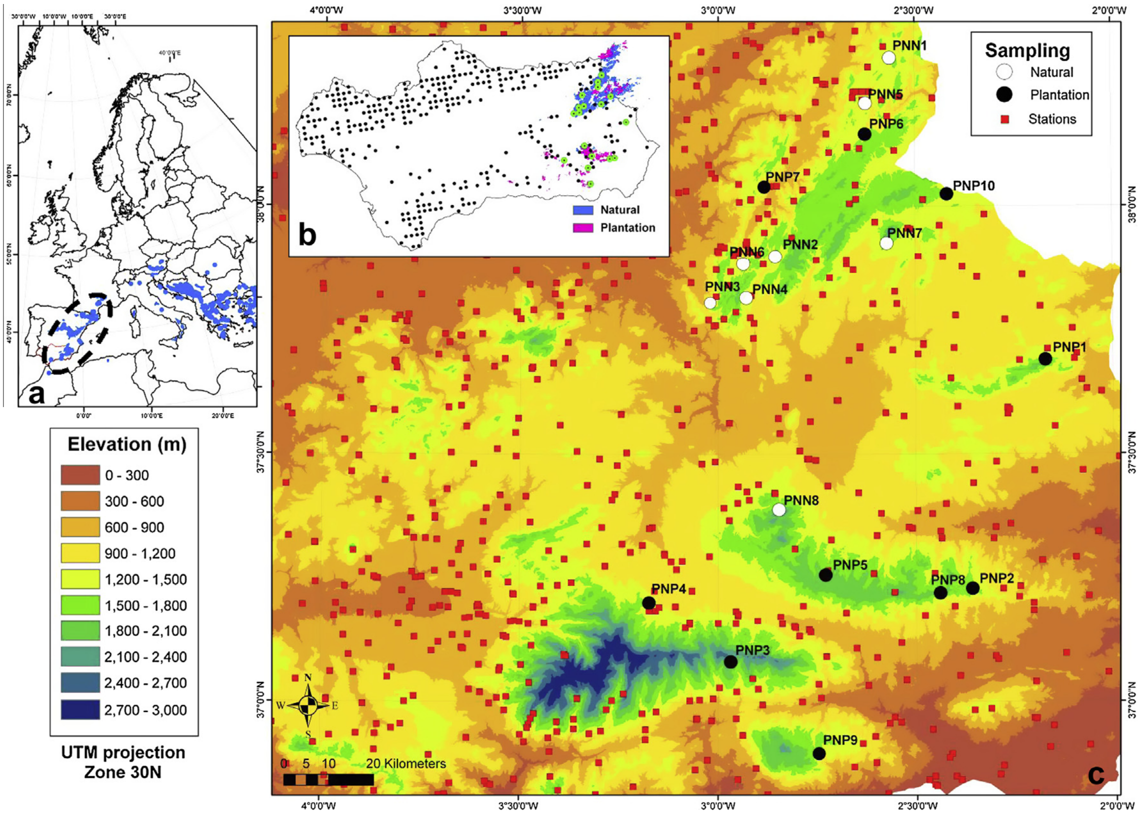

Fig. 1. Distribution of *P. nigra* in the Circum-Mediterranean area (a) (the subpspecies *P. nigra* subsp. *salzmannii* is mainly distributed in Spain and southern France – area delimited by the dashed line). Andalusian forest monitoring network (AFMN) plots (black circles) and the distribution of natural and planted *P. nigra* forests (b). Location of the study sites (natural stands, empty circles; planted stands, filled circles) and local meteorological stations (squares) used to derive the regional climatic series (c) (see sites codes in Table 1).

Spanish National Meteorological Agency-AEMET (total of 200 local meteorological stations) (Fig. 1c). Temporal trends of monthly temperature and precipitation were estimated to characterize the climate of each plot considering the nearest stations located not further than 20 km from each study site. To analyze trends separately for planted and natural forests at a regional scale, we homogenized the mean trends for precipitation and temperature datasets developed for each plot. To asses spatial and temporal climate variability within plots and natural vs. plantations two datasets were used. First, climatic data were spatially analyzed by implementing them in a Geographic Information System (GIS) with a 10-m spatial resolution. We used the average ratio of precipitation (P) to potential evapotranspiration (PET) from June to August as a proxy of summer drought stress (summer P/PET) and PET was calculated following Hargreaves and Samani (1985) method. Low and high values of summer P/PET correspond to dry and wet conditions, respectively (Martínez-Vilalta et al., 2008). Second, annual standardized temperature and precipitation anomalies (differences from the average for the period 1950–2010) were obtained for each plot considering the growing period from March to August (hereafter abbreviated as ATgrow and APgrow for temperature and precipitation, respectively) (see Vilà-Cabrera et al., 2011). This period was selected because the maximum radial-growth rates of *P. nigra* and other Mediterranean pine species occur during these months (Richter et al., 1991). The years with the most negative APgrow values, i.e., the highest water deficits, during the studied period were (natural vs. planted stands): 1983 (−1.53 vs. −1.54), 2005 (−1.54 vs. −1.41), 1987 (−1.29 vs. −1.28), 1994 (−1.27 vs. −1.23), 1999 (−0.95 vs. −1.24), and 1995 (−0.86 vs. −0.79). Since 1950, the years with the most positive APgrow values corresponding to those showing the lowest water deficits were (natural vs. planted stands): 1971 (2.22 vs. 1.95), 1975 (1.32 vs. 1.49), 1960 (1.63 vs. 1.12), 2004 (1.17 vs. 1.63), 1969 (1.63 vs. 1.12) and 1984 (1.53 vs. 0.71). We selected four recent dry years characterized by very low APgrow values (1994–1995, 1999 and 2005) to perform further analyses on growth responses to drought.

2.2. Sampling methods and dendrochronological analyses

We selected all the AFMN plots where *P. nigra* was dominant, which contained more than 14 trees per plot. This selection gave a total of 18 plots including 10 planted and 8 natural stands (Fig. 1c; Table 1). Planted and natural stands were distinguished by their contrasting structures, being characterized by coetaneous, spatially homogeneous and single-layered stands vs. multi-cohort, heterogeneous and multi-layered ones, respectively. On the selected AFMN plots the following assessments and measurements were carried out: annual crown condition assessments for the period 2000–2010 (see Appendix A); growth increment variables (height, dbh-diameter at breast height measured at 1.3 m) measured every fifth year and annual observations of recent disturbances (i.e., PPM defoliation, drought or frost damage). We excluded suppressed trees from the analyses and trees with physical damages due to storms, windy conditions or snow load. The intensity of PPM defoliation was assessed anually using a 6-degree scale of defoliation degree at the stand level adopted within the AFMN network and ranking from no defoliation (0) to complete defoliation (5). The PPM preferentially feeds on 1-year old needles during winter thus affecting radial growth the next spring (Hódar et al., 2003). We only considered the occurrence of strong defoliations (defoliation intensity >3) since these are the most important

Table 1
Sites description and characteristics of selected *P. nigra* plots sampled in Andalusia, southern Spain. Values are means (SD).

