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Abiotic factors modulate post-drought growth resilience of Scots pine plantations and rear-edge Scots pine and oak forests

Álvaro Rubio-Cuadrado^a, J. Julio Camarero^b, Rut Aspizua^c, Mariola Sánchez-González^d, Luis Gil^a, Fernando Montes^d

^aDepartamento de Sistemas y Recursos Naturales, Escuela Técnica Superior de Ingeniería de Montes, Forestal y del Medio Natural, Universidad Politécnica de Madrid. Ciudad Universitaria s/n, 28040, Madrid, Spain.

^bInstituto Pirenaico de Ecología (IPE-CSIC), Avda. Montañana 1005, 50080, Zaragoza, Spain.

^cAgencia de Medio Ambiente y Agua, Regional Ministry of the Environment and Land Management, Junta de Andalucía, C/Minerva 7, Edificio Zeus III, Granada, 18014, Spain.

^dINIA, Forest Research Centre, Department of Silviculture and Forest Management, Crta. La Coruña km 7.5, 28040, Madrid, Spain.

Corresponding author: Álvaro Rubio-Cuadrado (alvaro.rubio.cuadrado@upm.es).

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Abstract

The proportion of planted forests in the Mediterranean Basin is one of the largest in the world. These plantations are dominated by pine species and present a series of characteristics such as low elevation, high competition or small tree size that make them more vulnerable to droughts. However, quantitative assessments of their post-drought growth resilience in accordance with species, site factors and tree characteristics are lacking. In this study we sampled 164 trees at four forest sites located in the drought-prone Sierra Nevada, southeastern Spain. We compared growth responsiveness to drought in rear-edge planted vs. relic natural Scots pine (*Pinus sylvestris*) and coexisting Pyrenean oak (*Quercus pyrenaica*) stands. Our objective was to characterize and compare the different growth responses to drought between species and sites and the effect of the main physiographic factors (altitude, aspect, and slope) on these responses since the influence of these factors on post-drought resistance and resilience has received little attention to date. Our results reveal that the planted pine sites with the lowest mean growth rates displayed greater resistance during drought, and that higher altitude was associated with improved resistance and/or resilience for all species and sites. Natural pine and Pyrenean oak stands were better adapted to the dry climatic conditions of the Mediterranean region where the study was undertaken, displaying greater resistance and/or resilience and lower influence of drought on growth in comparison to stands of planted pines. These results suggest that promoting the conservation of high-elevation pine plantations and enhancing the regeneration of natural pine and oak may improve the resistance and resilience of these drought-prone forest ecosystems.

Keywords: resilience; resistance; recovery; dendroecology; Sierra Nevada.

1. Introduction

Dry spells and heat waves are linked to sharp growth reductions in drought-prone biomes such as Mediterranean forests (Herrero and Zamora, 2014; Marqués et al., 2016). In most of these biomes there have been recent cases of drought-triggered forest die-off (Allen et al., 2010), such cases being particularly abundant and well documented in Mediterranean southern Europe (Bréda et al., 2006; Camarero et al., 2015a; Peñuelas et al., 2001; Sangüesa-Barreda et al., 2015; Sarris et al., 2011, 2007). Ongoing climate change will increase the recurrence and severity of adverse climate extremes such as severe droughts, extreme heat events, and heat waves (IPCC, 2013). The aridification trends forecasted for the 21st century in the Circum-Mediterranean area will make many forests more vulnerable to warming-amplified drought stress (Sánchez-Salguero et al., 2017). In the Mediterranean region, the semi-arid region of southeastern Spain will be one of the most affected areas in Europe, with substantial drying and warming, especially in summer (Jacob et al., 2014).

The effects of droughts on tree growth are not uniform, but rather, vary significantly among species (Allen and Breshears, 1998), sites, forest types and even among coexisting individuals of the same species (Marqués et al., 2016). At tree level, previous studies have shown that the effect of droughts on tree growth varies according to tree size, age and canopy position (Orwig and Abrams, 1997). Growth responses to drought can also differ between natural and planted stands of the same species, particularly near the xeric or southernmost (rear edge) distribution limits of the species' range (Sánchez-Salguero et al., 2013).

Rear-edge tree populations serve as valuable models to assess the sensitivity of trees to drought (Sánchez-Salguero et al., 2012). In these populations, climate can be an important factor regulating the forest dynamic (Rubio-Cuadrado et al., 2018b) and

competition between species (Rubio-Cuadrado et al., 2018c). Moreover, it can underlie rapid shifts in tree species composition at landscape-scale (Allen and Breshears, 1998).

The proportion of planted pine forests in the Mediterranean Basin is one of the largest in the world and the area has a long history of planned forest management (FAO, 2006; Montero, 1997). These plantations were used to address the inherited deforestation resulting from negative woodland management in previous centuries (Valbuena-Carabaña et al., 2010). However, today certain characteristics of these plantations make them more vulnerable to drought damage such as low elevation, high stand density, low structural and genetic diversity and lack of local adaptation due to unknown seed origin (Benito Garzón et al., 2011; Gil et al., 2009). Approaches proposed to help mitigate the effects of climate on these ecosystems include thinning (Fernández-de-Uña et al., 2015) and species diversification, favoring the facilitation of broadleaved species (Gómez-Aparicio et al., 2009).

