



Resist, recover or both? Growth plasticity in response to drought is geographically structured and linked to intraspecific variability in *Pinus pinaster*

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Funding information

Ministerio de Economía y Competitividad, Grant/Award Number: CGL2007-62063, CGL2008-06005, CGL2011-27229, CGL2013-48843-C2-1-R, CGL2015-69186-C2-1-R, CGL2015-69985, IJCI-2015-25845, MINECO-FPDI 2013-16600; Consellería de Cultura, Educación e Ordenación Universitaria, Xunta de Galicia, Grant/Award Number: PGIDIT06PXIB502262PR; European Union Agency for Network and Information Security, Grant/Award Number: Interreg V-A POCTEFA 2014-2020-CANOPEE; Russian Science Foundation, Grant/Award Number: Grant 14-14-00219-P, Project "5-100", Grant N° M 2.2.

Editor: Matt McGlone

Abstract

Aim: We investigate the effects of the environmental and geographical processes driving growth resilience and recovery in response to drought in Mediterranean *Pinus pinaster* forests. We explicitly consider how intraspecific variability modulates growth resilience to drought.

Location: Western Mediterranean basin.

Methods: We analysed tree rings from a large network of 48 forests (836 trees) encompassing wide ecological and climatic gradients, including six provenances. To characterize the major constraints of *P. pinaster* growth under extremely dry conditions, we simulated growth responses to temperature and soil moisture using a process-based growth model coupled with the quantification of climate–growth relationships. Then, we related growth–resilience indices to provenance and site variables considering different drought events.

Results: *Pinus pinaster* displayed strong variation in growth resilience across its distributional range, but common patterns were found within each provenance. Post-drought resilience increased with elevation and drier conditions but decreased with spring precipitation. Trees from dry sites were less resistant to drought but recovered faster than trees from wet sites.

Main conclusions: Resilience strategies differed among tree provenances: wet forests showed higher growth resistance to drought, while dry forests presented faster growth recovery, suggesting different impacts of climate warming on forest productivity. We detected geographically structured resilience patterns corresponding to different provenances, confirming high intraspecific variability in response to drought. This information should be included in species distribution models to simulate forest responses to climate warming and forecasted aridification.

KEYWORDS

dendroecology, drought resistance, drought stress, forward growth models, post-drought recovery, provenances, resilience indices



1 | INTRODUCTION

The forecasted increase in global mean temperature and severe dry spells might make many forests types worldwide more vulnerable by reducing their post-drought resilience (Allen, Breshears, & McDowell, 2015). This loss in resilience, i.e. the capacity of a forest to resist disturbances and/or recover after them and maintain its structure and function (sensu Lloret, Keeling, & Sala, 2011), is very conspicuous in some drought-prone forests where water shortages induce a reduction in forest productivity and growth, often triggering dieback and mortality (Camarero, Gazol, Tardif, & Conciatori, 2015). Thus, it is challenging to predict if tree populations will be able to adapt to drought by increasing their resilience and how they will recover after drought events across different regions. To address these questions, forest-growth responses to drought must be explored in relationship to tree provenance (Lamy et al., 2014), as severe droughts act as selective forces by accelerating the rate of evolution of drought-adaptive traits in widely distributed tree species (Kremer, Potts, & Delzon, 2014).

The persistence of tree species under forecasted climate conditions will depend upon their phenotypic plasticity and their potential to adapt to drought (Gazol, Camarero, Anderegg, & Vicente-Serrano, 2017). The effects of drought on forest productivity highlight the need to investigate the relevant traits providing tolerance to temporary water shortages (e.g. radial-growth plasticity) and to assess how genetic variation and, consequently, phenotypic plasticity allow tree populations to cope with climate extremes (Valladares et al., 2014). Therefore, understanding how forests can resist drought and recover after it across different regions and in relation to their distinct genetic or geographical provenances (e.g., Gazol, Ribas, Gutiérrez, & Camarero, 2017) is crucial for understanding how drought will impact tree function and forest productivity at a global scale (Anderegg et al., 2015).

Different mechanisms allow tree species to address water deficits (Brodrribb, McAdam, Jordan, & Martins, 2014; Gazol, Camarero, et al., 2017). For instance, Scots pine (*Pinus sylvestris*) shows limited geographical plasticity in its xylem traits related to drought resistance (Martínez-Vilalta et al., 2009). This lack of plasticity is often associated with differences in growth resilience to drought (Gazol, Ribas, et al., 2017), which may be quantified by comparing the growth rates before, during and after drought events (Lloret et al., 2011). Those so-called resilience indices are surrogates of tree adaptation ability and phenotypic plasticity (Sánchez-Salguero, Camarero, Gutiérrez, et al., 2017; Sánchez-Salguero et al., 2015). In this sense, a trade-off between resistance and recovery in terms of drought can be expected, with some tree species displaying strong growth resistance and low growth recovery and vice versa (e.g., Gazol, Camarero, et al., 2017).

