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Analyses from stand to tree level allow disentangling the effects of age, size, origin and competition on tree growth sensitivity to climate in natural and afforested Scots pine forests

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ABSTRACT

The sensitivity of tree growth to climate is conditioned by several variables, often intermingled, such as the origin of the forest (natural vs. artificial), tree age, tree size and tree-to-tree competition. The effect of these variables is usually inferred from average growth series obtained at the stand level, thus ignoring the differences at the individual tree level and their drivers. Our objective is to disentangle the effects of stand origin, age, size, competition and social status on the sensitivity of tree growth to climate, including the effects of extreme climatic events, such as droughts, on resistance and resilience, and also to show the advantages of using a tree-level approach. To this end, we compared four stands of *Pinus sylvestris* with contrasting characteristics: young afforested, young of natural origin, old afforested and old of natural origin. We analyzed differences in growth sensitivity to climate at both stand and tree levels to compare both approaches. Our results show the great complexity of the relationships of the variables considered with the sensitivity of growth to climate. All these variables are important and with strong interactions between them, which makes their effects not unidirectional and strongly dependent on the site conditions. While the stand approach hides these interactions, the tree-level approach makes it possible to analyze them in detail. In general, the sensitivity of growth to climate increases with age, diameter, afforested origin, decreasing competition and higher social status; growth resistance increases with age, decreasing diameter, afforested origin, decreasing competition and higher social status; and growth resilience increases with age, diameter, natural origin, decreasing competition and higher social status. We show the usefulness of the analysis of data at individual tree level, which, combined with the joint analysis at stand level, allows us to obtain more accurate and detailed information.

1. Introduction

Ongoing climate change is leading to changes in forest growth responses. These changes may lead to adaptation to new conditions while maintaining stable growth (Rubio-Cuadrado et al., 2020a), or to a reduction in growth due to drought limitation, which could impact future forest dynamics and carbon uptake (Babst et al., 2019). Therefore, it is pivotal to disentangle the multiple drivers of tree growth response to climate to assess the vulnerability of forests to warming and drying conditions (e.g., Sánchez-Salguero et al., 2015, 2013). The sensitivity of

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tree radial growth to climate (both average climate conditions and climate extremes), is determined by a set of primary variables, with an obvious and widely studied influence, such as tree species and provenances, and soil and climate characteristics (Camarero et al., 2015; D'Orangeville et al., 2018; Gea-Izquierdo and Cañellas, 2014; Griesbauer et al., 2011; Orwig and Abrams, 1997; Sánchez-Salguero et al., 2018). But there are also other variables, whose influences on climate-growth relationships are less evident or may even have no influence at all under certain conditions. These variables include stand and tree characteristics, such as size, age, origin, stand structure, and competition, among others (Fritts, 1976), many of which are easily modifiable by management. The effect of these variables is poorly understood because they are often intermingled, making it difficult to disentangle the variables responsible for the different sensitivity of growth to climate (Carrer and Urbinati, 2004; Gómez-Aparicio et al., 2011; Sánchez-Salguero et al., 2015; Trouillier et al., 2019). Moreover, the studies that seek to analyze this effect are focused on one or some of these variables, but there are no studies that analyze all of them together with their interactions, and usually employ mean growth series for groups of trees, being these groups made up of trees from the same stand or with similar characteristics (e.g., size, age or species). However, considering the differences between individual trees allows us to study the whole range of individual responses among sampled trees and to understand those variables responsible for the different responses (Carrer, 2011; Galván et al., 2014; Rozas, 2014). All these elements make this issue a field of study that requires greater efforts and new methodological approaches to unravel the effects of each of these variables on the sensitivity of tree growth to climate.

Forest origin (natural or artificial) can have a great influence on the response of growth to climate (Camarero et al., 2021b; Sánchez-Salguero et al., 2013), and a relationship has been found between this variable and drought-induced mortality (Rubio-Cuadrado et al., 2021). However, this influence is not direct, but it is due to the effect of other related variables. Afforestations are often pure stands with elevated competition, a low coefficient of variation of tree diameter, inadequate seed origin in these afforestations made at the beginning and in the middle of the twentieth century, poor and superficial soils and, in some cases, they were established beyond the current climatic range limit of the species, all of which affect the sensitivity of tree growth to climate (Sánchez-Salguero et al., 2013). Likewise, cultural treatments carried out in nurseries, such as the repeated undercutting of the taproots of seedlings or different types of container, can affect the adequate development of the plant, modifying in this case the shape of the root system, and thus increasing the sensitivity of growth to climate (Zadworny et al., 2019). The number of variables interrelated with the origin of forests means that the results (in terms of their sensitivity to climate) obtained in a given afforestation may not necessarily be valid for another afforestation. This, together with the importance (e.g., ecological, social, and environmental) and extent of afforestations (FAO, 2006), and the current conditions of climate change, make it especially important to increase the research effort in this area.

Tree size and age are, in general, related to climate sensitivity, which increases up to a certain value of these variables after which it remains constant (Carrer and Urbinati, 2004; Rozas et al., 2009; Trouillier et al., 2019). However, relatively few studies have tested the influence of these variables in the climate–growth response, and conclusions vary among those that do exist (Dorman et al., 2015; Fritts, 1976; Galván et al., 2014; Rozas, 2014; Rozas et al., 2009; Sánchez-Salguero et al., 2015; Szeicz and MacDonald, 1994). In addition, age and size are strongly interrelated, which makes it difficult to disentangle their effects on the sensitivity of growth to climate. Most studies concerning this topic tend to focus on the age effect, however, age appears to have few direct effects on tree physiology as compared with size (Bond, 2000; Thomas, 2002). In contrast, size is related to hydraulic conductivity (Ryan et al., 2006; Ryan and Yoder, 1997), and changes in xylem anatomy due to tapering (Carrer et al., 2015). Therefore, there is ecophysiological background to support the role played by size on driving the sensitivity of growth to climate. Stem diameter could thus facilitate a more direct assessment of size effects (Trouillier et al., 2019).

Competition is a key process driving forest growth due to the limitation that this variable produces on obtaining soil water and nutrients and acquiring radiation (Orwig and Abrams, 1997; Weiner, 1990). Thus, trees may have different climate-growth sensitivities, depending on the different competition levels, including different structural attributes and social statuses (Andersen et al., 2009; Cherubini et al., 1998; Linares et al., 2010). However, the influence of this variable on growth, and thus on the sensitivity of growth to climate, is often confused with others variables, especially with the influence of climate itself (Gómez-Aparicio et al., 2011; Rubio-Cuadrado et al., 2020b; Sánchez-Salguero et al., 2015).

Tree-ring width data are widely used to assess climate-growth relationships (Fritts, 1976). One of the basic methodologies in dendroecology consists of extracting the common signal, which is considered to be mainly due to the climate, from the growth series of a group of trees of the same species and sampled in the same stand (stand approach), reducing as much as possible the unwanted variability (the noise, that is, the tree-to-tree variability not due to climate) (Fritts, 1976). For this purpose, researchers usually build robust averages of detrended individual growth series. This reduces the noise and considerably increases the climate signal, creating an artificial inflation to the climate sensitivity that can lead to unrealistic conclusions about the effect of climate on growth (Carrer, 2011). However, by using mean values we are losing all the information retained in the growth variability that occurs in each tree. On the contrary, by using individual growth series (tree-level approach) it is possible to analyze differences in sensitivity due to differences in competition, age, size, sociological class, genetic pool, microenvironmental conditions, etc., and analyze these differences statistically (Galván et al., 2014; Rozas, 2014).

In this study, we seek to disentangle the effect of these variables on the sensitivity of radial growth to climate. To this end, we compare four stands of Scots pine (*Pinus sylvestris* L.), one of the most important tree species in Eurasia in terms of extension, ecological value and timber production. The stands were selected based on their contrasting characteristics: young afforested, young of natural origin, old afforested and old of natural origin. We analyze the differences in growth sensitivity to climate both at the stand and tree levels. Our objectives are (i) to know the effect of origin, age, diameter and competition on the sensitivity of growth to climate, measured through growth-climate relationships and by considering the impacts of climate extremes such as droughts on growth, and (ii) to analyze the advantages or disadvantages of the stand and tree-level approaches.

2. Material and methods

2.1. Study area

The study area was located in "Sierra de Guadarrama" National Park (central Spain), where Scots pine forests dominate the landscape at mid to high elevations (1350–2000 m a.s.l.). Within these forests we looked for 4 stand types with contrasting characteristics: planted stands where most of the trees were less than 70 years old (young afforestation stand hereafter); young stands of natural origin (young natural stand hereafter); planted stands where most of the trees were at least 100 years old (old afforestation stand hereafter); and stands similar in structure and age to an old-growth forest (old natural stand hereafter) (Table 1). All these stands have been historically managed by shelterwood cuttings, although in the old natural stand the interventions have been minor and it is currently assigned to a protection district. The climate in the study area is continental Mediterranean with average temperature of 9.2 °C and annual precipitation of 687 mm (average data for the period 1950–2015, see Section 2.4). Soils are siliceous and acid in the four stands. Shrubs such as *Genista florida* L., *Juniperus communis* L.,

Table 1
Description of structural and dendrochronological variables (mean values) of cored trees for each stand type studied (young/old/natural/afforestation stands). Values in parentheses indicate standard deviations. Mean correlation with master refers to mean correlation of detrended growth series with master. Note that standard deviations are not shown for plot basal area in young natural and old afforestation stands because only a single plot was sampled in these stands.

	Young Natural	Young Affor.	Old Natural	Old Affor.
Number of sampled cores	63	74	102	62
Number of sampled trees	32	41	51	31
First year with growth data	1951	1970	1582	1890
Last year with growth data	2021	2015	2017	2021
Mean age at 1.3 m (years)	59 (8)	35 (7)	263 (162)	126 (6)
Mean DBH (cm)	29.3 (5.5)	25.1 (7.2)	55.3 (14.7)	44.1 (5.2)
Mean correlation with master	0.57	0.55	0.48	0.64
Mean inter-trees correlation	0.42	0.37	0.27	0.53
Mean tree-ring width (mm)	2.22 (0.86)	3.25 (1.63)	0.99 (0.73)	1.58 (1.08)
Mean BAI (cm^2)	15.68 (6.99)	15.12 (11.02)	15.36 (10.93)	14.76 (8.01)
Mean BAI 2006–2015 (cm^2)	16.73 (2.60)	14.66 (2.25)	11.67 (2.89)	9.34 (2.14)
Mean sensitivity	0.18	0.24	0.24	0.26
Expressed Population Signal	0.95	0.94	0.90	0.97
Signal to noise ratio	17.41	16.05	8.81	30.86
Plot basal area (m^2 ha^{-1})	50.18	33.53 (13.03)	49.54 (3.77)	41.16

Vaccinium myrtillus L. and *Cytisus oromediterraneus* Rivas Mart. dominated the understory.