Scots pine and Pyrenean oak display two main physiological strategies to cope with drought. The gymnosperm forms narrow xylem conduits (tracheids) and maintains leaf water potential above a threshold and within a narrow range (isohydric response) thus limiting C uptake during drought. The angiosperm forms ring-porous wood (with wide vessels susceptible to frost- or drought-induced cavitation) and reduces leaf water potential (anisohydric response) to maintain more constant rates of gas exchange although the risk of hydraulic failure increases (McDowell et al., 2008). In addition, pines often show a more rapid reduction in radial-growth in response to drought in comparison to oaks, which tend to present lagged growth declines (Anderegg et al., 2015).

In this study we compared growth responsiveness to drought in natural/planted-origin Scots pine (*Pinus sylvestris* L.) and natural-origin Pyrenean oak (*Quercus*

pyrenaica Willd.), in the rear-edge and relic stands of these species in Sierra Nevada (Southeastern Spain), where management aims to promote the establishment of Pyrenean oak to enhance diversity in vast pine plantations. The objectives of this study are (i) to evaluate the effect of drought on the growth of these species in the southern marginal populations; (ii) to analyze the effect of the main physiographic factors (altitude, aspect, slope) on growth responses to drought; (iii) to compare the differences between planted Scots pine, natural origin pine and Pyrenean oak with respect to their growth resistance to drought. We hypothesized that natural pine and Pyrenean oak are better adapted than planted pine to the climatic conditions of the study area. Since the influence of physiographic factors or tree variables on resistance and resilience remain poorly explored, understanding these influences may be important in order to accurately predict the response of forests to drought and to develop effective management strategies that enhance ecosystem stability in planted conifer stands.

2. Materials and methods

2.1. Study area

We compared planted and natural-origin (relict) Scots pine stands and natural-origin Pyrenean oak stands located in the National Park of Sierra Nevada (southeastern Spain). Four sampling locations were selected between coordinates 36° 58′ 15″ – 37° 9′ 53″ N, 3° 2′ 54″ – 3° 27′ 34″ W (**Fig. 1, Table 1**) at the sites of Aldeire, Cañar, Jérez del Marquesado and San Jerónimo (ALD, CAN, JER and SJE hereafter). At each site we selected pine plantations dating from the middle of the 20th century, some of which currently also contain Pyrenean oak recruitment. The seeds for these planted pines came from the Central mountain range (Valsaín, central Iberian Peninsula, 430 km north of Sierra Nevada) (Mesa Garrido, 2016). At the San Jerónimo site (SJE site hereafter)

there are two zones of relict natural-origin pine, described as *P. sylvestris* ssp. *nevadensis* (Ceballos and Ruiz de la Torre, 1971), and natural-origin Pyrenean oak forest, hence, both natural pine and oak stands were also selected at this site. In general, the tree cover is continuous over all studied zones except in the natural pine stands, where the density is lower (**Table 1**) and there are abundant gaps in the canopy with a dense, continuous shrub layer.

Figure 1. Maps showing the sampled plots at the four study sites (see codes in **Table 1**) and the outline of the Sierra Nevada National Park situated in southeastern Spain [the inset shows the location of the study area with respect to the Scots pine distribution area in Europe (EUFORGEN, 2009)]. Note that Scots pine plantations were studied at all sites, whereas natural Scots pine and pure oak stands were only sampled at the SJE site.

Climate is Mediterranean with annual mean temperature of 9.2° C and annual precipitation of 579 mm. The soil depth and soil horizons are similar in all locations studied: 15-20 cm A horizon, with decomposed organic material, and 50-70 cm B horizon. The lithofacies is slate or micacite in the oak and planted pine stands and is a calcareous, siliceous mixture in the natural pine stands [FOREDAF database (Chiti et al., 2012)].

2.2. Field sampling

To capture the environmental and structural variability of the studied forests we performed a complete field survey in the four selected zones consisting of 154 sampling plots in total (**Table 1**). These were systematically distributed on a square grid of 250 m × 250 m and sampling was conducted in 2015. In total, 10 plots of planted pine at the SJE and CAN sites had naturally recruited oaks. Great part of the pure oak and most of the mature natural pine areas located within the National Park were included in the study. Areas of young natural pine stands were not inventoried due to the likelihood of genetic mixture with the planted pine forests (Robledo-Arnuncio et al., 2009). The number of natural pine samples was low not only because of the limited area occupied by these trees but also due to restrictions imposed by the protected status of this relic population.

In each plot, a pair of stereoscopic hemispherical images was captured using ForeStereo to characterize the neighborhood and to estimate: basal area (BA), tree density (N) and the mean diameter at breast height (DBH_{stand}) (Rodríguez-García et al., 2014; Sánchez-González et al., 2016). ForeStereo is a device which allows trees located up to 15m from the center of the plot to be mapped and their size estimated (Rodríguez-García et al., 2014). In addition, two cores were extracted at 1.3 m (always

perpendicular to the maximum slope) from a dominant or codominant tree of each species nearest to the plot center using a Pressler increment borer, and the diameter at breast height (DBH_{cored}) was measured with a caliper. In total we sampled 135 planted pines, 7 natural pines and 22 natural oaks. In the light of the results obtained (see Section 3.2), it is considered that this sample size was appropriate. Topographical variables (altitude, slope and aspect) for each plot were obtained from a Digital Terrain Model (PNOA®, Instituto Geográfico Nacional, Spain) with a spatial resolution of 25 m and an altimeter error of less than 5 m (Horacio, 2010).