Stand type	Site code	Latitude (N)	Longitude (W)	Elevation (m a.s.l.)	Aspect	Slope (°)	Dbh (cm)[a]	Height (m)	Density (stems ha^{-1})	Tm (°C)	*P* (mm)
Plantation	PNP1	37°41′23″	2°10′15″	1389	E	10	20.8 (7.0)	7.8 (2.7)	650	11.4	430
Plantation	PNP2	37°13′47″	2°21′30″	1567	N	25	16.0 (2.6)	6.2 (0.7)	1100	11.3	398
Plantation	PNP3	37°04′52″	2°58′04″	2103	NW	15	21.4 (2.8)	9.6 (0.9)	1300	9.1	583
Plantation	PNP4	37°15′26″	2°43′43″	1338	E	5	17.3(6.1)	8.0 (2.3)	650	12.4	488
Plantation	PNP5	37°08′29″	3°04′15″	1884	S	16	16.5 (4.0)	9.7 (0.8)	1100	10.4	372
Plantation	PNP6	38°08′44″	2°37′35″	1428	SE	5	23.8 (3.5)	11.2 (1.1)	1000	11.3	920
Plantation	PNP7	38°02′21″	2°52′57″	1233	N	21	19.4 (3.3)	11.7 (1.3)	900	13.2	942
Plantation	PNP8	37°13′14″	2°26′23″	1891	SW	4	13.2 (3.2)	6.7 (0.6)	1200	10.8	393
Plantation	PNP9	36°53′47″	2°44′46″	1489	NE	29	13.7 (2.7)	6.6 (0.7)	1100	11.5	404
Plantation	PNP10	37°23′20″	2°50′45″	1484	NW	24	17.1 (4.7)	6.5 (1.6)	1000	11.0	760
Natural	PNN1	38°17′56″	2°33′49″	1383	SE	20	34.4 (6.9)	16.7 (2.8)	350	11.5	888
Natural	PNN2	37°53′54″	2°51′17″	1478	S	8	54.7 (19.0)	18.9 (6.1)	250	11.3	1000
Natural	PNN3	37°48′17″	3°01′12″	1053	SE	19	33.0(14.9)	14.9 (6.6)	900	13.7	835
Natural	PNN4	37°48′54″	2°55′43″	1430	NW	17	31.3 (6.7)	14.8 (1.4)	650	11.5	856
Natural	PNN5	38°12′28″	2°37′32″	1199	W	31	35.8 (11.4)	15.6 (3.4)	750	12.2	1010
Natural	PNN6	37°53′02″	2°56′10″	1209	S	20	41.7 (12)	17.8 (6.9)	800	12.4	931
Natural	PNN7	37°55′33″	2°34′19″	1517	W	9	29.6 (7.8)	18.1 (3.8)	450	11.0	569
Natural	PNN8	37°12′04″	3°10′27″	1966	SE	17	43.1 (13.7)	12.5 (4.1)	350	10.0	467

[a] Diameter at breast height measured at 1.3 m (data from the Andalusian Forest Monitoring Network). Abbreviations of variables: Tm, mean annual temperature; *P*, total annual precipitation.

for evaluating the PPM effects on radial growth (Hernández Alonso et al., 2005).

In each plot 12 trees were cored at 1.3 m with a Pressler increment borer and two cores were sampled per tree along the direction perpendicular to the maximum slope. Cores were air dried, sanded until tree-rings were clearly visible and visually cross-dated. Individual tree-ring width series were measured to the nearest 0.01 mm with a LINTAB measuring device (Rinntech, Heidelberg, Germany). Cross-dating quality was checked using the software COFECHA (Holmes, 1983) by checking the consistency of the different ring-width series among trees coexisting within the same plots. The trend due to the geometrical constraint of adding a volume of wood to a stem of increasing radius was corrected by converting tree-ring widths into basal-area increments by using the following equation:

$$\mathrm{BAI} = \pi(R_t^2 - R_{t-1}^2) \qquad (1)$$

where *R* is the radius of the tree and *t* is the year of tree-ring formation (Table 2). In the case of cores without pith, we estimated the missing rings by using a geometrical method and taking into account the mean growth rate of the innermost rings present in samples with pith.

To quantify climate–growth relationships, tree-ring widths were converted into indices by standardizing and detrending raw data for each tree and plot using the program ARSTAN (Cook, 1985). To assess the quality of tree-ring width series several dendrochronological statistics were calculated considering the common interval 1970–2010 (Fritts, 1976) (Table 2): AC, the first-order autocorrelation of raw tree-rings width data, a measure of the year-to-year growth similarity; MS, the mean sensitivity of residual chronologies which measures the relative year-to-year variability in width of consecutive rings; *rbt*, the mean between – trees correlation which quantifies the similarity in residual width indices among trees, PC1, the percentage of variance explained by the first principal component which is an estimate of the common variability in growth indices among all trees located within each site. The chronology segment with expressed population signal (EPS) values higher than 0.85 was regarded as reliable and used in further climate–growth analyses, where EPS is a measure of the statistical quality of the mean site chronology as compared with a perfect infinitely replicated chronology (Wigley et al., 1984). Finally, the shared variation among residual chronologies in the common period 1970–2010 was evaluated for both natural and planted stands using principal component analysis (PCA) based on covariance matrices.

We related tree-ring width indexed chronologies to monthly climate data at tree level for each plot (mean temperature and total precipitation, period 1970–2010) using Pearson correlation coefficients. Also, climate–growth correlations were calculated considering separately the average correlations among grouped trees between planted vs. natural stands at regional scale. Bootstrapped confidence intervals were calculated for these correlations (Fritts, 1976). Mean regression coefficients were regarded as significant ($P < 0.05$) if they were at least twice their standard deviation after 999 bootstrapped iterations. Climate–growth relationships were analyzed from August of the previous year up to September of the year of tree-ring formation based on previous dendrochronological studies in *P. nigra* (Creus and Puigdefabregas, 1983; Richter et al., 1991; Génova and Martínez-Morilla, 2002). Correlation and bootstrap confident intervals were calculated using the program Dendroclim2002 (Biondi and Waikul, 2004).