2.2. Field sampling

We carried out different sampling strategies in each stand type. For the young afforestation stand, we sampled 41 plots of 9.8-m radius (1.23 ha in total of sampled surface) in 2016 in a homogeneous area located between 40° 47′ 54″ – 41° 1′ 50″ N and 3° 52′ 53″ – 4° 7′ 47″ W, within the 1499–1810 m a.s.l. altitudinal range. All these plots were systematically distributed on a square grid of 250 m x 250 m and were located in young forests, although they were afforested in different years. For the old natural stand, we sampled 5 plots of 25-m radius (0.98 ha in total) in 2018 around the coordinates 40° 47′ 21″ N and 4° 2′ 17″ W, within the 1830–1960 m a.s.l. altitudinal range, located in areas with complete canopy cover and no apparent disturbance. Finally, for the young natural and old afforestation stands, we sampled a single plot in each stand of dimensions 60 m x 85 m (0.51 ha) and 70 m x 70 m (0.49 ha), respectively, located at coordinates 40° 49′ 6″ N, 4° 1′ 24″ W and 41° 2′ 46″ N, 3° 51′ 37″ W, respectively, and at an altitudes of 1355 and 1448 m a.s.l., respectively. The separation between the two furthest plots sampled was 35 km, having plots of young forest stands sampled along this entire length.

Sampling designs and altitudes were very different from stand to stand, but this is due to their specific characteristics. While the young afforestation forests are widely distributed in the study area, the other stand types are found in very limited areas. In addition, the old natural stand was located in a forest area with many gaps and a highly variable structure, which prevents the creation of a large plot and makes it necessary to make a non-systematic selection of smaller plots. In this stand, plots were located in areas without gaps and with a homogeneous stand structure of adult trees (**Fig. S1**), making their results comparable to those of the other stands.

In all plots, we measured diameters at breast height (at 1.3 m; DBH) and height for all trees, as well as azimuth and distance from the plot center, except in the young afforestation stand plots where we measured DBH only. In addition, we cored between 31 and 51 dominant or co-dominant trees within plots in each stand type, using a Pressler increment borer. In the young afforestation stand, we selected the bored trees from the plot center (1 tree per plot) so that the competition measured in the plot is representative of the competition experienced by the cored, focal tree. Two cores were extracted at 1.3 m from each sampled tree.

2.3. Growth data

Cores were taken to the laboratory, air dried, mounted on wooden supports and carefully sanded until tree rings were clearly visible. Tree rings were visually cross-dated and measured to the nearest 0.01 mm, using the semi-automatic LINTAB device with the TSAP-Win software (RINNTECH, Heidelberg, Germany), obtaining the tree-ring width (TRW) series for each tree. Cross-dating was further verified with the COFECHA program (Holmes, 1997).

TRW series were subsequently transformed into basal area increments (BAI) as this variable is better than tree-ring width for capturing growth trends and accounting for the increase in tree size and age (Biondi and Qeadan, 2008). The BAI was calculated as in the Eq. (1). When cores did not contain the pith, the missing core length was estimated to calculate the BAI by subtracting the core length to the tree radius measured in the field without bark. Bark thickness of Scots pine (BT_{Ps}; in mm) was estimated based on DBH (in mm) using the Eq. (2) fitted to the data of this species from the Second Spanish National Forest Inventory (DGCONA, 1998). The final BAI chronologies were built by averaging annual BAIs across all trees of the same stand types.

$$BAI = \pi\left(r_t^2 - r_{t-1}^2\right) \qquad \text{(eq. 1)}$$

$$BT_{Ps} = 0.0951\ DBH + 10.82 \qquad \text{(eq. 2)}$$

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

Since the BAI series may contain long-term trends due to non-climate variables (i.e. age or changes in competition), to determine the main climatic drivers of tree growth we used ring-width indices (RWI), removing the long-term trends of the raw tree-ring widths (TRW) for each stand using the *dplR* package (Bunn et al., 2016) in the R statistical software (R Development Core Team, 2022). For this end, we fitted a 32-year cubic smoothing spline to each TRW series, subsequently the TRW series were standardized by dividing them by the fitted spline, and then detrended series were pre-whitened fitting an autoregressive time series model (AR1 model). The residuals of this model were divided by its mean to yield a series with white noise and a mean of one (RWI). Finally, to obtain the RWI of each stand, averages of the individual RWI series were calculated using bi-weight robust means. This method efficiently eliminates long-term growth trends, such as biological trends or trends due to gradual changes in competition, as well as the effect on growth of those events that produce multi-year changes, such as thinning, but also eliminates the effects of long-term climate trends while preserving the short-term effects of annual non-climatic events, such as pests.

To estimate tree age, the ring widths in the missing part of each core were considered to be equal to the average width of the 5 innermost rings adjacent to this missing part. The missing core length was estimated in the same way as for the BAI calculation. The statistical quality of each chronology was checked via Expressed Population Signal (EPS) (Wigley et al., 1984) using *dplR* package (Bunn et al., 2016). Mean sensitivity of the detrended (but not pre-whitened) TRW series (Speer, 2012) and signal to noise ratio of the RWI series (Wigley et al., 1984) were also obtained. The current differences in BAI between sites were analyzed through ANOVA and Tukey post-hoc tests (after verifying that the normality assumption is met), based on the average growth for each stand in each year of the period 2006–2015.

2.4. Climate data

Due to the lack of long and complete series of local meteorological data from stations located in the study area, we used daily precipitation (P) and maximum (Tmax) and minimum temperature (Tmin) data from the 0.11º-gridded Spain02-v5 dataset (Herrera et al., 2016, 2012). This dataset reproduces climatological features, including weather extremes, thanks to the dense network of weather stations it uses, and covers from 1950 to the present. The Spain02-v5 dataset uses more than 3000 precipitation stations and over 250 temperature stations located along the Spanish surface. We obtained climate data from Spain02-v5 for the central coordinates of our study area.

To assess drought intensity we used the Standardised Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010a, 2010b) calculated from the Spain02-v5 climate dataset using the Hargreaves equation (Droogers and Allen, 2002) to estimate the monthly reference evapotranspiration (ETo) within the *SPEI* package in R (Beguería and Vicente-Serrano, 2017). High and low SPEI values correspond to wet and dry conditions, respectively. The SPEI drought index considers the effect of temperature on evapotranspiration rates and calculates a cumulative water deficit. The period from the arrival of water input (precipitation) to availability of a given usable resource (water absorption by the roots) differs considerably. Thus, the time scale over which water deficits accumulate becomes extremely important to calculate the SPEI. For this reason we used a range of time scales (from 1 to 20 months) during which the water deficit and surplus are accumulated (Vicente-Serrano et al., 2010a). For the rest of the document and for simplicity, we use the initials of the variable together with the time scale. Thus SPEI1, SPEI2… and SPEI20 refer to monthly SPEI variables calculated with a time scale of 1, 2… and 20 months.

2.5. Stand-level analyses

2.5.1. Climate-growth relationships

We calculated Pearson correlation coefficients for the common period between the RWI of each stand and mean monthly Tmax and Tmin, total monthly P and the SPEI using time scales from 1 to 20 months. The common period was from 1972, the first year with growth data in more than one tree in the young afforestation stand, until 2015, the last year with growth data in this same stand. Pearson correlation coefficients were calculated from October of the previous year to September of the growth year considering that: (i) tree growth is affected by the previous year climate, and (ii) growth of Scots pines may occur from April to September usually peaking in May-June (Aldea et al., 2017; Camarero et al., 2010, 1998; Sánchez-Salguero et al., 2015).

Radial growth is a continuous process that is not limited by monthly boundaries. Furthermore, the study of growth-climate relationships can give very different results depending on whether continuous periods of time are used or whether the climate of each month is analyzed separately (Rubio-Cuadrado et al., 2022). To address this issue, we calculated, for each climatic variable (Tmax, Tmin and P) and stand, the time period in which the growth-climate relationship is maximal (best climate window) using the *climwin* R package (Bailey and van de Pol, 2016; van de Pol et al., 2016), which offers important advantages in the field of dendroecology (Rubio-Cuadrado et al., 2022).

To select the best climatic window between a RWI stand series and a given climate variable, all possible linear models relating them were first fitted. In each model a different climate window with daily temporal resolution was tested. Then, the model that minimizes ΔAICc was chosen (Burnham and Anderson, 2004). ΔAICc is the difference between the corrected Akaike information criterion (AICc) of the selected model and the AICc of the baseline model. For the RWI series of each stand, we fitted both simple models, including a single climate variable in each model (in this case the baseline model was the null model that contains only the intercept), and multiple models. To create the multiple models, we first introduced the variable and the climate window with the lowest ΔAICc (i.e., we started from the best simple model, which was in this case the baseline model) and then added one by one the rest of the possible variables, in order to fit all possible two-variable models, and for each variable we tested all the possible climatic windows. Three-variable models were also fitted by repeating the process and in which the baseline model for each RWI stand series was the best two-variable model. The limits established for the beginning and closing of the climate window (windows open and close, respectively) were the same as those established in the monthly climate analysis (from October 1 of the previous year to September 30 of the growth year). The models were also fitted for the same period used in correlation analyses, i.e., 1972–2015. We used the mean (for minimum and maximum temperatures) and the total (for precipitation) of each time window considered as the aggregate statistic. We established a minimum period of 15 days between windows open and close. The large numbers of models that were fitted to test all possible climatic windows increases the possibility of obtaining models with low ΔAICc by chance. To solve this problem, randomization tests were performed on all the models obtained using 1000 repetitions. The randomization test determines the expected distribution of ΔAICc values in a data set where no response to climate exists, and provides a probability value (p AICc) which determines the likelihood that the ΔAICc value of the selected model has occurred by chance (van de Pol et al., 2016). As randomization tests require a high computational power, we used the “Magerit” High Performance Computer of “Universidad Politécnica de Madrid” (www.cesvima.upm.es, Madrid, Spain) to derive these analyses.

2.5.2. Growth response

We analyzed the sensitivity of the growth series to abrupt environmental changes, whether these changes are due to climate extremes (e.g., droughts) or to forest disturbances (that imply changes in competition). The responses to climate extremes was analyzed by defining pointer years and calculating growth resistance and resilience indices (Lloret et al., 2011), while the responses to disturbances was analyzed by detecting growth releases (Nowacki and Abrams, 1997).