Table 1. Main characteristics of the study sites. Data are means per site and their margins of error for a 95% confidence interval. The age of the oaks isolates growing in planted pine stands are 57 ± 16 . All oaks are of natural origin.

Site	Aldeire	San Jerónimo	San Jerónimo	San Jerónimo	Jérez del Marquesado	Cañar
Code	ALD	SJE	SJE	SJE	JER	CAN
Stand type	Planted pine	Pure oak	Natural pine	Planted pine	Planted pine	Planted pine
Number of plots	49	12	7	26	29	31
Latitude (North)	37° 7' 43''	37° 5' 48''	37° 5' 47''	37° 6' 21''	37° 9' 53''	36° 58' 15''
Longitude (West)	3° 2' 54''	3° 26' 16''	3° 27' 34''	3° 25' 49''	3° 12' 48''	3° 24' 45''
Mean altitude (m a.s.l.)	1953 ± 36	1726 ± 37	1720 ± 197	1895 ± 23	1850 ± 28	1896 ± 34
Altitude range (m a.s.l.)	1677-2161	1637-1817	1445-1952	1759-1988	1709-1993	1773-2163
Aspect (°)	226 ± 36	306 ± 16	43 ± 21	248 ± 17	127 ± 39	153 ± 19
Slope (°)	17.0 ± 1.3	26.5 ± 4.1	21.4 ± 7.1	20.1 ± 2.6	17.2 ± 1.9	19.0 ± 1.9
DBH _{stand} (cm)	20.3 ± 0.9	21.9 ± 2.2	35.3 ± 21.5	20.8 ± 1.7	21.8 ± 1.1	24.3 ± 1.6
Basal area (m ² ha ⁻¹)	24.1 ± 2.8	30.5 ± 13.4	22.3 ± 53.4	28.9 ± 5.0	33.1 ± 5.1	39.6 ± 7.6
Density (stems ha ⁻¹)	686 ± 76	712 ± 278	375 ± 322	771 ± 142	796 ± 118	775 ± 151
Tree age (years)	50 ± 1	64 ± 11	98 ± 56	48 ± 1	46 ± 1	73 ± 1

2.3. Dendrochronological analyses

Wood cores were mounted on wooden supports and carefully sanded until tree rings were clearly visible. Tree-ring widths were then measured to the nearest 0.01 mm using the semi-automatic Lintab device with the TsapWin software (Rinntech, Heidelberg,

Germany). Tree rings were visually cross-dated and measured, and cross-dating was further verified with the COFECHA program (Holmes, 1997).

We calculated ring-width series for each individual and these series were subsequently transformed into basal area increments (BAI) as this variable captures growth trends better than tree-ring width (Biondi and Qeadan, 2008). The BAI was calculated as follows (Marqués et al., 2016):

$$BAI = \pi(r_t^2 - r_{t-1}^2) \quad (1)$$

where r_t and r_{t-1} are the stem radius at the end and the beginning of a given annual ring increment.

When cores did not contain the pith, the length of the missing radius was estimated for BAI calculation as the distance to the geometric center of the tree, assuming concentric growth. Estimation was carried out by subtracting the corresponding cored length to the radius measured in the field. The final chronologies of planted pine (differentiating between sites), natural pine and oak were built by averaging individual BAI measurements.

Tree age was estimated as follows: In planted pine stands at each site we considered the maximum number of years counted through cross-dating of the rings as the age of all trees. For natural pine and oaks, in those cases where cores reached the pith, age estimation was also performed through cross-dating of the rings. In the other cases (two natural-origin *Pinus sylvestris* and four *Quercus pyrenaica*), the current age was determined by subtracting the annual increments from the current DBH and minimizing the sum of squared residuals of the exponential growth model fitted to the DBH-age data.

2.4. Climate data

Monthly data for precipitation and mean temperature from 99 meteorological stations covering the study area were interpolated at the sampling locations using spatio-temporal Universal Kriging. The generalized product-sum model (De Iaco et al., 2002) was fitted to the space-time variogram. The altitude and the projected coordinates XY, as well as the interactions “altitude $\times$ X” and “altitude $\times$ Y” were included as auxiliary variables in the trend function. The year was also included to reflect possible temporal trends in the climatic data. The variogram model parameters and trend function coefficients were estimated using Iterative Re-Weighted Generalized Least Squares procedure (Gotway and Stroup, 1997; Neuman and Jacobson, 1984).

We calculated the Standardised Precipitation Evapotranspiration Index (SPEI) on 12-month scales (Vicente-Serrano et al., 2010) to estimate the drought intensity. We chose this scale based on previous analyses (Pasho et al., 2011). The SPEI drought index considers the effect of temperatures on evapotranspiration rates and the cumulative water deficit and was calculated based on the 0.5°-gridded Climatic Research Unit dataset (Harris et al., 2014). We selected the grid with coordinates 37.0°-37.5° N and 3.0°-3.5° W. High and low SPEI values correspond to wet and dry conditions.

2.5. Climate- and drought-growth relationships

To determine the main climatic drivers of tree growth, we first removed biological trends in growth by calculating the residual ring-width chronologies for each species using the `detrend.series` function in the *dplR* package (Bunn et al., 2016) in R software (R Development Core Team, 2017). We used a double detrending procedure to remove long-term growth trends. First we fitted a negative exponential curve to raw ring-width data, and then we fitted a 32-year cubic smoothing spline. Observed ring-width values

were divided by fitted values to obtain ring-width indices. The autocorrelation of the resulting residuals was removed using first-order autoregressive models.