2.3. Growth patterns and sensitivity to drought

To estimate tree growth response to drought we quantified the relative mean reduction in BAI of natural and planted forests as related to selected severe droughts (1994–1995, 1999 and 2005). We calculated the percent BAI reduction (BAI_{red}) as follows:

$$\mathrm{BAI}_{red} = 100((\mathrm{BAI}_D - \mathrm{BAI}_{D-1})/(\mathrm{BAI}_D + \mathrm{BAI}_{D-1}))/2 \qquad (2)$$

where BAI_D and BAI_{D-1} are the BAI values for the drought year and the previous one, respectively. In all cases BAI_D was lower than BAI_{D-1}. In the case of the consecutive droughts in 1994 and 1995 the BAI_D value was considered as the mean BAI value for those two years.

In order to characterize different aspects of resilience to drought we calculated four resilience indices following Lloret et al. (2011) (BAI resistance, BAI_{Rt}; BAI recovery, BAI_{Rc}; BAI resilience, BAI_{Rs}; and relative BAI resilience, BAI_{RRs}). We calculated these indices using ratios between post-drought and pre-drought BAI values of natural and planted forests and using the following formulae:

$$\mathrm{BAI}_{Rt} = \mathrm{BAI}_D/((\mathrm{BAI}_{D-1} + \mathrm{BAI}_{D-2} + \mathrm{BAI}_{D-3})/3) \qquad (3)$$

Table 2
Age and growth features and related dendrochronological statistics based on radial-growth series for each studied plot. The statistics and mean basal area increment (BAI) values were calculated for the common period 1970–2010. All dendrochronological statistics were calculated for residual series excepting AC which was obtained for raw tree-ring width data.

Stand type	Site code	Age (SD) (years)	BAI (SD) (cm^2 $year^{-1}$)	Dendrochronological statistics				
				AC[a]	MS	*rbt*	PC1 (%)	EPS
Plantation	PNP1	48 (4)	2.27 (0.66)	0.683	0.330	0.700	60.87	0.979
Plantation	PNP2	28 (2)	6.40 (2.72)	0.733	0.278	0.761	53.53	0.982
Plantation	PNP3	35 (2)	7.09 (2.67)	0.823	0.289	0.722	56.32	0.977
Plantation	PNP4	40 (2)	2.95 (1.01)	0.747	0.366	0.656	63.72	0.975
Plantation	PNP5	29 (3)	6.27 (3.57)	0.830	0.264	0.612	64.56	0.977
Plantation	PNP6	44 (3)	5.05 (1.92)	0.736	0.232	0.661	41.58	0.983
Plantation	PNP7	–[b]	–	–	–	–	–	–
Plantation	PNP8	28 (1)	3.96 (1.70)	0.852	0.247	0.571	45.68	0.959
Plantation	PNP9	–	–	–	–	–	–	–
Plantation	PNP10	30 (3)	4.57 (2.56)	0.764	0.322	0.621	81.99	0.965
Natural	PNN1	111 (31)	10.86 (6.79)	0.603	0.570	0.514	42.15	0.915
Natural	PNN2	134 (38)	16.06 (5.01)	0.630	0.467	0.597	58.63	0.901
Natural	PNN3	–	–	–	–	–	–	–
Natural	PNN4	80 (11)	6.65 (1.78)	0.766	0.325	0.626	50.68	0.939
Natural	PNN5	55 (14)	7.95 (1.63)	0.705	0.502	0.485	49.53	0.923
Natural	PNN6	70 (43)	8.60 (2.02)	0.604	0.319	0.493	47.65	0.952
Natural	PNN7	109 (27)	7.84 (0.55)	0.612	0.478	0.438	51.64	0.908
Natural	PNN8	124 (28)	7.62 (1.75)	0.528	0.456	0.579	77.64	0.930

[a] AC, first-order autocorrelation; MS, mean sensitivity; *rbt*, mean between-trees correlation; PC1, variance accounted for by the first principal component; EPS, Expressed Population Signal.

[b] Plots without enough tree-ring data for the dendrochronological statistics.

$$\mathrm{BAI}_{Rc} = ((\mathrm{BAI}_{D+1} + \mathrm{BAI}_{D+2} + \mathrm{BAI}_{D+3})/3)/\mathrm{BAI}_D \quad (4)$$

$$\begin{aligned}\mathrm{BAI}_{Rs} &= (\mathrm{BAI}_{D+1} + \mathrm{BAI}_{D+2} + \mathrm{BAI}_{D+3})/(\mathrm{BAI}_{D-1} + \mathrm{BAI}_{D-2} + \mathrm{BAI}_{D-3}) \\ &= \mathrm{BAI}_{Rt} \times \mathrm{BAI}_{Rc} \quad (5)\end{aligned}$$

$$\begin{aligned}\mathrm{BAI}_{RRs} = {} & ((\mathrm{BAI}_{D+1} + \mathrm{BAI}_{D+2} + \mathrm{BAI}_{D+3}/3) - \mathrm{BAI}_D)/((\mathrm{BAI}_{D-1} \\ & + \mathrm{BAI}_{D-2} + \mathrm{BAI}_{D-3}/3) - \mathrm{BAI}_D) \times (1 - (\mathrm{BAI}_D/(\mathrm{BAI}_{D-1} \\ & + \mathrm{BAI}_{D-2} + \mathrm{BAI}_{D-3}/3)) \\ = {} & \mathrm{BAI}_{Rs} - \mathrm{BAI}_{Rt} \quad (6)\end{aligned}$$

where BAI_D, BAI_{D-t} , BAI_{D+t} are the BAI values for the drought year, the previous t ones and t years after the drought, respectively.

2.4. Growth–defoliation modeling

Linear Mixed-effects Models (LMM) were used to assess how tree size (log-transformed dbh), (log-transformed) age, crown condition (including PPM defoliation), stand development and competition (assessed as current stand density which was considered as a proxy of past management) and climatic variables (APgrow, ATgrow and summer P/PET) affected growth (log-transformed BAI) in natural vs. planted stands at regional scale. We focused on BAI trends for the period 2000–2010 for which annual crown status records were available for all studied trees and plots. The predictor variables and their interactions were introduced as fixed effects. First, BAI was modeled as a function of time and age. Second, we introduced tree dbh and density variables one by one to contrast the individual contribution of each of these variables to BAI variability. Lastly, we explored the influence of crown condition data and climatic variables (APgrow, ATgrow and summer P/PET) on BAI. Furthermore, to test the influence of several variables (age, elevation, drought severity, dbh, temperature conditions) on BAI in natural and planted stands as related to the spatial distribution imposed by AFMN plots we repeated the same analyses considering only the most drought sensitive populations (located below 1500–1600 m) also showing similar tree density values. This allowed us to verify if the effects of those variables on BAI changed under similar site conditions.