We considered as negative/positive pointer year those years with a TRW decrease/increase of at least 25 %, relative to the average TRW of the 4 preceding years –relative growth change method (Schweingruber et al., 1990)– in at least 60 % of the sampled trees in the stand. The growth response to these negative pointer years and the ability to recover pre-disturbance growth levels after the disturbance were estimated for the TRW series through the resistance (*Rt*) and resilience (*Rs*) indices (Lloret et al., 2011):

$$Rt = TRW_i / TRW_{i-4} \tag{eq. 3}$$

$$Rs = TRW_{i+4} / TRW_{i-4} \tag{eq. 4}$$

where TRW_i is the TRW value of the i year. These indices were calculated with 4-year pre- (i-4), and post-disturbance (i+4) periods, based on previous studies (Rubio-Cuadrado et al., 2020a, 2018), using the *pointRes* package in R (van der Maaten-Theunissen et al., 2015). The differences between sites were analyzed through Levene’s test (to study the differences in variance) and ANOVA test with Bonferroni post hoc test, after verifying that the normality assumption is met.

To reconstruct forest disturbances, growth releases were detected through the study of abrupt growth increments (releases) using the *TRADER* package in R (Altman et al., 2014). Running yearly comparisons of sequential 10-year BAI means were used to quantify the growth increases using the formula (Nowacki and Abrams, 1997):

$$GC = (M_2 - - M_1) / M_1 \tag{eq. 5}$$

where GC is the growth change between preceding and subsequent 10-year BAI means, M_1 is the preceding 10-year mean BAI, and M_2 is the subsequent 10-year mean BAI. We consider that there has been a moderate or major release when GC is greater than 0.25 and 0.5, respectively. We used BAI instead of TRW series because in these comparisons spanning 20 years (10 years before and 10 years after a given year), the decreasing trend of ring widths with age, which is very pronounced in young trees, may affect the result.

2.6. *Tree-level analyses*

Within each stand there are variations in the competition experienced by each tree, and in the size and age of trees. To control for this variability and analyze how it influences the sensitivity of growth to climate, we repeated the previous climate-growth relationships analyses, but this time using the RWI of each tree instead of those of each stand. The period 1990–2015 was considered for these analyses for all trees to make the results comparable and to be able to use the growth series of the largest possible number of trees in the young afforestation stand (of the 41 trees sampled in the stand, 34 have at least growth data since 1990 but in 7 of them their first growth is after this year). In this way, we obtained the ΔAICc and the slope of the best simple models for each tree ($\Delta AICc_{BM}$ and $Slope_{BM}$ hereafter). ΔAICc was obtained in the same way as explained in Section 2.5.1, but in this case the RWI of each individual tree was related to climate and only simple models (with one climate predictor) were used. $\Delta AICc_{BM}$ and $Slope_{BM}$ are therefore the series (one value per tree) of ΔAICc and slope, respectively, of the models with the best climate window (the one that minimizes the AICc). $\Delta AICc_{BM}$ and $Slope_{BM}$ were obtained only for the climatic variable P, since it is the variable that shows the greatest relationship with growth in this case. We also obtained the correlations (this time by Spearman instead of Pearson due to the lack of fulfillment of the normality assumption in some trees) between the RWI of each tree and the different SPEI variables (from SPEI1 to SPEI20) and the slopes of the simple linear models relating these variables (with RWI as response variable). Within these correlations and models calculated with the different SPEI variables, we chose the results (correlation and slope) of that SPEI variable that maximizes correlation for each tree ($SPEI_{max}$ correlation and $SPEI_{max}$ slope hereafter) as representative of the sensitivity of the growth of that tree to drought.

As variables that may influence on the climate-growth relationships, we have considered the diameter of the cored trees (DBH_c), their age and height, the ratio between DBH_c and the average diameter of the neighboring trees (DBH_n) as a measure of their sociological status as well as of the historical competition that a tree has suffered, especially in even-aged stands, and the competition suffered by each tree measured as the total basal area of the neighboring trees (BA). For the calculation of BA and DBH_n, all adult trees (DBH > 7.5 cm) were considered, excluding the rest of the vegetation, which is scarce in the studied stands. Among the different plot sizes used in the field sampling, the smallest is the one used in the young afforestation stand, with a radius of 9.8 m, which is approximately twice the average crown diameter of Scots pine according to data from the Second Spanish National Forest Inventory (DGCONA, 1998). Therefore, this is the surface that has been considered to calculate DBH_n and BA of the neighboring trees. Thus, DBH_n and BA values were obtained directly for each of the plots sampled in the young afforestation stand. In the rest of the stands, within the sampled plots (all of them larger), 9.8-m radius subplots were established centered on each of the bored trees, and DBH_n and BA values were calculated for each of the subplots. For the spatial analyses and calculations of the variables in the subplots, the *spatstat* package in R was used (Baddeley and Turner, 2005).

To analyze the relationships between these variables and climate sensitivity, Pearson correlations were calculated for each stand by relating these variables to the $\Delta AICc_{BM}$, as well as to the related values of windows open, close and length (number of days between windows open and close), the $SPEI_{max}$ correlation, and the resistance and resilience values, both in each of the pointer years and the mean values (mean for each bored tree of the Rt and Rs values of the pointer years 1979, 1986, 1991, 2004 and 2013).

In order to obtain generalizable results, we also fitted multiple regressions to evaluate the predictors that influence growth and climate sensitivity, including all the data from all the stands together. As response variables we used the log-transformed BAI, $\Delta AICc_{BM}$ (in absolute values), $Slope_{BM}$, $SPEI_{max}$ correlation, $SPEI_{max}$ slope, and mean resistance and resilience. BAI was log-transformed to meet normality assumptions since this variable has a gamma distribution. We used the absolute value of $\Delta AICc_{BM}$ for ease of interpretation. In this way, $|\Delta AICc_{BM}|$ and $SPEI_{max}$ correlation measure the sensitivity of growth to climate in the same direction, with greater sensitivity to climate when higher $|\Delta AICc_{BM}|$ (but lower $\Delta AICc_{BM}$) and $SPEI_{max}$ correlation values are obtained. As predictors, we used the same variables in all (saturated) models: BA, DBH_n, DBH_n/DBH_c, age, stand origin (as dummy variable, taking values 0 and 1 for the natural and afforested stands, respectively) and the possible two-by-two interactions between them. We did not consider height because it was not measured for the Young Afforestation stand. For the BAI model, we used the growth values of the 10 years comprised in the period 2006–2015, since we consider that in general the current competition values will be valid for the last decade. Given the relationship between DBH_c and age, for the models we have used the residuals of the potential function relating age and DBH_c (Eq. (6)).

$$Age = 0.1222 \ \ DBH_c^{\ 1.8389} \qquad \text{(eq. 6)}$$

To identify the best-supported model for each response variable we constructed all possible combinations of alternative models from the saturated model. Then we selected the best model by minimizing the AIC. The existence of multicollinearity among predictors was evaluated by calculating the variance inflation factor (VIF) (Dormann et al., 2013), which was always lower than 5. These analyses were performed in R software with the *MuMIn* (Barton, 2012), *car* (Fox and Weisberg, 2011) and *effects* (Fox, 2003) packages.

3. Results

3.1. *Stand structure and tree growth*

The current basal areas in the young afforestation and young natural stands are 33.53 and 50.18 $m^2\ ha^{-1}$, respectively, being the stands with the lowest and highest competition respectively (Table 1). In any case, it must be taken into account that in the young afforestation stand different plots were sampled in which the basal area varied between 7.46 and 69.68 $m^2\ ha^{-1}$. Likewise, in the old natural stands, different plots were sampled and in them the basal area varied between 43.19 and 53.85 $m^2\ ha^{-1}$, being, in any case, larger than in the old afforestation stand (41.16 $m^2\ ha^{-1}$).

Trees of young and old afforestation stands showed larger TRW values than trees of young and old natural stands, respectively (Fig. 1), due to the lower age, size and competition of trees in these stands (Table 1). However, this growth (in TRW) is equalized within each age category (old/young) between natural and afforested stands during the last years despite differences in age, size and competition. The BAI values were similar among the four stands in the period 2006–2015, although growth rates were significantly higher in the young versus old stands ($p < 0.001$ in both ANOVA and pairwise Tukey post-hoc tests, except for the young afforestation-old natural pair, in which $p = 0.069$). Within each age category, natural stands also showed a higher BAI than afforested stands during this period, although these differences were not significant. The common growth signal varied greatly among the stands studied, with a maximum signal to noise ratio of 30.86 for the old afforestation stand and a minimum of 8.81 for the old natural stand,