Pearson correlation coefficients were then calculated between the residual chronologies (mean series of the residual ring-width indices calculated for planted pine at each site and for natural pine and oak) and monthly climate variables (mean temperatures and total precipitation) for the 1975–2014 period. We only analyzed the common period 1975–2014 in order to avoid the first years of growth of the planted pines, which presented very low BAI increments. Correlation coefficients were calculated from October of the previous year to September of the growth year considering that: (i) climate during the previous year affects growth during the following year in both species (Bogino et al., 2009; Camarero et al., 2015b; Olivar et al., 2015), and (ii) growth can occur from April until September (Aldea et al., 2017).

2.6. *Impact of droughts on tree growth*

We analyzed the most important reductions in BAI of the tree-ring series: 1995 and 2005. These are the only years in which at least 60% of the BAI series of oak (except in 2005), natural pine and planted pine showed a decrease in BAI of at least 40% relative to the average BAI in the 4 preceding years [relative growth change method (Schweingruber et al., 1990)]. The growth response to these unfavorable years and the ability to recover pre-disturbance growth levels after the disturbance were estimated for the tree-ring series of the planted pine at each site, natural pine and oak, through the resistance (R_t), resilience (R_s) and recovery (R_c) indices (Lloret et al., 2011):

$$R_t = BAI_i / BAI_{i-4} \quad (2)$$

$$R_s = BAI_{i+4} / BAI_{i-4} \quad (3)$$

$$R_c = BAI_{i+4} / BAI_i \quad (4)$$

These indices were calculated with 4-year pre- and post-disturbance periods, based on previous studies (Rubio-Cuadrado et al., 2018a,b), using the *pointRes* package in R (van der Maaten-Theunissen et al., 2015).

We used the *t*-test for independent samples, when the model assumptions are met, and the Mann-Whitney *U* test for independent samples, where they are not met, to compare the *Rt* and *Rs* means between oak, natural pine and planted pine.

2.7. Growth modeling

We used linear mixed-effects models to evaluate the factors that influence the BAI (the response variable) of planted pine, natural pine and oak with the following variables as fixed effects: DBH_{cored}, as tree growth of mature trees is driven by tree size (Diaconu et al., 2015; Mencuccini et al., 2005), altitude, aspect (calculated as the cosine of the magnetic bearing, 1 indicates north and -1 south) and slope. In addition, we introduced the dummy variable Stand type (pure oak stand or oak isolate growth in planted pine stand) for the oaks. We considered the period 1975-2014 for the model. We did not include competition variables in the models (such as basal area or density) because the studied forests have been thinned in recent years. Only the year was considered as a random component (1|Year) in all models in order to reduce the effect of the climate variability. In addition, in the planted pine model we also considered site as a random component (1|Site|Year).

The form of the fitted linear mixed-effects models with random intercept and fixed slope was as follows:

$$y_{ij} = \alpha + a_j + \beta z_{ij} + \varepsilon_{ij} \quad (5)$$

where y_{ij} represents $\log(\text{BAI}+1)$ (for the planted pine and for the oak, which showed Gamma distribution for BAI) or BAI (for the natural pine, which showed normal

distribution for this variable) for tree i and year j , α is the general intercept, a_j is the random intercept, β is the vector of general slopes, z_{ij} is the vector of fixed effects and ε_{ij} is the error with a first-order temporal autocorrelation [AR(1)] structure.

To identify the best-supported model we constructed all possible combinations of alternative models from the full model considering fixed and random effects. As the restricted maximum likelihood method (REML) estimates an unbiased variance but does not allow models to be compared by minimizing the Akaike Information Criterion (AIC), we first fitted all possible models using the Maximum Likelihood method (ML), then selected the best model by minimizing AIC and finally fitted it again using the restricted maximum likelihood method (REML) (Zuur et al., 2009). The existence of multicollinearity among explanatory variables was evaluated by calculating the variance inflation factor (VIF) (Dormann et al., 2013), which was always lower than 4 (VIF values larger than 10 indicate high collinearity among variables). The marginal pseudo- R^2 (R^2_m - the percentage of BAI variance explained by the fixed effects) and the conditional pseudo- R^2 (R^2_c - the percentage of BAI variance explained by the fixed and random effects) were estimated according to Nakagawa and Schielzeth (2013). These analyses were performed with the *nlme* (Pinheiro et al., 2018), *MuMIn* (Barton, 2012) and *lmerTest* (Kuznetsova et al., 2017) packages in R.

We also used linear models of BAI (log-transformed for the planted pine and for the oak but not for the natural pine) to analyze altitudinal trends in growth from 1975 to 2014 through the interaction between the year and the altitude. Effects of the interactions are plotted using the *effects* package in R (Fox and Hong, 2009).

2.8. Resilience modeling

We carried out regressions between the response variables, resistance and resilience of each tree for the years 1995 and 2005, and the predictor variables DBH_{cored}, age of the cored trees at the year of each annual radial growth, altitude, aspect and slope. We also considered the following dummy variables: site (for the planted pines), stand type (pure oak stand or oak isolate growth in planted pine stand), and year. Resilience was normalized through the inverse transformation $1/(Rs+1)$. Six different models were fitted: one for each response variable (R_t and R_s) and type of stand (planted pine, natural pine and oak). To do this, we constructed all possible combinations of alternative models and selected the models with the lowest AIC. The model assumptions and the absence of multicollinearity were checked (all variables had a VIF lower than 2). These analyses were performed using R software (R Development Core Team, 2017). We did not use mixed models for these analyses because when the random effects have few levels (and the factor “year” only has two levels), it is advisable to use classical regressions (Gelman and Hill, 2006; Zuur et al., 2007).