A final composite model was built using all fixed factors, retaining only the significant effects, including age and a first-order autocorrelative term to account for the effects of temporal autocorrelation on BAI. Mean spatial Moran indices (MI) of the residuals of the growth model were calculated to deal with the effect of spatial autocorrelation on growth at stand level following Qian and Kissling (2010). To choose the most parsimonious model, we selected that with the lowest Akaike Information Criterion (AIC) (Burnham and Anderson, 2002). Statistical analyses were carried out with the packages *nlme*, *MuMIn* and *corAR1* of the R software (R Development Core Team, 2013). Significance for statistical analyses was accepted at $\alpha < 0.05$.

2.5. Factors contributing to Pinus nigra decline

We used structural equation modeling (SEM) to quantify the effects of multiple correlated drivers, expressed as standardized path coefficients (usually drawn as arrows), to the last one drought-induced forest decline event that occurred in 2005 (Grace, 2006). We first constructed an *a priori* model of our system wherein the growth variables or predictands (ratio between the 2005 and mean 2000–2004 BAI values; mean crown defoliation over 2006–2010 period) were entered as a function of predictors as water availability (mean value of the APgrow over the 2000–2010 period), management as reflected by current competition (mean stand density for the period 2000–2010) and PPM defoliation (binary variable: absence or presence of severe PPM defoliations).

Then, we selected those models with the best fit by comparing the actual covariance matrices representing the relationships between variables and the estimated covariance matrices for each type of stand. The best fitted model was selected based on several goodness of fit indices: a high probability value (P) related to the χ^2 test which compares the observed and modeled covariance matrices, a low AIC indicating a parsimonious model, and a high (close to 1) Goodness-of-Fit Index (GFI) and a low (close to 0) robust root mean square error of approximation (RMSEA) (Grace, 2006). Since SEM does not allow correcting for the effects of spatial autocorrelation on significance levels of path coefficients, alternatively we validated each path by using spatially explicit LMMs following

Bartomeus et al. (2011). We fitted SEMs throught maximum likelihood estimation with multinomial errors using AMOS 19 (Arbuckle, 2010).

3. Results

3.1. Climate trends

In the study area we observed significant ($P < 0.05$) and opposite trends in ATgrow (increasing) and APgrow (decreasing) anomalies since 1950 (Fig. 2). The drying trend was mainly due to the long-term decrease in spring rainfall over the second half of the 20th century. The mean temperature increased at average rates per plot of +0.02 and +0.06 °C yr^{-1} for natural and planted stands, respectively (Fig. 2). The reduction in precipitation amount during the growing period was more intense in planted (−0.9 mm yr^{-1}) than in natural stands (−0.3 mm yr^{-1}). Overall, the early 1960s (mean APgrow anomaly in natural vs. planted = 0.20 vs. 0.25) and 1970s (0.35 vs. 0.36) were wet decades and the 1990s (−0.36 vs. −0.37) and 2000s (−0.07 vs. −0.19) were very dry decades (Fig. 2).

3.2. Structure, growth patterns and sensitivity to drought

The sampled *P. nigra* forests in the natural (planted) sites were on average 97 (35) years old and their mean dbh and height were 37.9 cm (17.9 cm) and 16.2 m (8.4 m), respectively (Table 1). The sites with highest density values were plantations (1000 stems ha^{-1} vs. 560 stems ha^{-1} in natural stands) (Table 1). The mean BAI for the period 1970–2010 was significantly lower ($F = 12.1$, $P < 0.05$) in planted (4.82 cm^2 year^{-1}) than in natural stands (9.37 cm^2 year^{-1}).

The first-order autocorrelation (AC) of the tree-ring width individual series was higher in planted than in natural stands ($F = 22.3$, $P < 0.05$), suggesting a higher year-to-year persistence in growth of the former forests, whereas the mean sensitivity (MS) was higher in natural than in planted stands ($F = 13.3$, $P < 0.05$) indicating a higher inter-annual variability of radial growth in the natural stands (Table 2). The mean correlation between trees (*rbt*) and the expressed population signal (EPS) were higher in planted than in natural stands ($F = 14.7$, $P < 0.05$) confirming a higher growth coherency among trees in plantations than in natural stands.

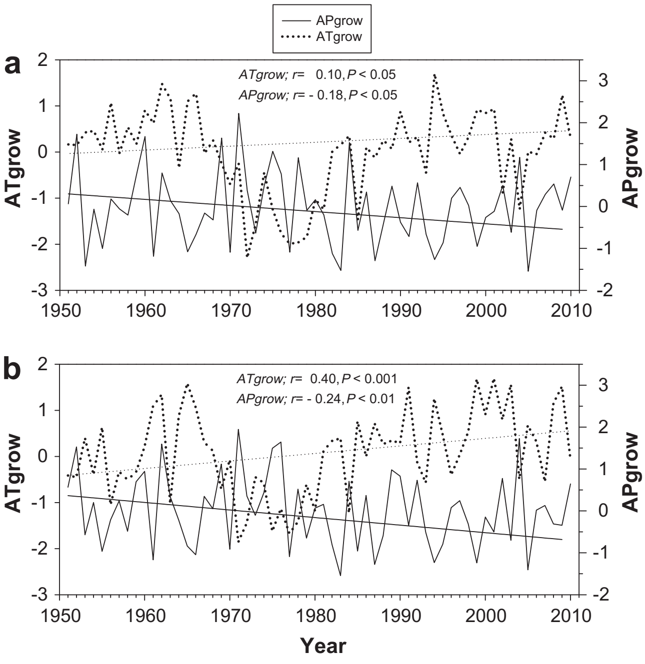

Fig. 2. Trends in the study area of precipitation (APgrow – continuous lines) and temperature (ATgrow – dashed lines) anomalies during the growing season (from March to August) for the period 1950–2010 in natural (a) and planted (b) *P. nigra* stands.

The selected dry years during the late 20th century (1994–1995, 1999 and 2005) coincided with sharp reductions in tree-ring width indices in both planted and natural stands (Fig. 3a). The maximum reduction in growth was detected for trees from natural stands in response to the 2005 drought, being significantly higher than in the rest of dry years (Fig. 3a). The PCA showed that natural and planted stands presented different growth patterns. The first and the second principal components (PC) accounted for 29.5% and 22.1% of the total variation in growth, respectively (Fig. 3b).