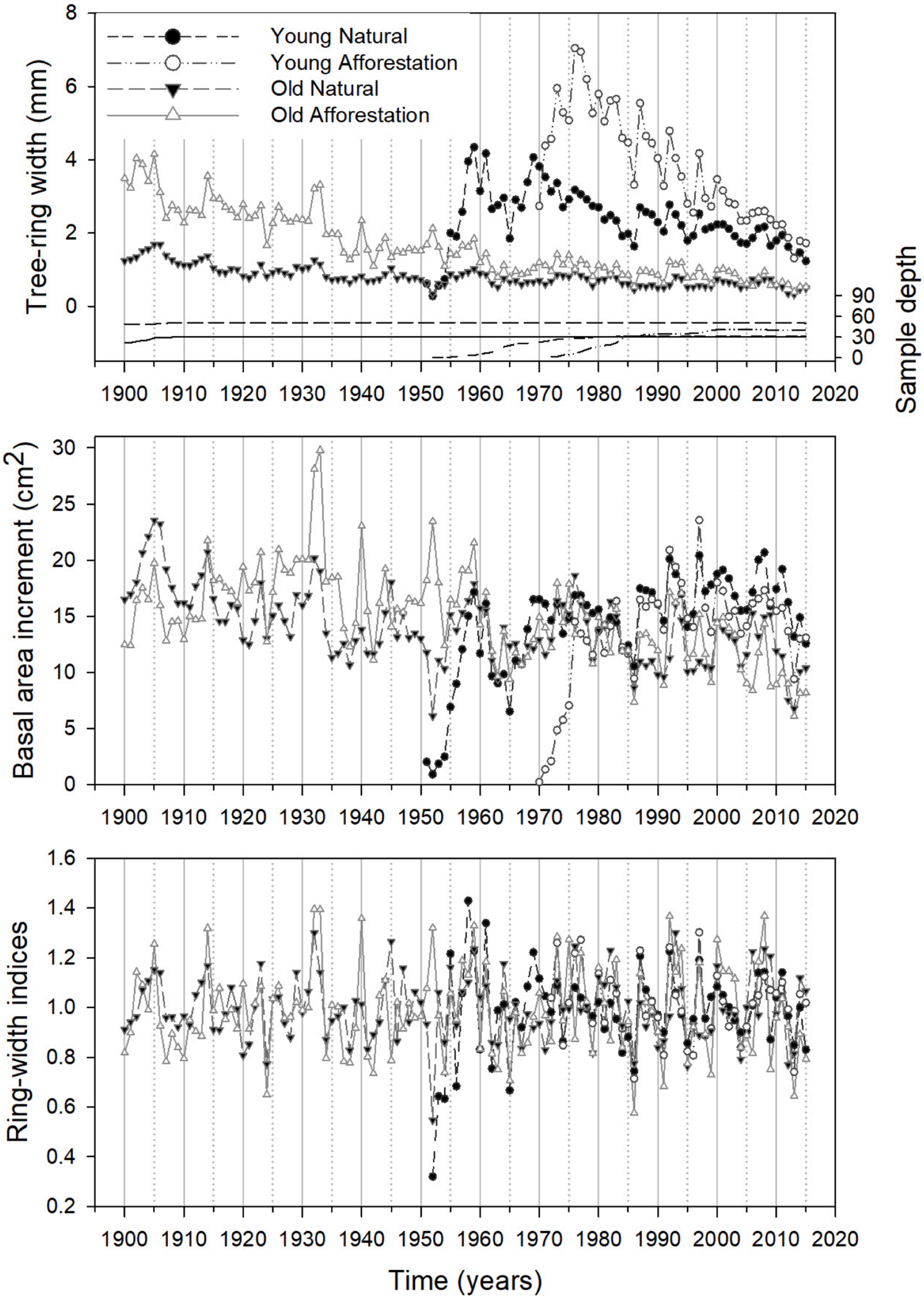


Fig. 1. Growth trends and patterns (tree-ring width, basal area increment and ring-width indices) for the four studied stand types since 1900 and sample depth (number of cored trees; right *y* axis in the upper panel).

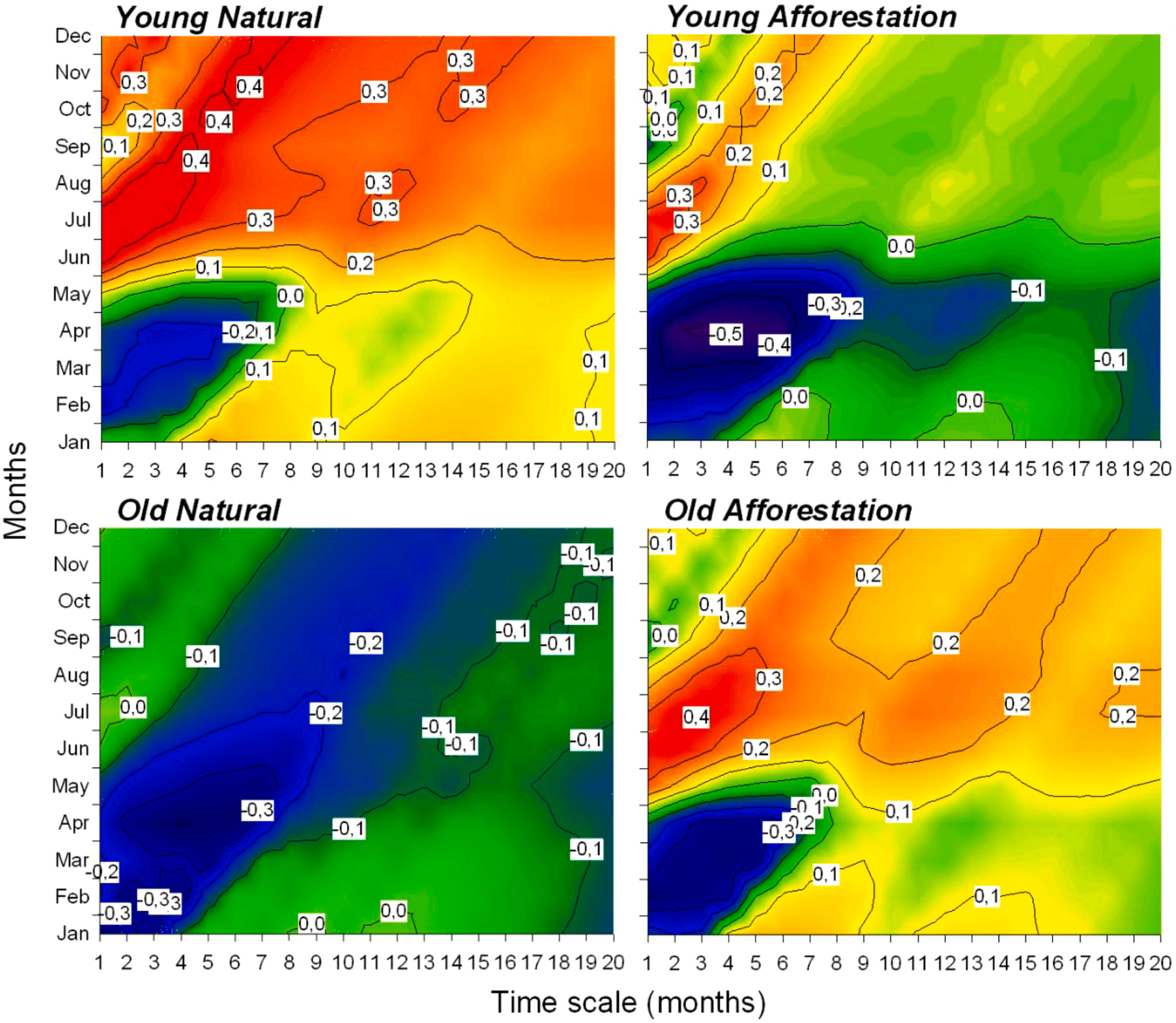
taking intermediate values in the young stands (Table 1). In all cases the Expressed Population Signal was larger than the 0.85 threshold, commonly considered in tree-ring studies to represent well-replicated chronologies.

Stand structure varied considerably (**Fig. S1**). The structure was irregular in the old natural stand, with a similar density of trees for all DBH classes between 12.5 and 62.5 cm, decreasing in density above this DBH value up to the 90 cm class. In contrast, the other three stands showed a regular structure, with a greater presence of trees in the intermediate DBH classes, and with a distribution curve with positive symmetry (i.e., with values more separated from the mean to the right or to the higher DBH classes). The DBH classes present in the old afforestation, young afforestation and young natural stands are 35–65, 10–55 and 10–45 cm, respectively.

3.2. Stand-level analyses

3.2.1. Climate-growth relationships

There has been an increase in drought conditions in recent decades, especially since 2000, according to the SPEI (**Fig. S2**). In the two young stands and also in the old afforestation stand the growth responses to climate were similar, whereas the old natural stand presented different responses to climate and correlations were lower (Figs. 2 and **S3** and **Tables 2** and **S1**). In general, in the young stands and in the old afforestation stand, growth is higher in years with rainy springs and summers and mild winters and summers (**Fig. S3**). On the contrary, in the old


Young Natural

Young Afforestation

Old Natural

Old Afforestation

Fig. 2. Pearson correlations calculated by relating mean ring-width indices (RWI) of the four studied stand types to the SPEI drought index from January to December (*y* axes) and for time scales between 1 and 20 months (*x* axes). Only the common period 1972–2015 was considered. Correlation values higher than 0.30, 0.38 and 0.48 are significant at 0.05, 0.01 and 0.001 significance levels, respectively.

natural stand, there were hardly any significant ($p < 0.05$) climate-growth relationships, and these only occurred during the autumn prior to the growth year (e.g., negative relationships with November precipitation and December minimum temperature).

Modeling growth as a function of daily climate showed that the most important variables in all stands were spring and summer precipitation, which accounted for 37–40 % of the growth variability, except in the old natural forest where the explained variability dropped to 16 % and where the relationship of growth with precipitation (in this case of previous autumn and winter) was inverse (**Tables 2** and **S1** and **Fig. S4**). The second most important climatic variable was maximum temperature (Tmax), which explained 10–19 % of the variability, although it was only significant (p AICc < 0.05) in the young afforestation stand. The period (climatic window) during which Tmax was positively related to growth varied among stands, encompassing winter and early spring in the young afforestation stand. In the other stands the climatic window was very small (about 20 days, a value close to the pre-established minimum), indicating that the result obtained may be due to randomness rather than to an actual effect of climate on growth, which is corroborated by the p AICc values. No model with more than two variables was shown because no significant p AICc values were obtained in any case.

Correlation analyses between the SPEI drought index and mean RWI generally corresponded to inverse relationships for the January-April period (significant relationships in all stands except the young natural) and direct relationships with June and July SPEI (significant relationships in all stands except the old natural) (Fig. 2). In the young natural stand, the maximum correlation corresponded to July SPEI2 ($r = 0.57$, $p < 0.001$). In the young afforestation stand April SPEI3 showed the minimum correlation ($r = -0.52, p < 0.001$), and July SPEI2 showed the maximum correlation ($r = 0.40, p = 0.007$). In the old natural stand, April SPEI4 showed the minimum correlation ($r = -0.41$, $p = 0.006$). Finally, in the old afforestation stand, February SPEI1 showed the minimum correlation ($r = -0.37$, $p = 0.013$) and the maximum correlation corresponded to July SPEI3 ($r = 0.41$, $p = 0.006$).

3.2.2. *Growth responses to climate extremes and disturbances*

Considering the common time period, the afforested stands showed a greater occurrence of abrupt drops in growth (negative pointer years) compared to the natural stands (**Fig. S5** and **Table S2**). Within the natural stands, the growth of the young stand showed greater stability, in which there was a single pointer year and where the variability of the resistance indices was smaller. Considering all the negative pointer years shared by the two afforested stands (1979, 1986, 1991, 2004 and 2013), both stands showed similar resistance indices, but the old afforested stand showed higher resilience despite also showing higher variability in both resistance and resilience indices (**Table S2** and Fig. 3). This stand showed even higher resilience indices in 1991 and 2013 than the young natural stand, which did not show abrupt drops in growth (negative pointer years) in these years. Considering the negative pointer years shared by the old natural stand with the two afforested stands (1979, 1986 and 2013), the three stands showed similar resistance indices and, again, the old afforested stand showed higher resilience, with the old natural and the young afforestation stands having similar resilience values. Due to the absence of negative pointer years in the young natural stand, it showed higher resistance values (Fig. 3), showing however a more variable behavior in the resilience indices. The negative pointer years of 1986 and 2013 occurred in dry years (**Fig. S2**).

Regarding positive pointer years, whether related to changes in climatic conditions or to competitive releases, these were mainly detected in the old stands (**Fig. S5** and **Table S2**). Considering the growth releases, these occurred in all four stands, although to a greater extent in the old stands, with the old natural stand having the highest percentages of releases, the highest percentages of major releases and the highest frequency of clustered release events (**Figs. S6** and **S7**).