3. Results:

3.1. Climate

Temperatures for the sites were similar but precipitations varied between locations (**Fig. 2**). The CAN site had the highest precipitation and ALD and JER sites had the lowest precipitation through the year. SPEI data showed a gradual increase in drought over recent decades (**Fig. 2c**). In fact, southeastern Spain, where the study area was located, is one of the most drought affected areas in Europe (**Fig. S1** of the Supplementary material).

Figure 2. Comparison of the mean monthly temperatures (a) and total monthly precipitation (b) between locations. Data are the average values for the 1975-2014 period. Temporal variability of the SPEI drought index in the study area since 1950 (c). This index was calculated using 12-month-long scales with negative values indicating dry conditions.

3.2. Radial growth

The greatest growth reductions occurred during the 1995 and 2005 droughts followed by the 1999 and 2012 droughts (**Figs. 2c** and **3**). Twenty of the sampled cores presented a missing ring corresponding to 1995 (16 at CAN site, 3 at SJE site and 1 at ALD site), two cores revealed no growth in the years 2005 and 2014 and one core sample with a missing ring was found for each of the years 1999, 2008 and 2010. While in the period 1975-1994 there were neither growth declines nor missing rings, in the period 1995-2014 there were four periods of decreased growth due to the increased recurrence of severe droughts (**Fig. 2c**).

The dendrochronological characteristics of the samples are shown in **Table 2**. With a threshold value of Expressed Population Signal (EPS) > 0.85 , the chronologies were considered reliable and well replicated (Wigley et al., 1984), and the sample size was considered appropriate (Speer, 2012). As regards the 1975-2014 period, the mean Pearson correlations between the master chronologies (mean site series) of the four planted pine stands is 0.56 ($P < 0.01$ in all comparisons), between the master chronologies of the natural pine and the four planted pine stands is 0.71 ($P < 0.001$ in all comparisons) and between the master chronologies of the oaks and the five pine stands (including both natural and planted pine stands) is 0.55 ($P < 0.01$ in all comparisons).

Figure 3. Growth patterns and response to drought presented either as mean basal area increment (a, BAI) or as residual chronologies (b, ring-width indices) for natural oak and Scots pine stands and also for the four pine plantations (SJE, JER, CAN and ALD sites). The right y axis in the lower plot (b) shows the cumulative precipitation, averaged for all sites, from the previous December up to May of the year of tree-ring formation (bars).

Table 2. Description of dendrochronological variables of cored trees.

	Oak	Natural pine	Planted pine
Number of cored trees	22	7	135
Number of sampled cores	44	14	270
Mean / maximum length of series (years)	61/124	98/165	46/73
Mean correlation with master chronologies	0.53	0.66	0.55
Mean sensitivity	0.28	0.41	0.31
Expressed Population Signal (EPS) since 1975	0.92	0.85	0.99

3.3. Climate-growth relationships

In general, growth in the two species was directly related with warm conditions in the previous winter (December-February) and in the late growing season (September) and temperate conditions in late spring and early summer (**Fig. 4**). Wet winter and spring conditions were directly related with pine growth whereas oak was less responsive to climatic conditions.

Figure 4. Pearson's correlation coefficients for oak, natural pine and the four pine plantation sites (SJE, JER, CAN and ALD) between ring-width indices and monthly climatic variables (a, mean temperature; b, total precipitation). We considered the period 1975-2014. The dashed lines show the 0.05 significance thresholds. The temporal window covers the period from October of the previous year (abbreviated by lowercase letters) up to September of the year of tree-ring formation.

3.4. Growth response to droughts: resilience indices

The R_t and R_s indices were significantly higher ($P = 0.018$ and 0.001 respectively) in oak ($R_{t-oak} = 0.53$; $R_{s-oak} = 0.89$) than in pine ($R_{t-pine} = 0.43$; $R_{s-pine} = 0.74$), and R_s was also significantly higher ($P = 0.033$) in natural ($R_{s-natural} = 0.87$) as opposed to planted pines ($R_{s-planted} = 0.73$). Natural and planted pines had similar R_t values. As regards the SJE site, R_t were significantly higher ($P < 0.001$ in both) in oak and natural pine ($R_{t-oak (SJE)} = 0.48$; $R_{t-natural} = 0.39$) than in planted pine ($R_{t-planted (SJE)} = 0.23$), but natural pine and oak had similar R_t values and there were no differences in R_s values of oak, natural pine and planted pine at the SJE site. In general R_t and R_s values for 1995 and 2005 were similar although R_c showed lower values in the 2005 drought in comparison to the 1995 drought (**Figs. 5** and **S2** of the Supplementary material).

Figure 5. Box plots showing the three resilience indices (R_t , R_c and R_s) calculated for radial-growth data (BAI) of oak, natural pine and the four pine plantations (SJE, JER, CAN and ALD sites). The indices were calculated considering the 1995 and 2005 droughts. The plot of the recovery index (R_c) presented numerous outliers due to the abundance of missing rings.