The mean relative reduction in BAI (BAI_{red}) in response to the selected droughts was significantly higher (Mann–Whitney *U* test = 4.00, $P = 0.005$) in planted (53.4 ± 5.5%) than in natural stands (35.7 ± 7.5%). The maximum BAI_{red} was also detected for planted stands, particularly in response to the 1994–1995 (51.3%) and 1999 (61.1%) droughts. However, natural stands showed higher BAI_{red} values in 2005 (63.5%) than planted ones (48.8%) (Fig. 3a). Declines in growth during the selected droughts episodes were in average significantly ($U = 10.00$, $P = 0.003$) lower in natural (0.78 ± 0.06), i.e., showing a higher BAI resistance (BAI_{Rt}), than in planted trees (0.48 ± 0.03) (Fig. 3a). The maximum BAI_{Rt} was found in natural stands in response to the 1994–1995 droughts. The BAI recovery (BAI_{Rc}) after the selected droughts episodes in plantations was lower than observed in natural stands, but it was significantly lower in 1999 for plantations. As a result, natural stands were more resilient (higher BAI_{Rs}) than planted ones both in 1994–1995 (natural vs. planted = 1.39 vs. 0.73) and 1999 (1.25 vs. 0.83), but not in 2005 (1.13 vs. 1.07) (Fig. 3a). The relative resilience (BAI_{RRs}), which accounts for the impact of the selected droughts, showed higher divergences between natural and planted trees in 1994–1995 (0.67 vs. 0.21) and 1999 (0.45 vs. 0.20), but again did not differ between stand types in 2005 (0.62 vs. 0.57) (Fig. 3a).

3.3. Climate–growth relationships

Current May and June precipitation were positively related to growth, and the mean climate–growth correlations for these months were significantly higher in planted than in natural stands, whereas June temperature was significant and negatively associated with growth only in planted stands (Fig. 4, see also Appendix B). Tree growth was enhanced by wet and cold conditions (low mean and maximum temperatures) during the previous autumn (September) and by warm conditions (high minimum temperature) during late winter and early spring (February), being these relationships stronger in natural than in planted stands (Fig. 4). Wet and cold conditions in January also favored growth of planted stands.

3.4. Linear mixed models for BAI and defoliation

The selected LMMs for BAI (planted stands, AIC = −251.3; natural stands, AIC = 40.7) showed similar negative and positive responses to years with low (e.g., 1994–1995, 1999, 2005) and high (e.g., 1992, 1997) water availability, respectively (Fig. 3a). However, the divergence in BAI between natural and planted stands was evident after the 1990s droughts. According to these models, time showed significantly divergent effects on BAI. There was significant positive (negative) effect on BAI for dbh (Age) being higher in planted than natural stands (Table 3). As expected, BAI decreased as crown dieback increased and this negative effect significant in planted but not in natural stands (Appendix B, Fig. B1).

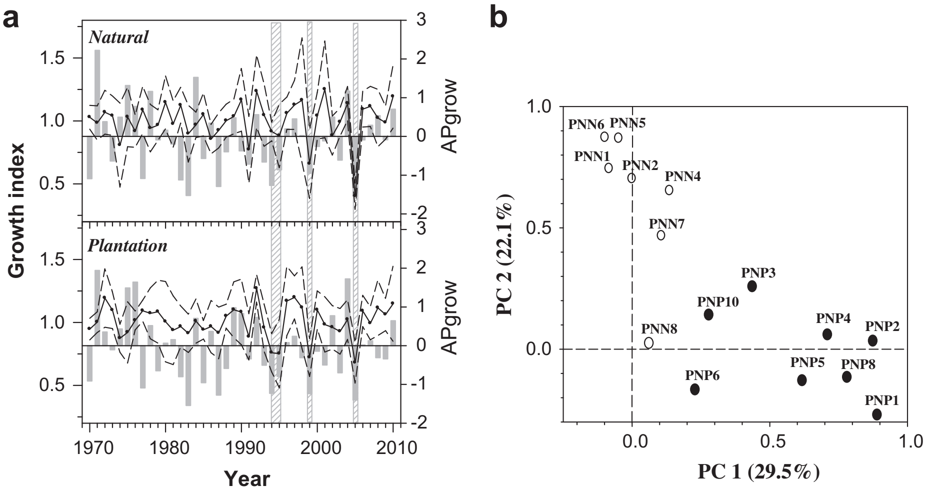

Fig. 3. Residual tree-ring width mean chronologies (±SD) of natural and planted *P. nigra* stands (means in black, SDs are dashed lines) as related to severe droughts (1994–1995, 1999 and 2005 – vertical hatched areas) and precipitation (APgrow, gray bars) (a). Loadings in the first two principal components obtained from comparing tree-ring width indexed series (period 1970–2009) for natural (empty circles) and planted (filled circles) stands (b). The percentage of variance explained by the two first components is shown. The sites codes are the same than in Table 1.

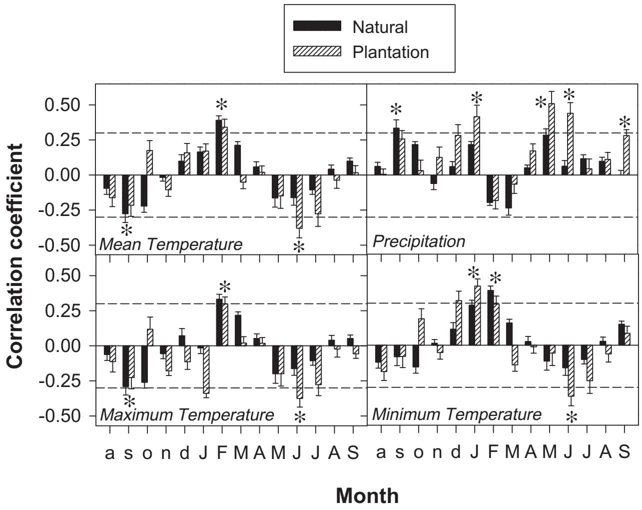

Fig. 4. Relationships (Pearson correlation coefficients ± SE) obtained by comparing radial growth (tree-ring width indices) and monthly climatic data (mean temperatures, mean maximum and minimum temperatures, total precipitation) for natural (black bars) and planted *P. nigra* stands (hatched bars). Growth is related with monthly climatic data from the previous (months abbreviated by lowercase letters) to the current (months abbreviated by uppercase letters) years, where the current year is the year of tree-ring formation. The bars surpassing dashed lines and the asterisks indicate significant ($P < 0.05$) correlation coefficients.

BAI also decreased in response to increasing stand density being this effect particularly strong in the case of planted stands (Table 3).