3.3. Tree-level analyses

The tree-level analyses show the relationships between individual variables (age, DBH, height and sociological status of the bored tree and competition suffered by it) and the sensitivity of radial growth to climate. The sensitivity was measured as ΔAICc and slope of the best models relating growth with daily climate data, the highest correlation for each tree (and the slope of the model resulting from relating the same variables) obtained between growths and the different SPEI variables, and values of the resistance and resilience indices in the pointer years. In the correlation analyses between these variables, different results were obtained for each stand and, as for the resistance and resilience variables, there were significant correlations only in some of the pointer years (**Table S3**). The different results obtained for each pointer year indicate a high level of variability caused by other variables (e.g. the time of year when the drought occurred, the drought intensity or the climate of previous years), variability that cannot be statistically analyzed with our data due to the small number of pointer years. In these analyses (**Table S3**) sociological status did not influence the sensitivity of growth to climate in old stands or in the young natural stand, being only important in the young afforestation stand, where a worse sociological status (higher DBH_n/DBH_c) was related to a lower sensitivity to the mean climate (lower correlations with SPEI) and to a lower resistance and resilience. In the young natural stand, an opposite relationship was found with resilience in 2013, but this was only marginally significant ($p < 0.10$). In general, age, as well as DBH_c and height, were directly related to greater response or sensitivity to mean climate conditions and greater resistance and resilience, except in the young afforestation stand, where higher ages were related to lower resistances, and in the height-resilience relationships, which had opposite directions depending on the year considered. Although age, DBH_c and height are variables related to each other, however the relationships between these variables and 2004 resilience in the Old Natural stand were opposite (*r*-values of 0.33, 0.32 and −0.34 for age, DBH_c and height, respectively). Finally, competition (measured as subplot basal area) showed few and opposite relationships, being directly related to resistance in the old

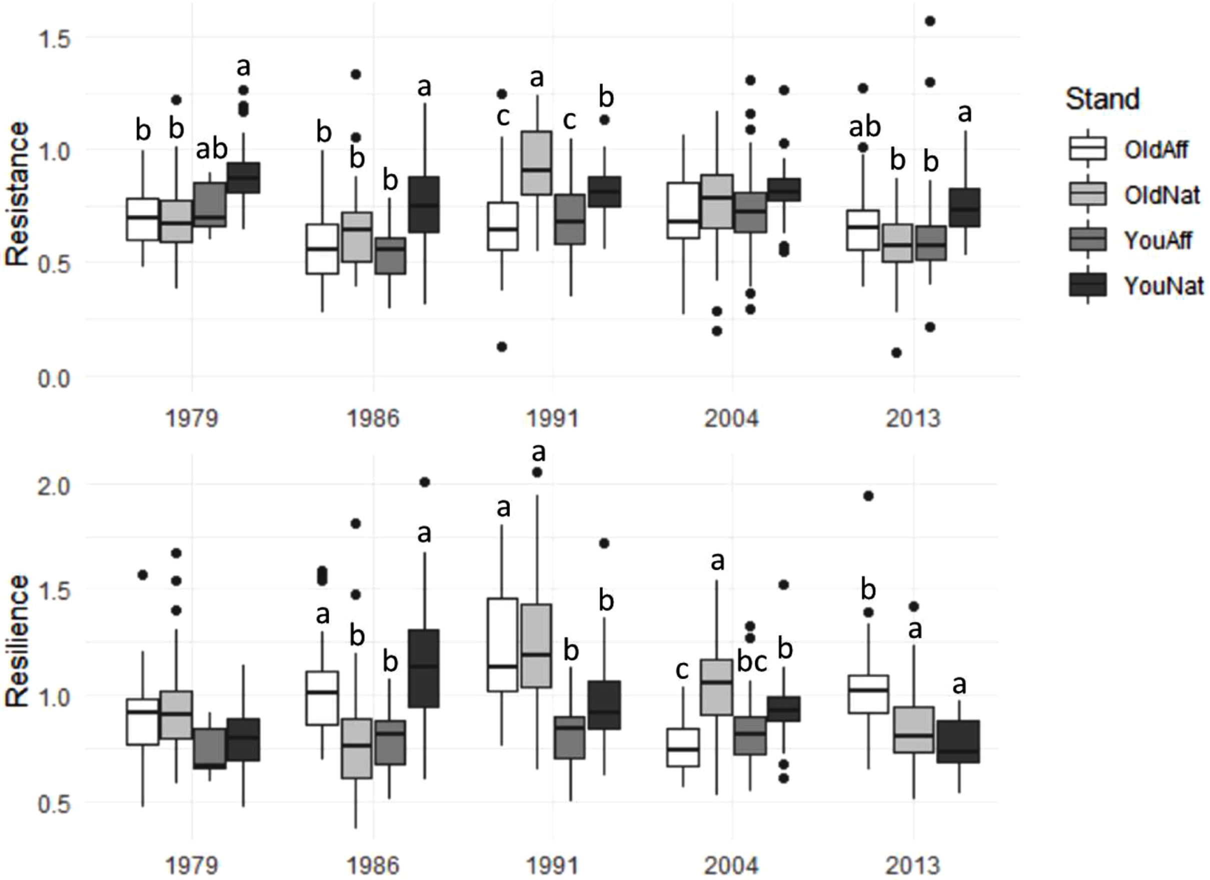


Fig. 3. Resistance and resilience indices for the four studied stand types considering the repeated negative pointer years among the different stands. For 2013, resilience values in YouAff are missing due to lack of growth data in this stand after 2015. YouNat, YouAff, OldNat and OldAff refer to the young natural, young afforestation, old natural and old afforestation stands, respectively. Letters show significant differences (using ANOVA with Bonferroni post hoc test) of resistance and resilience indices between the different stand types.

natural stand but inversely related to resilience in young stands. Increased competition, poorer sociological status, older age or higher height were related to an earlier opening or closing of the climatic window, although these relationships strongly varied among stands (**Table S4**).

We built seven models including the data of all trees of the four stands (Table 3). In addition to the six variables related to the sensitivity of growth to climate considered ($\Delta AICc_{BM}$, $Slope_{BM}$, $SPEI_{max}$ correlation, $SPEI_{max}$ slope, and values of the mean resistance and mean resilience), we used growth (BAI) as a response variable to compare the results obtained with the climate sensitivity variables with the relationships of the variables on growth, since the amount of growth is not necessarily related to the sensitivity of growth to climate (**Table S5**). The fact that DBH and age covaried led us to use the residuals of one of the two variables. The DBH was left in its original form as this variable was more important in all the models that have been tested, and age was transformed, as this variable was less important than DBH.

According to the BAI model, the higher the DBH_c and age (residual), the lower the growth rate, especially in the afforested stands (Table 3 and Fig. 4). Furthermore, these two predictors interact with each other in such a way that the higher the DBH_c the lower the growth in trees with low residual age, but the relationship was inverse in trees with high residual age. Finally, the higher the competition (BA), the lower the growth in large trees (with high DBH_c), but not in small trees. It must be taken into account that, working with residual age, a tree with a higher or lower value does not correspond exactly to a young or old tree, respectively.

Resistance was influenced (the model explains 33.6 % of the total variability) by all the variables considered (Table 3). Competition from neighboring trees negatively influenced resistance when the sociological status was worse (higher DBH_n/DBH_c) and vice versa, i.e., a worse sociological state reduced resistance when competition was high (Fig. 5). On the contrary, in trees with high residual age this effect of both competition and sociological status was compensated or even reversed. Finally, DBH_c had a negative effect on resistance in stands of natural origin (in afforested stands the effect was not significant).

The resilience model explained the greatest variability (38.9 %), where DBH_c and its interaction with the stand origin were the most influential variables (with the highest coefficients; Table 3 and Fig. 5). The higher the DBH_c, the higher the resilience, especially in afforested stands. Higher competition (BA) and worse sociological status decreased resilience, although the effect of the DBH_n/DBH_c variable was compensated or even reversed by age (residual). The greater the DBH and residual age, the greater the resilience, especially in afforested stands.

If interactions are not considered, the influence of the predictors was similar in the $AICc_{BM}$ and $SPEI_{max}$ correlation models (Table 3). Sensitivity to climate increased with afforested stand origin, better sociological status, smaller DBH and greater competition. However, the $AICc_{BM}$ model does not include interactions and explains a very small percentage of variability (3.9 %), while the $SPEI_{max}$ correlation model explains 22.5 % of the variability. The interactions in this model show that increasing BA increases the climatic signal in small trees (but no significant relationship in large trees) but reduces it when the sociological status is poor (high DBH_n/DBH_c values) (Fig. 6). DBH_c showed opposite effects depending on stand origin; in afforested stands the climatic signal increased as DBH_c did, while in natural stands higher values of this variable decreased the signal.

$Slope_{BM}$ and $SPEI_{max}$ slope models included different predictors but their results were concordant (Table 3 and Fig. 6). Diameter and residual age strongly increased the effect of climate on growth in afforested stands but decreased it in natural origin stands. Poorer sociological status and higher competition decreased the effect of climate, although in the latter case, only with medium or high DBH_c values.

4. Discussion

The models that included the strength of the growth-climate relationship as a response variable ($\Delta AICc_{BM}$ and $SPEI_{max}$ correlation) and those that included slope ($Slope_{BM}$ and $SPEI_{max}$ slope) showed concordant results (Table 3 and Fig. 6). Although the predictors may vary between the models, the effect of the predictors on the response variables were similar, with the sign of the regression coefficients of each predictor being maintained in almost all cases between the four models. This means that the coefficient of the same predictor (e.g. DBH_n/DBH_c or origin), and also the same interaction (e.g. DBH_c : origin), maintains the same sign (negative for DBH_n/DBH_c and positive for both origin and the interaction DBH_c : origin) and therefore the same effect in the four