3.5. Growth models

The coefficients of the variables for the most parsimonious BAI model for oak, natural pine and planted pine are shown in **Table 3**. The intercepts of the random effect -site- for the planted pine stands were as follows: -0.127, -0.080, 0.061 and 0.147 for ALD,

CAN, JER and SJE sites respectively. Taking into account the three selected models, the most important predictors of growth were: altitude, aspect, DBH_{cored} and stand type (for oak). According to the growth models, oak BAI increases in pure oak stands, and it is positively associated with DBH_{cored} and negatively associated with altitude and aspect; natural pine BAI is also positively associated with DBH_{cored} and negatively associated with altitude and aspect; and planted pine BAI is positively associated with DBH_{cored}, altitude and aspect. The lowest average growths in the planted pine forest occur in the ALD and CAN sites and the greatest in the SJE and JER sites.

Table 3. Regression coefficients of the fixed effects (standard errors are shown in parentheses), standard deviation of the random effects, marginal (R^2_m) and conditional pseudo- R^2 (R^2_c) for the best linear mixed-effects models of basal area increment for oak, natural pine and planted pine, considering the 1975–2014 period. The factor -stand type- takes values 0 and 1 for the pure oak stand and the planted pine stand, respectively. Predictors are standardized. Pyrenean oak series include both the pure oak stands and the natural oak isolates in planted pine stands. Significance levels: $**P < 0.01$ and $***P < 0.001$, respectively.

		Pyrenean oak	Natural pine	Planted pine
Fixed effects	(Intercept)	2.300 (0.040) ***	43.024 (1.621) ***	2.531 (0.075) ***
	Altitude	-0.142 (0.023) ***	-4.369 (1.267) ***	0.120 (0.007) ***
	Aspect	-0.215 (0.020) ***	-5.768 (1.351) ***	0.030 (0.009) **
	DBH _{cored}	0.428 (0.016) ***	16.647 (1.662) ***	0.384 (0.009) ***
	Stand type	-0.600 (0.047) ***		
Random effects	Site			0.138
	Year	0.204	8.445	0.362
	Residual	0.482	14.94	0.456
R^2_m		0.514	0.542	0.294
R^2_c		0.578	0.653	0.590

The linear regression with altitude $\times$ year interaction shows an increase in BAI from 1975 to 2014 at high altitudes and a decrease in BAI from 1975 to 2014 at low altitudes for planted pines, while natural pine showed the reverse pattern (**Table 4**, **Fig. 6**). Oak had a positive BAI trend with no significant interaction of altitude $\times$ year.

Table 4. Regression coefficients (standard errors are shown in parentheses) and adjusted R^2 for the linear models of BAI for oak, natural pine and planted pine. “ $\times$ ” indicates interactions. All models are highly significant ($P < 0.001$). Significance levels: n.s. $P > 0.10$, ** $P < 0.01$ and *** $P < 0.001$, respectively.

	Pyrenean oak	Natural pine	Planted pine
(Intercept)	-12.470 (4.301) **	-10080 (2175) ***	328.200 (36.390) ***
Altitude	-0.004 (< 0.001)	6.118 (1.261) ***	-0.169 (0.019) ***
Year	0.011 (0.002) ***	5.029 (1.089) ***	-0.164 (0.018) ***
Altitude $\times$ Year	n.s.	-0.003 (< 0.001) ***	0.00008 (< 0.00001) ***
R^2 of the model	0.234	0.216	0.025

Figure 6. Effects of the interactions between year and altitude on radial growth (BAI) for planted (a) and natural pines (b). Shaded bands indicate the 95% confidence intervals. Positions of the data along the x axis are denoted by tick marks.

3.6. Resilience models

According to the fitted models, oak resistance increased in pure oak stands and showed a positive association with DBH_{cored}; natural pine resistance showed positive association with altitude and negative with DBH_{cored} (association marginally significant); and planted pine resistance was positively associated with altitude and DBH_{cored} (association marginally significant), and presented greater values in the ALD site and lower values in the SJE site (**Table 5**). In the CAN and JER sites, resistance presented intermediate values. The effect of the year was significant in the oak and natural-pine.

Table 5. Regression coefficients (standard errors are shown in parentheses) and adjusted R^2 for the best linear models of the resistance index (Rt) for oak, natural pine and planted pine, considering the 1995 and 2005 dry years. The factor -stand type- takes values 0 and 1 for the pure oak stand and the planted pine stand, respectively, and the factor -dry years- takes values 0 and 1 for the years 1995 and 2005, respectively. Predictors are standardized. Oak and planted pine models were highly significant ($P < 0.001$), whereas the natural-pine model was significant ($P = 0.017$). Significance levels: • $P < 0.10$, * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$, respectively.

	Pyrenean oak	Natural pine	Planted pine
(Intercept)	0.433 (0.039) ***	0.451 (0.036) ***	0.568 (0.027) ***
Altitude		0.144 (0.045) *	0.031 (0.016) *
DBH _{cored}	0.076 (0.025) **	-0.087 (0.045) •	0.030 (0.018) •
CAN site			-0.194 (0.050) ***
JER site			-0.186 (0.042) ***
SJE site			-0.343 (0.046) ***
Stand type	-0.141 (0.049) **		
Dry years	0.194 (0.049) ***	-0.162 (0.051) *	
Adjusted R^2	0.490	0.589	0.286

Due to the inverse transformation of R_s , the relationships between the resilience index (without transformation) and the coefficients of **Table 6** were also inverse. According to the models, oak resilience was positively associated with DBH_{cored} and altitude (both associations are marginally significant); natural pine resilience increased in the year 1995 and showed a negative relationship with altitude and aspect; and planted pine resilience was greater in the year 1995 and at the SJE site and was lower in the CAN site. In the ALD and JER pine plantations, resilience presented intermediate values. The effects of the interactions in the planted pine model are shown in **Fig. S3** of the Supplementary Material.