Lastly, regarding the climatic variables, BAI increased with precipitation during the growing period (APgrow) and decreased with warmer conditions during this period (high ATgrow values) in both types of stands. Summer P/PET also significantly enhanced BAI, being its positive effect on growth higher in planted than in natural stands. Furthermore, the interactive effect of stand density and summer P/PET also affected BAI this influence being particularly marked in planted stands, i.e., in planted stands tree-to-tree competition modulated the positive effect of wet summer conditions on growth. Finally, the interaction between anomalies in temperature and precipitation during the growing period (ATgrow × APgrow) affected BAI in different ways showing negative and positive effects in planted and natural stands, respectively. This suggests that tree growth in plantations is particularly sensitive to the negative effects of high temperatures (Fig. 4; Table 3, Appendix B, Table B1), irrespective of water availability. Further, the effects of the interaction between age and summer P/PET also affected negatively BAI being this effect on growth higher in planted than in natural stands, suggesting that age modulated the positive effect of wet summer conditions on growth. The same analyses considering only the most drought sensitive stands located at elevations below 1500–1600 m showed similar results (data not shown).

3.5. Factors contributing to Pinus nigra decline

The conceptual model of tree growth and crown condition in natural and planted stands provided a robust framework to obtain adequately fitted SEMs for trees from natural and planted stands (Fig. 5). The Moran indices indicated that spatial autocorrelation was not significant ($P > 0.05$) in the selected SEMs neither for planted nor for natural stands. The SEMs with the best fit included the direct effects of water availability during the growing period, and tree density on BAI and crown condition, the direct effect of PPM on defoliation, and the indirect effects of water availability and tree density mediated by BAI on crown dieback. These relationships were able to explain from 77% (planted stands) to 83% (natural stands) in crown status variability and from 75% (natural stands) to 87% (planted stands) in growth variability, respectively. The respective positive and negative effects of water availability and crown dieback on BAI were stronger in planted than in natural stands. The negative effect of tree density on BAI was also more important in planted than in natural stands (Table 3; Fig. 5). Defoliation was mainly driven by PPM outbreaks, being this effect more relevant in natural than in planted stands. Again, these results were similar for the most drought sensitive populations located below 1500–1600 m (data not shown).

4. Discussion

4.1. Climate and growth trends

The ultimate causes of the reported differences in tree growth between natural and planted stands – which may include tree genotype, establishment type, sites chosen for planting, tree

Table 3
Statistical parameters of the evaluated fixed factors and selected interactions in linear mixed-effects models fitted to basal-area increment data for the period 2000–2010. Significant ($P < 0.05$) factors are presented in bold characters.

Fixed effects	Estimate Stand type		SE Stand type		*P* Stand type	
	Planted	Natural	Planted	Natural	Planted	Natural
Intercept	**4.0305**	**3.8800**	1.4184	0.8134	0.0070	<0.001
Time	**0.0062**	−**0.0341**	0.0025	0.0112	0.0292	0.0068
Age	−**0.6054**	−**0.4903**	0.1468	0.1773	<0.001	0.0018
Dbh	**2.0696**	**0.6748**	0.0272	0.0247	<0.001	0.0066
Crown dieback	−**0.0021**	−0.0008	0.0007	0.0001	0.0120	0.5426
Tree Density	−**0.0230**	−**0.0010**	0.0022	0.0003	<0.001	0.0359
APgrow	**0.0039**	**0.0022**	0.0006	0.0005	0.0141	0.0308
ATgrow	−**0.6256**	−**0.3458**	0.1618	0.1110	<0.001	0.0020
Summer *P*/PET	**2.6399**	**1.1457**	1.1289	0.3931	0.0198	0.0377
Density × summer *P*/PET	−**0.0201**	−0.0050	0.0094	0.0014	0.0034	0.4401
ATgrow × APgrow	−**0.0025**	**0.0036**	0.0005	0.0009	<0.001	<0.001
Age × summer *P*/PET	−**0.5947**	−**0.2748**	0.3427	0.1638	0.0388	0.0342

Abbreviations of variables: Dbh, diameter at breast height; APgrow and ATgrow, annual anomalies of standardized precipitation and mean temperature for the growing period (from March up to August); summer *P*/PET, ratio of precipitation to potential evapotranspiration in summer (from June up to August).