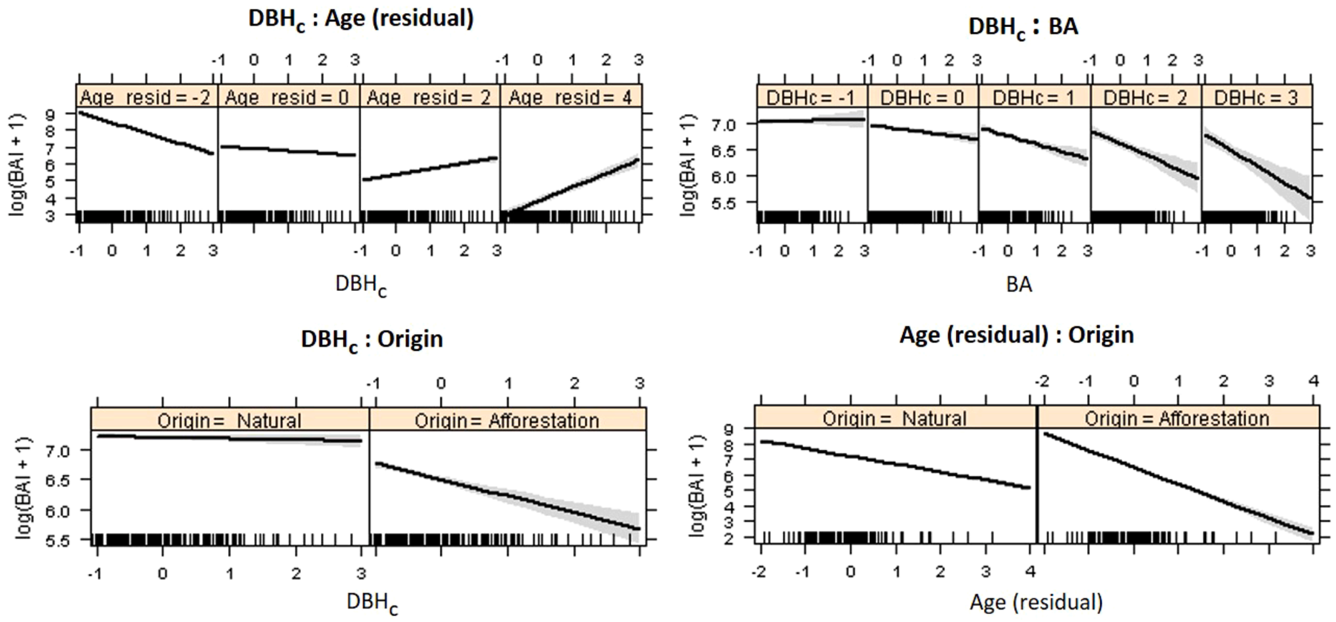


Fig. 4. Effects of the interactions between predictors on radial growth. Origin refers to the stand origin of the plots (natural or afforestation), Age (residual) are the residuals of the nonlinear model relating Age and DBH_c, BA is the subplot basal area, and DBH_c is the diameter at breast height of the cored trees. The predictors are standardized. Shaded bands indicate the 95 % confidence intervals. Positions of the data along *x* axis are denoted by tick marks.

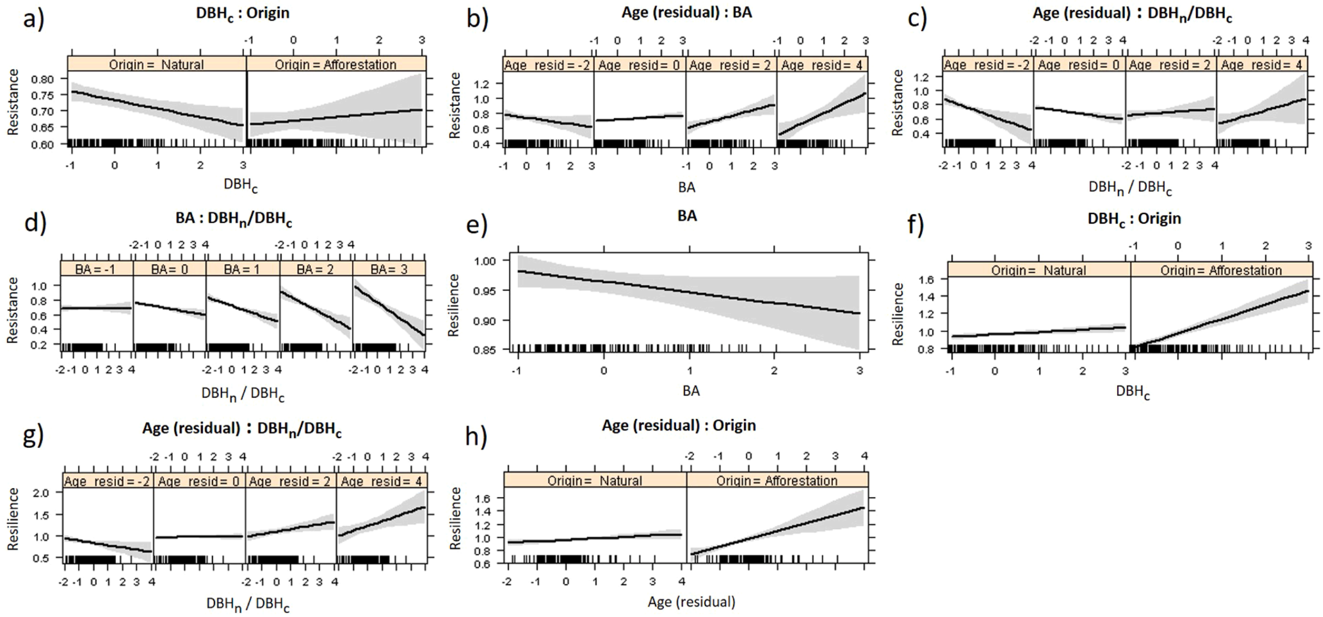


Fig. 5. Effects of the interactions between predictors on resistance (a-d) and resilience (e-h). Origin refers to the stand origin of the plots (natural or afforestation), Age (residual) are the residuals of the nonlinear model relating Age and DBH_c, BA is the subplot basal area, DBH_c is the diameter at breast height of the cored trees, and DBH_n/DBH_c is the ratio between mean diameter of the subplot and the diameter of the cored tree. The predictors are standardized. Shaded bands indicate the 95 % confidence intervals. Positions of the data along *x* axis are denoted by tick marks.

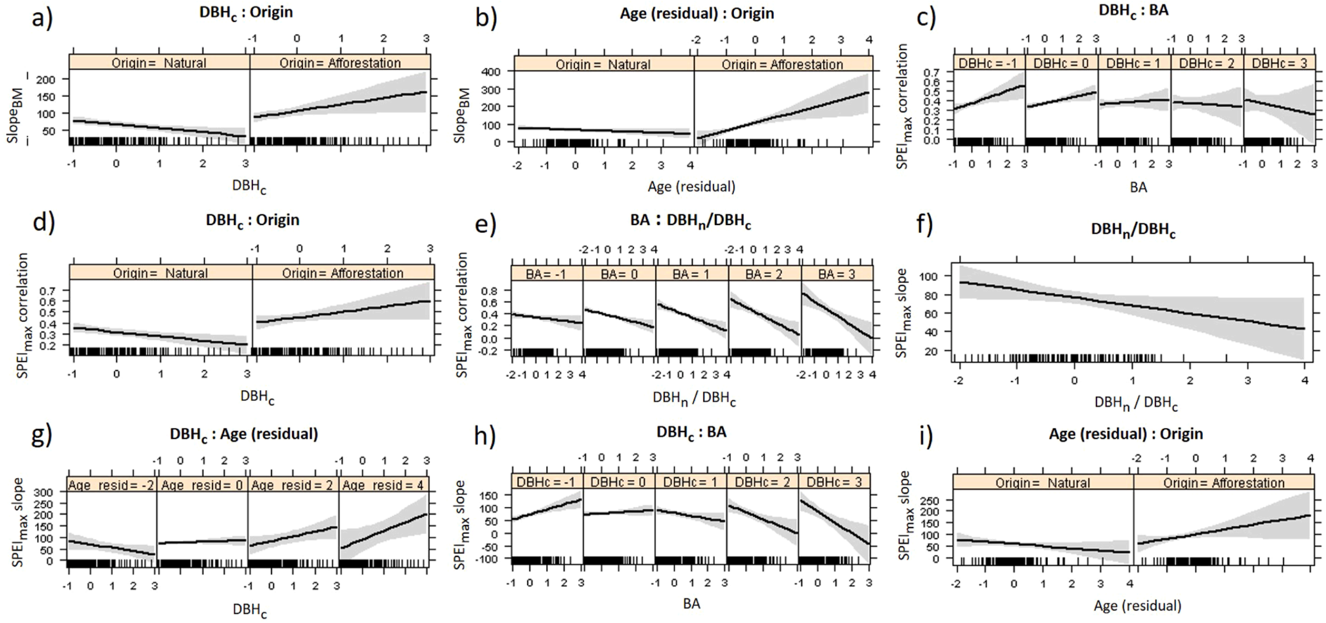


Fig. 6. Effects of the interactions between predictors on $Slope_{BM}$ (a-b), $SPEI_{max}$ correlation (c-e) and $SPEI_{max}$ slope (f-i). Origin refers to the stand origin of the plots (natural or afforestation), Age (residual) are the residuals of the nonlinear model relating Age and DBH_c, BA is the subplot basal area, DBH_c is the diameter at breast height of the cored trees, and DBH_n/DBH_c is the ratio between mean diameter of the subplot and the diameter of the cored tree. The predictors are standardized. Shaded bands indicate the 95 % confidence intervals. Positions of the data along *x* axis are denoted by tick marks.

models. Therefore, we will discuss together the results obtained in the models that analyze the strength and slope of the relationships ($\Delta AICc_{BM}$, $SPEI_{max}$ correlation, $Slope_{BM}$ and $SPEI_{max}$ slope).

The values of $\Delta AICc_{BM}$, $SPEI_{max}$ correlation, $Slope_{BM}$ and $SPEI_{max}$ slope were obtained by relating tree growth to drought indices (in the case of $SPEI_{max}$ correlation and $SPEI_{max}$ slope) and to temperature and precipitation (in the case of $\Delta AICc_{BM}$ and $Slope_{BM}$; note that although temperature is considered, these values are obtained by relating growth to precipitation because this variable fits better than temperature). However, as the modeling results for these variables are similar and are therefore discussed together, the generic term climate is used throughout the discussion rather than referring to temperature, precipitation or drought index. Note that although we use the term climate, we do not consider other important climatic variables such as radiation.

4.1. Stand and tree-level approaches

Based on the results of the stand level analysis, we can state that the afforested stands and the young natural stands showed similar relationships with climate (Figs. 2 and **S3**) and, among them, the young afforestation stand was the most sensitive to climate which explained 58 % of the growth variability (Table 2). This result is in line with previous studies (Sánchez-Salguero et al., 2013). On the contrary, the old natural stand showed very little sensitivity to climate. In addition, natural stands had fewer pointer years, especially the young natural stand (**Fig. S5** and **Table S2**), while the old afforestation stand showed the highest resilience (Fig. 3). In a traditional analysis, comparing different stands, it would be speculative to try to reach more detailed conclusions about the specific effect of age, diameter or origin. To try to go further it is necessary to perform tree-level analysis which allows us to analyze independently the effect of each variable, including competition or social status, which cannot be analyzed at stand level. Furthermore, in the stand-level approach we can only make comparisons between 4 datasets (4 stands), which prevents us from studying interactions, whereas in the tree-level approach we can make comparisons between more than 150 datasets (from the more than 150 trees sampled; Table 1). The number of series we can use in the tree-level approach allows us to model their relationships, including interactions. Within the tree-level analysis, one of the most evident results is the complexity of the relationships. Indeed, the effect of the variables studied on growth is not unidirectional, being this multidirectional effect dependent on third variables that interact and make the interpretation of the results difficult (**Table 3**; see also Castagneri et al., 2022).