Table 6. Regression coefficients (standard errors are shown in parentheses) and adjusted R^2 for the best linear models of the transformed resilience index ($1/(R_s+1)$) for oak, natural pine and planted pine, considering the 1995 and 2005 dry years. The factor -dry years- takes values 0 and 1 for the years 1995 and 2005, respectively. Predictors are standardized and “×” indicates interactions. Both pine models were highly significant ($P < 0.001$), whereas the oak model was marginally significant ($P = 0.056$). Significance levels: • $P < 0.10$, * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$, respectively. The relationship between the resilience index (without transformation) and the coefficients are inverse (with opposite signs) due to the transformation of R_s .

	Pyrenean oak	Natural pine	Planted pine
(Intercept)	0.547 (0.011) ***	0.497 (0.008) ***	0.551 (0.010) ***
Altitude	-0.021 (0.011) •	0.056 (0.008) ***	
Aspect		0.042 (0.008) ***	
DBH _{cored}	-0.023 (0.011) •		
CAN site			0.048 (0.017) **
JER site			-0.014 (0.016)
SJE site			-0.037 (0.018) *
Dry years		0.114 (0.012) ***	0.078 (0.014) ***
CAN site × Dry years			-0.067 (0.024) **
JER site × Dry years			0.030 (0.023)
SJE site × Dry years			0.013 (0.026)
R^2 of the model	0.113	0.910	0.304

4. Discussion

4.1. Growth trends

Natural pines showed the greatest BAI values for all the period (**Fig. 3a**), mainly due to the lower plot basal area and density and greater age and size (DBH_{stand}, see **Table 1**). The higher growth values exhibited by pines in comparison to oaks is in accordance with previous studies based on seedlings (Castro-Díez et al., 1998; Zavala et al., 2000).

Pines presented significant growth trends (**Fig. 3a** and **Table 4**), which change from negative to positive (in planted stands) or vice versa (in natural stands) as altitude increases (**Fig. 6**). The interaction of the planted pine growth trend with altitude was probably related with the increasing temperature and drought occurrence as well as lower precipitation as altitude decreases. Negative growth trends in similar Mediterranean pine and oak species, associated with climate warming, have been described in other mountainous areas (Gea-Izquierdo et al., 2014; Sarris et al., 2011, 2007). However the interaction of the natural pine growth trend with altitude may not be related with climate, since it was influenced by the relationship between altitude and age (Pearson correlation = 0.96, $P < 0.001$). This relationship was not significant either in pine plantations or in the oak stands.

In contrast, oak showed a positive BAI trend and its growth trend was not affected by altitude (**Table 4**). This rising growth trend in Pyrenean oak under conditions of climate change would appear to be characteristic of elevated locations where wet, cool conditions prevail and mitigate drought stress (Fernández-de-Uña et al., 2015).

4.2. Growth responses to climate

There were no significant differences in the climate-growth correlations between natural and planted pine stands. Pines displayed an overall positive response to precipitations along with a positive response to mild winter, late spring and early summer conditions (**Fig. 4**). This behavior is characteristic of mountainous Mediterranean environments (Bogino et al., 2009; Olivar et al., 2015). However, Pyrenean oak showed low sensitivity to climate in comparison to other studies (Gea-Izquierdo et al., 2015). Furthermore, this sensitivity to climate was lower than that of pine in this study. This

finding, and the fact that all sampled trees were dominant or codominant, suggests that environmental conditions were favorable for oak growth. Pine is more affected by heat and drought than oak, as reported in other studies where functionally similar pairs of gymnosperm-angiosperm tree species coexisted (Eilmann et al., 2009; Gea-Izquierdo et al., 2015).

4.3 Growth reactions to severe droughts

Oaks and natural pines showed similar resistance and resilience in response to droughts and both showed greater resistance than planted pine at the SJE site (**Fig. 5**). However, when considering all the planted pine sites, these showed lower resilience and similar resistance to natural pines and lower resistance and resilience than oaks. In accordance with this, Taeger et al. (2013) found low variability in resistance but large differences in resilience between Scots pine provenances. In any case, our results reveal better adaptation of oak and natural pine to drought stress compared to planted pine, pointing to the suitability of using local provenance Scots pine and oak regeneration as a management option to enhance the resistance and resilience of these forests to droughts, the frequency and severity of which may increase in the future.

4.4 Factors influencing radial growth

Tree size and site variables are recognized as key factors influencing tree radial growth (Diaconu et al., 2015; Marqués et al., 2016). Planted pines displayed the opposite relationship between growth and altitude and aspect to that shown by natural pines and oak (**Table 3**). These relationships indicate that planted pines respond better to colder conditions whereas natural pines and oak better tolerate warmer conditions, which could lead to warming-induced decline episodes at lower altitudes in planted pine (Bakkenes

et al., 2002; Linares and Tiscar, 2010). In fact, planted pine stands showed negative growth trends at low altitude where climate conditions are warm and dry (**Table 4** and **Fig. 6**).