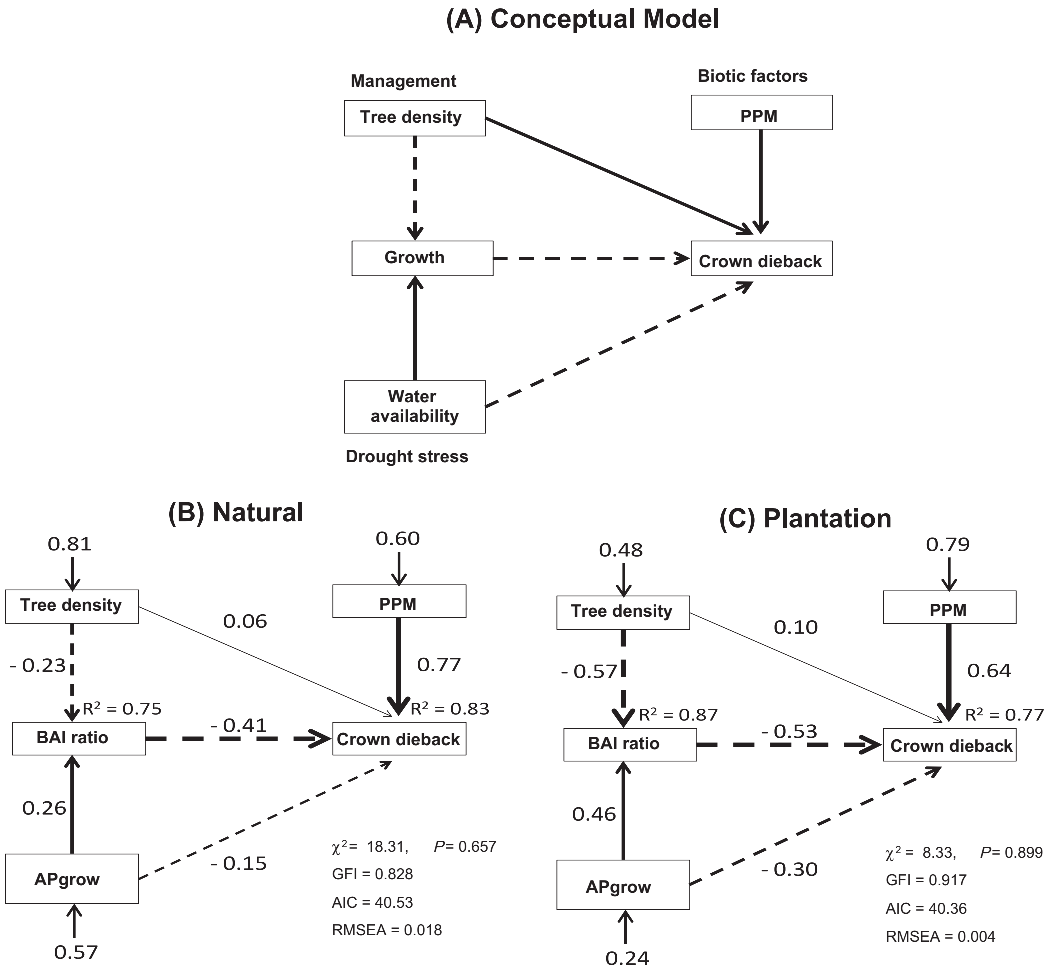

Fig. 5. Conceptual model (a) representing the hypothesized causal relationships among explanatory (*drought stress* – APgrow – *management* – tree density- and *biotic factors* (strong defoliations by the Pine Processionary Moth – PPM) and response (growth–BAI ratio, crown dieback) variables. Selected structural equation models for (b) natural and (c) planted *P. nigra* stands. The standardized path coefficients displayed over arrows are significant ($P < 0.001$) and show how strongly changes in one variable modify another one, whereas the arrow width is scaled proportionately to the strength of this association (solid and dashed arrows correspond to positive and negative relationships, respectively). The arrows pointing measured variables indicate the error terms associated with their measurement, i.e. unexplained variance. The proportion of variance explained (R^2) is interpreted similarly to a regression analysis. The model goodness of fit indices are shown in the lower right side (see text for more details; note that high *P* values correspond to models with satisfactory fitness parameters).

density, tree age – cannot be determined in this study. But our findings provide evidence that sharp growth reductions in *P. nigra* may be triggered by spring and early summer precipitation which have steadily declined in the study area (De Luis et al., 2009). Spring precipitation enhances radial growth of *P. nigra* and other pine species in xeric areas as reported in other Spanish pine forests

(Andreu et al., 2007; Bogino and Bravo, 2008; Candel-Pérez et al., 2012; Olivar et al., 2012; Sánchez-Salguero et al., 2012b), in Scots pine forests from the dry inner Swiss Alps (Eilmann et al., 2009), and in Aleppo pine forests from Greece (Sarris et al., 2010). Further, water shortage in spring and summer may enhance crown dieback as has been observed in Norway spruce (Solberg, 2004).

Natural and planted pine forests in the Mediterranean Basin are likely to experience strong negative effects on growth associated with warming-enhanced drought stress (Lindner et al., 2010). Droughts might be expected to affect more severely populations located near the species rear edge, where trees face the species' aridity tolerance limit, and this drought stress may be particularly exacerbated in dense stands (Vilà-Cabrera et al., 2011; Sánchez-Salguero et al., 2012a,b). Several authors have found forest dieback episodes and changes in climate–growth relationships in relation to severe droughts during the last 30 years in Spain (Tardif et al., 2003; Camarero et al., 2004; Peñuelas et al., 2007; Martín-Benito et al., 2010a). Growth is currently limited by temperature in high elevation Mediterranean forests and it could experience increases as a result of warming (Tardif et al., 2003; Linares and Tíscar, 2010). However, the productivity of Mediterranean mountain tree species might be also constrained by severe spring-summer droughts (Férnandez-Cancio et al., 1996; Martínez-Vilalta et al., 2008). Further, recurrent droughts reduce the carbon uptake by trees and increase their respiration rates thus reducing their capacity to grow (Breda et al., 2006; McDowell et al., 2008; Galiano et al., 2011; Moreno-Gutiérrez et al., 2012).

The assessed climate–growth associations showed different patterns among natural and planted stands (Fig. 4). The radial growth in planted forests showed a high sensitivity to water availability in the previous winter and current spring, whereas growth in natural stands responded more to previous autumn precipitation and late-winter minimum temperature before tree-ring formation started (Fig. 4). However, both high temperatures and precipitation amounts in January enhanced growth in planted stands suggesting that wet and warm late winters either improve carbohydrate synthesis and storage for earlywood formation in spring or increase the soil water reserves for cambial resumption during the growing period (Galiano et al., 2011; Pasho et al., 2011).

Our results agree with those of other authors suggesting that species' responses to climate are site dependent and may be modulated by the stand density (Martín-Benito et al., 2010a; Camarero et al., 2013). It also agrees with the contention that *P. nigra* is a drought-sensitive species susceptible to both rising temperatures and decreasing precipitation (Linares and Tíscar, 2010; Esteban et al., 2012) being the species' vulnerability (resilience) to drought higher (lower) in densely planted than in natural forests.

4.2. Factors contributing to Pinus nigra decline: increased vulnerability and resilience loss

Manion's (1981) conceptual model has proven difficult to test in the field (Dobbertin, 2005), particularly in plantations (Sánchez-Salguero et al., 2012a). We found that several drivers act synergistically and in different ways on *P. nigra* growth and crown condition in natural vs. planted stands (Fig. 5). Drivers of tree growth and crown dieback act differently in both densely planted and natural stands but, overall, spring–summer water deficit and tree density were the most important drivers of tree growth (Linares and Tíscar, 2010; Martín-Benito et al., 2010a; Sánchez-Salguero et al., 2012a), presumably acting as inciting and long-term predisposing factors, respectively. Crown dieback was associated with additional inciting and contributing factors such as drought stress and PPM defoliation, respectively. Thus, despite punctual PPM outbreaks increased defoliation and reduced growth, extreme drought events and stand structure were the main drivers of decline and determined the long-term differences in vulnerability and resilience between natural and densely planted forests (Table 3; Fig. 5).

In agreement with previous studies (e.g., Carnicer et al., 2011; Sánchez-Salguero et al., 2012a,b) our results confirm that decline is negatively driven by low water availability and high temperatures during the growing period, and also by summer drought intensity. In wet years warmer temperatures enhanced growth in natural stands but not in planted ones subjected to similar site conditions (but see Martín-Benito et al., 2010a). Water availability per unit of basal area is likely to be lower in plots with higher tree density and hence increase competition (Martín-Benito et al., 2010b), being this effect higher in planted than in natural stands (Table 3; Fig. 5). The relatively high tree density in the studied planted stands is likely the result of management abandonment during the last decades, as a consequence of the reduction of thinning intensity and frequency in this area since the 1980s (Montero, 1997). The existence of significant interactions between drought stress and density on growth, defoliation or mortality suggests that competition and plot-level water availability exert additive effects on growth in very dense planted stands, in contrast with low density natural ones.