4.2. Age and diameter effects

Age influenced the strength of the climate signal (**Tables S3** and **S4**), but once the variability explained by DBH$_c$ was removed, it had no influence (it did not appear in the ΔAICc$_{BM}$ and SPEI$_{max}$ correlation models; Table 3). It must be taken into account that the residual age indicates whether a tree is younger or older than the age that would correspond to its DBH, and therefore the characteristics of the microsite will have an important influence on this variable. Residual age influenced the slope of the climate-growth relationship, decreasing it in stands of natural origin, but strongly increasing it in afforested stands and in trees with higher DBH$_c$ (Fig. 6). Diameter influenced both the strength of the climate signal (Table 3), and the slope of the growth-climate relationship, and its influence was similar to that exerted by age, i.e., it decreased the strength and slope of growth-climate relationships in stands of natural origin, but increased them in afforested stands and trees with high residual age (Fig. 6). Therefore, and contrary to what we expected, residual age influenced growth-climate relationships in a similar way to DBH$_c$ (also, non-residual age and diameter correlate similarly with the strength and slope of growth-climate relationships; **Table S3**), possibly because both variables are proxies or are related to tree height (Schuster and Oberhuber, 2013), which would be the variable that best explains changes in physiology and also in climate-growth relationships (Trouillier et al., 2019). The fact that height showed in our data greater relationships (than age and DBH$_c$) with growth response to climate (**Table S3**) would support this idea. However, these relationships are not coincident among these three variables and in some cases are opposite, indicating that age and DBH$_c$ provide additional or partially different information to that provided by height.

The increase in climate sensitivity with increasing age/DBH$_c$ that occurred in afforested stands was previously described (Carrer and Urbinati, 2004; Linares et al., 2013; Rozas et al., 2009; Trouillier et al., 2019). This sensitivity increased up to a certain age/size, at which point sensitivity to climate did not change anymore. Effectively, in young natural and afforestation stands, the correlations between SPEI$_{max}$ correlation and DBH$_c$ were of 0.31 and 0.36, respectively, while in old stands this correlation decreased to 0.07 (for old natural stand) and 0.11 (old afforestation stand) (**Table S3**). This increase in sensitivity with age is at least partially explained by increased maintenance respiration costs (Hunt et al., 1999) and by hydraulic limitation, which increases as the height and complexity of the tree structure increase (Ryan and Yoder, 1997; Zhang et al., 2009), due to a several variables including gravity, a longer and more complex hydraulic path length through stems and branches, and reduced allocation to roots (Carrer and Urbinati, 2004). In addition, increased hydraulic resistance is related to earlier stomata closure, compared to younger or smaller trees (Ryan and Yoder, 1997), which may increase their sensitivity to climate. The decrease in climate sensitivity observed in the natural stands (Fig. 6) is possibly influenced by the specific characteristics of the sites sampled and, in particular, by the low sensitivity to climate shown by the old natural stand (Figs. 2 and **S3** and Table 2), which has a similar structure to that of an old-growth forest (this aspect is discussed in detail in Section 4.5).

The effect of residual age and DBH$_c$ on resilience was approximately similar, but the results differed in terms of the effect on resistance. Higher residual age was related to increased resistance and resilience in general terms (Table 3 and **Fig. 5**; also compare resilience values of afforested stands in Fig. 3), although competition and sociological status interacted with age (only DBH$_n$/DBH$_c$ interacts in the case of resilience), so that with high values of BA and DBH$_n$/DBH$_c$, resistance and resilience increased strongly with increasing residual age, but with low values of these variables, resistance and resilience decreased slightly with increasing residual age. However, the effect of diameter on resistance and resilience was opposite. While higher DBH$_c$ decreased resistance in stands of natural origin (the effect is not significant in afforested stands), on the contrary, it increased resilience irrespective of origin, although the effect was more pronounced in afforested stands (Fig. 5 and Table 3). Regardless of the interactions between variables, in the old afforestation

Table 2
Characteristics of the simple (relating residual series of ring-width indices and daily total precipitation, Prec) and multiple linear models (relating residual series of ring-width indices with Prec and mean daily maximum temperatures, Tmax) fitted for the best time window. In all stands, simple models with Prec (compared to the models with Tmax or mean daily maximum minimum temperatures, Tmin) and multiple models with Prec and Tmax (compared to the models with Prec and Tmin) showed the lowest ΔAICc. ΔAICc is the difference between the AICc of the fitted linear model and the baseline model (null model for the simple linear model, and the latter for the multiple linear model), windows open and close (W. open and close, respectively) show the selected climate window (in Julian days of the year) from the prior (*t-1*) to the current (*t*) year, *p* and R^2 refer to the model values, and *p* AICc is the *p*-value of the randomization test (probability of obtaining a similar ΔAICc value by chance). For the OldNat stand, only the simple model is shown since no significant relationships (*p* AICc < 0.05) were found with any of the climatic variables. YouNat, YouAff, OldNat and OldAff refer to the young natural, young afforestation, old natural and old afforestation stands, respectively. Regression coefficients of the best linear model for each stand are shown in **Table S1**.

Stand	Model	Variable	ΔAICc	W. open	W. close	*p*	R^2	*p* AICc
YouNat	Simple	Prec	−20.18	140	214	< 0.001	0.40	**0.003**
YouNat	Multiple	Tmax	−5.82	185	205	0.001	0.50	0.546
YouAff	Simple	Prec	−19.64	184	215	< 0.001	0.39	**0.003**
YouAff	Multiple	Tmax	−13.32	33	132	< 0.001	0.58	**0.042**
OldNat	Simple	Prec	−5.61	305 (t-1)	122	0.006	0.16	0.664
OldAff	Simple	Prec	−17.98	123	243	< 0.001	0.37	**0.004**
OldAff	Multiple	Tmax	−9.47	54	73	< 0.001	0.52	0.169

Table 3

Regression coefficients (standard errors are shown in parentheses), adjusted R^2 and *p*-value for the best linear models of the log-transformed basal area increment (BAI), the mean resistance and resilience, $|\Delta AICc_{BM}|$ (absolute value of ΔAICc of the best models relating growth with daily climate data; the higher the absolute value, the higher the sensitivity to climate), $Slope_{BM}$ (slope of the best models relating growth with daily climate data), $SPEI_{max}$ correlation (the highest correlation obtained between growths and the different SPEI variables; the higher the value, the higher the sensitivity to climate) and $SPEI_{max}$ slope (slope of the model relating growth, as response variable, to the most correlated SPEI variable). DBH_c is the diameter at breast height of the cored trees, Age (residual) are the residuals of the nonlinear model relating Age and DBH_c, BA is the subplot basal area, and DBH_n/DBH_c is the ratio between mean diameter of the subplot and diameter of the cored tree. The variable "afforestation" takes values 0 and 1 for the natural and afforested stands, respectively. Predictors were standardized prior to fitting the models and ":" indicates interactions. Interaction effects are shown in Figs. 4, 5 and 6. Significance levels: ■$p < 0.10$, *$p < 0.05$, **$p < 0.01$ and ***$p < 0.001$, respectively.

	Log(BAI)	Resistance	Resilience	$\|\Delta AICc_{BM}\|$	$Slope_{BM}$	$SPEI_{max}$ correlation	$SPEI_{max}$ slope
Intercept	7.213 (0.022) ***	0,734 (0,011) ***	0,958 (0,012) ***	9068 (0,483) ***	68,373 (4462) ***	0,319 (0,017) ***	58,678 (5167) ***
DBH_c	−0.019 (0.02)	−0,026 (0,009) **	0,027 (0,009) **	−0,674 (0,381) ■	−11,649 (3845) **	−0,039 (0,014) **	3049 (3469)
Age (residual)	−0.514 (0.029) ***	−0,014 (0,01)	0,023 (0,011) *		−5382 (3516)		−9183 (6669)
BA	−0.066 (0.018) ***	0,019 (0,009) *	−0,018 (0,01) ■			0,037 (0,014) **	4216 (3954)
DBH_n/DBH_c		−0,028 (0,009) **	0,002 (0,01)	−0,666 (0,409) ■		−0,049 (0,013) ***	−8485 (4223) *
Afforestation	−0.709 (0.041) ***	−0,063 (0,021) **	0,015 (0,026)	1647 (0,795) *	38,826 (8801) ***	0,134 (0,03) ***	41,729 (10,698) ***
DBH_c : Age (residual)	0.241 (0.017) ***						8694 (4083) *
DBH_c : BA	−0.081 (0.022) ***					−0,025 (0,017)	−15,817 (4229) ***
DBH_c : Afforestation	−0.258 (0.047) ***	0,038 (0,019) *	0,138 (0,021) ***		30,566 (9285) **	0,088 (0,034) **	
Age (residual) : BA		0,03 (0,012) *					
Age (residual) : DBH_n/DBH_c		0,022 (0,01) *	0,027 (0,011) *				
Age (residual) : Afforestation	−0.581 (0.059) ***		0,099 (0,033) **		47,662 (13,47) ***		29,777 (12,731) *
BA : DBH_n/DBH_c		−0,028 (0,008) ***				−0,025 (0,011) *	
R^2	0.351	0.336	0.389	0.039	0.182	0.225	0.154
P	< 0.001	< 0.001	< 0.001	0.038	< 0.001	< 0.001	< 0.001

stand there is a direct relationship between DBH_c and resilience (**Table S3**). The existing literature on the effect of size or age on growth resistance and resilience is scarce and its results are contradictory, ranging from a negative influence of these variables on growth resistance and resilience (Bosela et al., 2021; Carnwath and Nelson, 2017; D'Amato et al., 2013; Sohn et al., 2016) to a positive effect (Carnwath and Nelson, 2017; Merlin et al., 2015; Orwig and Abrams, 1997; Rubio-Cuadrado et al., 2018), which shows the importance of the specific characteristics of each study site in this type of relationship, such as species, forest type, climate conditions, competition, soil, slope, aspect or latitude (Carnwath and Nelson, 2017; Gazol et al., 2017; Rubio-Cuadrado et al., 2018; Sohn et al., 2016). Taking into account the meta-analysis by Sohn et al. (2016), larger trees have lower average resistance due to their higher water demand, their lower hydraulic efficiency and the higher radiation and evaporation their canopies experience compared to smaller trees. However, it could be also argued that larger trees have greater capacities to store (hydraulic capacitance) and capture water and nutrients by forming bigger root systems and reaching deep soil water sources (Goldstein et al., 1998; Ripullone et al., 2020), which could make them more resistant, and may take faster advantage of improved conditions after drought events, leading to higher average resilience. The possible protective effect of high BA and DBH_n/DBH_c values on drought is discussed in Section 4.4 below. In any case, only trees of a certain size, that is to say, with a root system developed enough to be able to face a drought event in better conditions, are benefited by the competition.