Oak growth was lower in planted pine stands than in pure oak stands (**Table 3**). However, previous studies have reported a positive mixture effect, with higher rates of growth for both tree species in mixed as opposed to pure stands (del Río and Sterba, 2009). In addition, Pyrenean oak is less sensitive to competition (Sánchez-Gomez et al., 2008) and more shade tolerant than Scots pine (Hansen et al., 2002; Rodríguez-Calcerrada et al., 2007). Thus we expected higher oak growth in pine stands. This behavior, opposite to what was expected, may be caused by the possible sprout origin of the sampled oaks (Valbuena-Carabaña and Gil, 2013). The sprout origin affects the oaks vigor and their ability to compete with pine due to the age of the stump and also entails a disproportionate root system (Bravo et al., 2008; Salomón et al., 2017) as well as over-gaining and growth stagnation in some stools (Corcuera et al., 2006). In addition, the higher growth rate of pine can increase the competition for light. Furthermore, interspecific competition can change with climate, tree size, stand structure or stocking degree (Condés et al., 2013; del Río et al., 2014; Manso et al., 2015; Pretzsch et al., 2013a). Reducing competition through thinning in pine plantations may favor the oak growth and improve the stand stability by increasing its structural and functional diversity.

4.5 Factors influencing post-drought growth resilience

The factors that influence growth may change or may even have the opposite effect on growth resistance and resilience indices (**Tables 5** and **6**). In this regard, increasing altitude and north-facing sites, which are associated with colder and wetter conditions,

changed from having a positive to a negative effect on the R_s with respect to R_t of the natural pine. Similar behavior has been described in a previous study on Mediterranean pine ecotones (Marqués et al., 2016). In addition, we observed that the resistance and resilience indices were not explained by the same factors. In general, pine and oak resistance was positively associated with altitude, as in Marqués et al. (2016), although natural pine resilience showed negative association with altitude and aspect. The factors that influence resistance and resilience may also vary among the oak, natural and planted pine stands, probably due to the different locations and stand structures. As reported in previous studies (Carnwath and Nelson, 2017; Merlin et al., 2015) less resistance in a year did not imply less resilience in the same year and vice versa. Oak showed lower resistance in the 1995 drought but its resilience was similar in 1995 and 2005, whereas planted pine displayed lower resilience in 2005 but showed similar resistance in both dry years.

Tree size (DBH_{cored}) had a negative effect on natural pine resistance and a positive effect on oak and planted pine resistance and oak resilience (**Tables 5 and 6**). A similar positive effect of tree size on resistance and resilience has been reported in some pine and oak species, among others (Merlin et al., 2015; Orwig and Abrams, 1997), although in general it has a negative effect (Sohn et al., 2016), possibly due to shifts in carbon allocation associated with tree size (Meinzer et al., 2011) and due to the increase in the total hydraulic resistance making trees less water-use efficient (Ryan and Yoder, 1997), as well as to increasingly negative water potentials associated with longer path lengths as trees enlarge (McDowell et al., 2008). In any case, the relationships between tree size, resistance and resilience remain poorly explored and can even change between different drought events (Merlin et al., 2015). On the other hand, we found no effect of age in our models.

The lower growth rates of oaks in pine stands (**Table 3**) had a negative effect on growth resistance (**Table 5**), reducing growth stability when compared with pure oak stands. Superior performance in mixed stands is assumed because of niche complementary (Kelty, 1992) and facilitation of one species by the other (Holmgren et al., 1997). However, this behavior changes depending on species and site conditions. For instance, an increase in the effect of drought has been reported in *Quercus petraea*–*Pinus sylvestris* mixed stands (Toigo et al., 2015) and a slight reduction in resilience of *Fagus sylvatica* when mixed with *Picea abies* (Pretzsch et al., 2013b).

4.6. Differences among sites

The sampling performed in the planted pine forest was very broad and representative of this type of stand across the whole Sierra Nevada. In addition, as stands of natural pine and oak have only been preserved in very localized areas of Sierra Nevada, our survey can also be considered representative of both types of forest.

The ALD site, which had the lowest annual precipitation and was one of the sites with the highest temperatures (**Fig. 2**), and the CAN site, with better climatic conditions but on a south-facing slope, had the lowest average BAI values (see the intercepts of the random effects in Section 3.5). In contrast, the SJE site had the highest average BAI values. The sites with lowest growth had greater *Rt* values (**Table 5**), although they also exhibited lower resilience following drought. Previous studies have reported that growth resistance during drought increased and growth performance following drought decreased with site aridity (Sohn et al., 2016), possibly due to changes in carbon allocation in trees adapted to drier conditions, which may store and mobilize non-structural carbohydrates to use them as osmolytes or as carbon sources for meristems (Maguire and Kobe, 2015).

5. Conclusions

The planted pine sites with the lowest mean growth rates displayed greater resistance during drought, indicating a possible adaptation of these trees to dry conditions. Natural pine and Pyrenean oak stands were better adapted to the dry climate conditions of the study region and the growth of these stands was also found to be less affected by drought than planted pines. Higher altitude was associated with improved resistance and resilience, with the exception of resilience in the natural pine stands which decreased as altitude increased as well as on north-facing slopes. Thus, forest management should promote natural regeneration of oak and pine or the enrichment of pine plantations using trees of local, natural-origin/provenance, especially at lower altitudes, on south facing slopes and, in general, at the sites with worse climate conditions.

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