Previous drought events may have also predisposed by weakening trees (Bréda and Badeau, 2008) leading to defoliation and decline at the driest sites during the severe 1990s and 2000s droughts (Sánchez-Salguero et al., 2012b). The differential spatio-temporal vulnerability and resilience (here assessed as growth and vigor losses) for natural and planted stands in response to extreme droughts was linked with a warming trend during the growing period, particularly in planted stands in agreement with our hypothesis (Table 3). Long-term warming has been pointed out as a major decline driver in other Mediterranean tree species (Sarris et al., 2007; Gómez-Aparicio et al., 2011; Sánchez-Salguero et al., 2012b).

Our study provides further evidence about vulnerability and resilience of Mediterranean pine forests to climate change by introducing the performance of different growth-decline components in the comparison of natural vs. densely planted forests (see also Lloret et al., 2011). Tree growth was relatively higher in natural stands (Table 2) and, as expected, the basal area increment was positively related with time in planted stands comprising mostly young trees but not in natural ones including mainly old trees (Candel-Pérez et al., 2012). Our results agree with previous studies showing that planted trees suffer greater growth reductions during droughts (e.g., Sánchez-Salguero et al., 2012b), and with the notion that the recovery rate after disturbance in natural forests can be high (Granda et al., 2013). We also observed that planted trees retained proportionally lower growth rates up to three years after the drought, and their resilience was therefore lower than trees from naturally regenerated stands. Hence, trees from non-planted stands perform better after low growth periods and are more resistant to low growth periods than planted trees. Thus, the ability of natural trees to recover to pre-drought levels is notably greater than that of planted trees (Fig. 3a). The lower resistance of densely planted trees could reflect reduced vigor, which is consistent with the well-documented drought-induced decline process of rear-edge forests (Andreu et al., 2007; Sánchez-Salguero et al., 2012a). In spite of the variability in the response to different drought episodes, we found that factors that influence individual performance through time (competition) persist through successive episodes in planted forests (Fig. 5). Ultimately, age effects did not affect the growth resistance, recovery or resilience abilities since old trees did not show significant differences in those variables as compared with young ones irrespective of the stand type (results not presented).

As expected tree age was negatively related to basal area increment, but this effect was higher in planted than in natural stands.

Recent growth patterns are also related to the tree crown status (Drobyshev et al., 2007) (Table 3, Fig. 5). Needle loss could be triggered by drought as an avoidance mechanism to maintain a favorable water balance by reducing transpiring needle area (Bréda et al., 2006), being this a key mechanism to differentiate the responses of natural vs. planted stands (Dobbertin, 2005; Martín-Benito et al., 2008) (Fig. 5). Our hypothesis that these dense plantations would show a high risk of decline under severe water deficit is therefore in agreement with the discussed growth–defoliation models and the resilience-vulnerability growth indices.

4.3. Drought and past management are driving forest decline in rear-edge pine forests

Our data suggest that past management leading to very dense stands may act as stressor acting continuously on tree performance through increased competition for water, particularly in drought-prone areas, and that this condition could be intensified by warmer conditions. Clearly, structural attributes modulate the adaptation, vulnerability and resilience of forests to climate-induced stress. The decline processes taking place in Andalusian Spanish planted *P. nigra* forests were likely predisposed by the absence of thinning. On the other hand, a strong interaction between stand structure and climate–growth relationships was also detected (see Linares et al., 2010). Furthermore our results suggest that the negative effects of current climate conditions may be related to threshold effects on specific components of resilience such as loss of resistance rather than to a gradual loss of overall resilience over time.

The lack of silvicultural management (reduced or null thinning) of the studied plantations led to the existence of dense *P. nigra* stands at sites that may be currently too xeric for the performance of this species (Fernández-Cancio et al., 2011). Even in cases of severe spring-summer drought, however, drought stress was not the sole factor causing decline but rather a long-term factor that weakens the vigor of the trees and, in combination with unfavourable site conditions, renders them susceptible to additional stressors such as PPM defoliation. The amount of green needles and carbon reserves may render a positive feedback that constrains the recovery of trees and explains the delayed effects of drought on tree growth, which have been reported elsewhere (e.g., Bréda et al., 2006; Bigler et al., 2007). Thus, densely planted stands may face inevitable constrains on growth when crown height and water are simultaneously limiting (Lines et al., 2012). In forest ecosystems, a tradeoff between resistance and recovery after drought episodes could also occur if both resistance and recovery depend in part on the amount of stored carbohydrates (Galiano et al., 2011). Long-term warming stress could impose further challenges to overcoming drought events (Allen et al., 2010), such as a requirement for superior carbon balance when faced with the need to recover from drought or the loss of needles induced by insect outbreaks (Franklin et al., 1987). However, carbohydrate consumption required to sustain growth and respiration will increase due to rising temperatures (Adams et al., 2009; McDowell et al., 2008), potentially increasing the negative effects of warming-induced drought in planted forests.

4.4. Implications for management

Altogether, these results constitute new information which not only furthers our understanding of Mediterranean forests, but will also aid in developing new guidelines for adapting forests to withstand climate warming (Millar et al., 2007). Thinning of drought-prone planted forests should reduce competition between trees for soil water and enhance the species' adaptive capacity (increasing resilience and decreasing vulnerability) to withstand drought stress. Planting mixed stands dominated by species resistant to drought stress is also advisable. Further studies of climate change effects on tree growth performance must necessarily consider stand origin and the period of establishment of trees, something that has seldom been done so far.

5. Conclusions

In southeastern Spain, annual temperature has increased and spring precipitation has declined during the growing period since 1950 leading to a long-term reduction in water availability. These regional climatic changes affected differently natural and planted *P. nigra* stands at a regional scale. Trees from planted stands experience stronger growth reductions during severe drought episodes than those from natural ones with similar site conditions. Trees from natural stands showed a more plastic response to drought by reducing growth and recovering faster after drought than densely planted trees. Growth in natural stands experienced less inertia in response to climate than in plantations, and this may explain why planted trees were more vulnerable and showed less resilience to drought stress than trees from natural stands. High tree-to-tree competition as a result of past reduced thinning and drought are the major drivers of forest decline in rear-edge *P. nigra* populations. The decline probability of a *P. nigra* tree is conditioned by the stand type (natural vs. planted), the tree size, the competition degree it is subjected to and drought severity. We evidence the vulnerable character of planted *P. nigra* stands compared to natural ones and suggest this may be a common feature in the forecasted warmer and drier conditions for the Circum-Mediterranean region.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.foreco.2013.09.050.

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