4.3. *Stand origin effect*

The strength of the climate-growth relationship was greater in afforested stands, with higher $|\Delta AICc_{BM}|$ and $SPEI_{max}$ correlation values obtained in these stands (Table 3 and Fig. 6). Its effect on slope was also similar between $Slope_{BM}$ and $SPEI_{max}$ slope models, increasing the effect of climate on growth in afforested stands in medium or large trees (Fig. 6). This result is possibly related to these trees having the lowest BAI (Fig. 4). In fact, for each of the age types (young-old), afforested and natural stands had similar growth (TRW) in recent years despite the afforested stands having lower competition, age and size (Fig. 1 and Table 1). The more limiting conditions in which trees in afforested stands grow make them more sensitive to climate. The most limiting conditions would not be related to the uniformity of these stands, since the young afforestation stand shows a similar structure (**Fig. S1**), nor to the differences in competition, since the afforested stands have lower BA (Table 1), nor to the origin of the seed, since the seed of the afforested stands belongs to the region of provenance that encompasses the study area (Mesa Garrido, 2016; Rubio-Cuadrado et al., 2020a). Therefore, the limiting conditions are probably due to the worse soil conditions, since the stands that were treeless before afforestation would have suffered high soil losses during the periods in which they were not forested. However, differences between forests according to their origin often did not imply changes in sensitivity to climate (Camarero et al., 2021b; Ni et al., 2023).

Stands of natural origin had fewer pointer years (**Fig. S5** and **Table S2**) and, for the pointer years considered, trees of natural origin with lower DBH_c had higher resistances (Table 3 and Fig. 5) in accordance with previous studies (Navarro-Cerrillo et al., 2018; Rubio-Cuadrado et al., 2018; Sánchez-Salguero et al., 2013). On the contrary, trees of afforested origin and medium or high DBH_c (or age) had higher resilience (see also Fig. 3). These results contradict those obtained in previous studies (Navarro-Cerrillo et al., 2018; Rubio-Cuadrado et al., 2018; Sánchez-Salguero et al., 2013), in which either no differences due to origin were found, or resilience was higher in natural stands (but see Navarro-Cerrillo et al., 2023). Because of this contrast with the literature, our results are possibly not related to the origin of the stand, but to the particular conditions (such as the microclimate) that affect the old afforestation stand.

4.4. Competition and social status effect

In general, the higher the BA and the worse the social status (higher DBH_n/DBH_c), the lower both the strength and the slope of the climate-growth relationship (Table 3 and Fig. 6). That is, suppressed trees with high competition showed little climate-driven growth variability, maybe because their low growth rates or because they could take advantage of the climate conditions buffering relative to the closed and densely foliated canopy, which could reduce thermal stress and transpiration during summer, and thus sensitivity to drought (Aussenac, 2000; Bréda et al., 2006; Lebourgeois et al., 2014; Niinemets, 2010). In addition, trees that have grown under high competition may modify structural properties of their hydraulic architecture (Tyree and Zimmermann, 2002), increasing for example the proportion of latewood, in which tracheids are capable of storing significantly more water than are earlywood tracheids (Domec and Gartner, 2003), or increasing the proportion of conductive sapwood (Carnwath and Nelson, 2016). Likewise, changes in carbon allocation can occur in trees living with worse environmental conditions that allow them to better cope with unfavorable periods of the year (Maguire and Kobe, 2015). Related to these anatomical and physiological adaptations, previous studies have shown that stands located in areas with poorer environmental conditions may be less sensitive to climate (Martínez-Vilalta et al., 2012; Rubio-Cuadrado et al., 2020a).

On the contrary, in trees with lower DBH_c an increase in BA produced an increase in both the strength and slope of the climate-growth relationships (Table 3 and Fig. 6). In this sense, previous studies showed that increased competition fundamentally affects the availability of water resources for the tree, strengthening the relationships between growth and soil water availability (Aussenac, 2000; Cescatti and Piutti, 1998; Kholdaenko et al., 2023; Lebourgeois et al., 2014; Martín-Benito et al., 2010). In small trees, with a less developed root system, this competition for water may be more limiting than the protective effect of the neighborhood. In our climate-growth models fitted to each tree, the introduced climate variable was either SPEI or precipitation, since this variable has shown greater relationships than temperature. However, while high levels of competition increased the effect of precipitation on growth, a low level of competition may increase the effect of temperatures by increasing canopy exposure (Cescatti and Piutti, 1998; Kholdaenko et al., 2023; Martín-Benito et al., 2010). Possibly because of this, the young afforestation stand, which had the lowest competition values (Table 1), showed the highest relationship with Tmax (Table 2). With respect to the interaction that occurred with DBH_c, Matisons et al. (2017) showed how in mature trees the effect of social status is greater than in smaller trees, strongly changing the climate-growth relationships and significant influence period (in this regard see also **Table S4**).

Resistance and resilience showed a similar response to variation in BA and DBH_n/DBH_c. In general, the higher the value of these two predictors the lower both resistance and resilience (Fig. 5 and **Tables 3** and **S3**), due to the greater drought stress because of greater root competition for soil moisture (Carnwath and Nelson, 2017; Kloeppel et al., 1993; Martín-Benito et al., 2008; Sohn et al., 2016). Effectively, during extreme climatic events, having a good social status (low DBH_n/DBH_c values), which is related to a larger root system and, therefore, to a greater capacity to acquire scarce belowground resources, including access to deep soil water (Carnwath and Nelson, 2017; Ripullone et al., 2020), may be more important for growth resistance than the possible protective effect of the neighborhood. In fact, it seems that only these trees with better social status are able to benefit from the protective effect of the neighborhood during extreme weather events, since for these trees, the higher the BA, the higher the resistance (Fig. 5). This agrees with a recent meta-analysis showing a reduced resistance with higher competition (Castagneri et al., 2022).

4.5. Other effects

Stand forest structure is another important variable that can influence climate-growth relationships, although this topic is a gap in the literature that remains poorly studied. A diverse forest structure, with the presence of multiple vertical strata, including above-ground and underground stratification, often implies a better use of resources and a decrease in average competition for water, nutrients and light (Dănescu et al., 2016; Ercanli, 2018; Laurans et al., 2014), although there are multiple other variables that may influence the effect of this variable (Bohn and Huth, 2017). The old natural stand, which presented characteristics of age and structure similar to an old-growth forest (Table 1 and **Fig. S1**), showed a much lower and very different response to climate than the rest of the stands studied (Figs. 2, **S3** and **S4** and Table 2). Therefore, in this stand the greater structural complexity would reduce competition for water, making this resource not limiting (in this stand there are no significant direct relationships between growth and precipitation), with radiation appearing as the limiting variable for growth. Although we do not have radiation or cloudiness data, these variables would be those behind the inverse relationships between growth and precipitation or SPEI. Such a relationship is probably due to the fact that this stand was sampled at the highest elevation in the coolest site. In any case, although structural diversity reduced competition, it was still important for growth, with the old natural stand showing the greatest growth response due to releases (**Figs. S6** and **S7**).

The structure had no appreciable influence on the resistance and resilience values (Fig. 3) (but see Itter et al., 2017). Although a complex structure may decrease competition for resources, on the contrary, it may increase evapotranspiration by decreasing the protective effect of the neighborhood. However, a complex forest structure can have a protective effect against extreme climate events such as windstorms or snowstorms, due to the lesser slenderness of the trees growing in uneven-aged stands and the increased vulnerability of homogeneous afforested stands (Camarero et al., 2021a; Kenk and Guehne, 2001; Martín-Alcón et al., 2010; Mason, 2002).

There are variables that have not been considered here, but that interact with those we have studied in the present work, as can be deduced from the fact that we found an inverse relationship between DBH_c and growth rates (Table 3 and Fig. 4), contrary to what is usually observed in the literature (Monserud and Sterba, 1996; Rubio-Cuadrado et al., 2020a). Those additional variables include tree height, height of neighboring trees, soil characteristics, microenvironmental conditions, etc. As we have seen, the variables interact strongly with each other and it is inappropriate to offer general conclusions valid for all conditions and forest types. It is necessary to continue in the wake of the present work by expanding both the number of variables studied and, especially, the number of species, stands and sites, in order to understand precisely the variables that influence on the sensitivity of growth to climate and its effects and interactions.

5. Conclusions

Our results illustrate the great complexity of the relationships of age, diameter, stand origin, competition, social status, structure, etc., with the sensitivity of tree growth to climate and the effect of climate on growth, including the effect of extreme climatic events (e.g., droughts) on resistance and resilience. All these variables are important and with strong interactions between them, which makes their effects not unidirectional and strongly dependent on the site conditions. In general, the sensitivity of growth to climate and the effect of climate on growth increases with age, diameter, afforested origin, decreasing competition and higher social status. The old natural stand has a very different relationship with climate compared to the rest of the stands. This stand, with a structure similar to that of an old-growth forest, has a very low sensitivity to climate. In general, growth resistance increases with age, decreasing diameter, afforested origin, decreasing competition and higher social status. In general, resilience increases with age, diameter, natural origin, decreasing competition and higher social status. However, the interactions between variables cause the effect of one variable to change depending on the value of the other variables. Finally, with this work we show the usefulness of the analysis of data at individual tree level, which, combined with the joint analysis at stand level, allows us to obtain more accurate and detailed information.

CRediT authorship contribution statement

Álvaro Rubio-Cuadrado: Conceptualization, Formal analysis, Investigation, Methodology, Software, Writing – original draft, Writing – review & editing. **Fernando Montes:** Conceptualization, Investigation, Resources, Writing – review & editing. **Iciar Alberdi:** Conceptualization, Investigation, Writing – review & editing. **Isabel Cañellas:** Conceptualization, Funding acquisition, Investigation, Resources, Writing – review & editing. **Isabel Aulló-Maestro:** Investigation. **Raúl Sánchez-Salguero:** Investigation, Writing – review & editing. **Andrea Hevia:** Investigation, Writing – review & editing. **César Pérez-Cruzado:** Investigation, Writing – review & editing. **Juan Alberto Molina-Valero:** Investigation, Writing – review & editing. **J. Julio Camarero:** Conceptualization, Methodology, Writing – review & editing.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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Data availability

Data will be made available on request.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2024.110148.

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