Maritime pine (*Pinus pinaster* Ait.) is a keystone species in the western Mediterranean (WM), combining a wide climate niche with limited genetic variability between populations and limited phenotypic plasticity for cavitation resistance across the whole species

distribution (Lamy et al., 2011, 2014). In addition, secondary growth in this species is very sensitive to drought, which reduces cambial activity and is linked to a decrease in tracheid lumen area (e.g. Bogino & Bravo, 2008; Campelo, Vieira, & Nabais, 2013; Rozas, Zas, & García-Gonzalez, 2011; Rozas, Zas, & García-González, 2011; Sánchez-Salguero, Navarro-Cerillo, Camarero, & Fernández-Cancio, 2010). It could be hypothesized that *P. pinaster* displays different growth strategies to cope with severe droughts across its broad distribution range. These characteristics make this conifer an excellent model to study intraspecific variation in drought response (Serra-Varola et al., 2015, 2017).

To explore the among-provenance variability in growth responses to severe drought, we evaluate the post-drought growth resilience across the WM *P. pinaster* forests. This species has a fragmented distribution in the WM region, where it inhabits sites subjected to a wide range of climatic conditions (Barbéro, Loisel, Quézel, Richardson, & Romane, 1998). The scattered distribution of this species results in limited gene flow among populations, leading to clearly defined provenances (Alía, Moro, & Denis, 1997; Bucci et al., 2007). To provide a mechanistic understanding of growth responses to drought, we use the Vaganov–Shashkin model of tree-ring formation, hereafter VS-Lite (Vaganov, Anchukaitis, & Evans, 2011; Vaganov, Hughes, & Shashkin, 2006). The VS-Lite forward growth model is one of the simplest models for understanding growth responses to climate at regional scales (Breitenmoser, Brönnimann, & Frank, 2014; Mina, Martin-Benito, Bugmann, & Cailleret, 2016; Sánchez-Salguero, Camarero, Carrer, et al., 2017; Tolwinski-Ward, Anchukaitis, & Evans, 2013; Tolwinski-Ward, Evans, Hughes, & Anchukaitis, 2011).

Here, we combine VS-Lite mechanistic models with resilience growth indices to characterize *P. pinaster* responses to drought. Our objectives are to: (1) analyse *P. pinaster* growth responses to climate and drought across the WM over a wide diversity of climate conditions, (2) assess the impact of drought events on growth by calculating resilience indices using growth responses to soil moisture obtained from the VS-Lite growth model and (3) evaluate whether resilience to drought varies among different provenances and depends upon site factors. We expect that *P. pinaster* growth responses to drought depend upon forest provenance and hypothesize that forests from drought-prone sites have lower growth resistance to drought (i.e. a low growth rate) and show higher recovery after drought than forests from mesic sites.

2 | MATERIALS AND METHODS

2.1 | Study sites and sampling design

The study area includes most natural populations of *P. pinaster* in the WM (Barbéro et al., 1998) (Figure 1a; see also Table S1). This species inhabits a wide range of elevations, from sea level up to 2,000 m a.s.l., and a wide range of hydroclimates (200–1,700 mm) and mean annual temperatures (9–16°C; Table S2). The species is ecologically very versatile, growing on a variety of substrates but

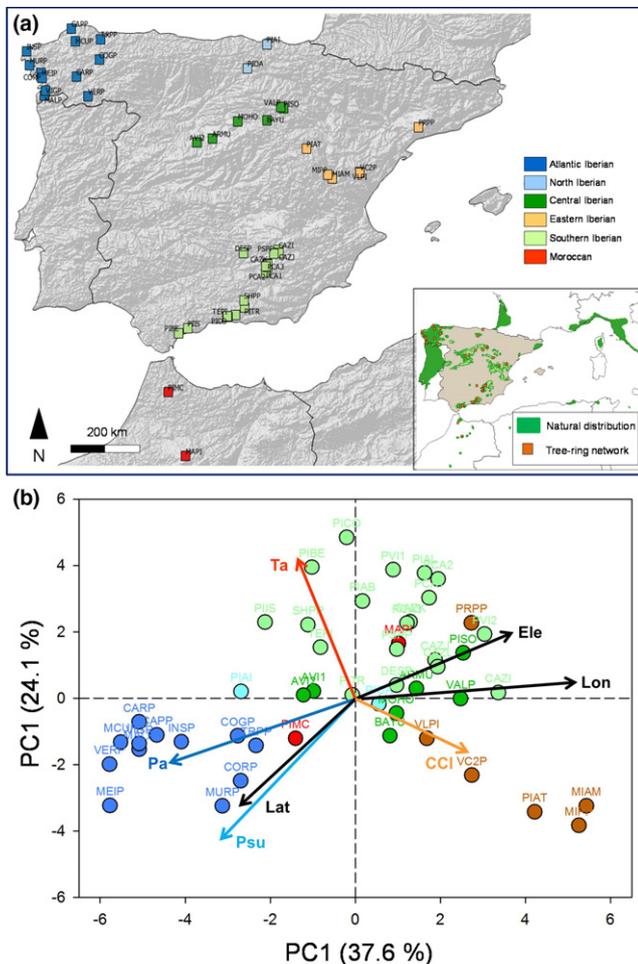


FIGURE 1 (a) Distribution of the studied Maritime pine (*Pinus pinaster*) sites and provenances (cf. Alía et al., 1997; Serra-Varela et al., 2015) along the natural distribution range of the species in Spain and northern Morocco. The inset map shows the location of the species distribution area in south-western Europe. (b) Scatter plots of the first two axes of a Principal Component Analysis (PCA) showing the observed tree-ring width indices (TRWi) for each provenance (colours) and sites (1950–2006 period). The PCA arrows show climatic (*Pa* and *Ta*, mean annual precipitation and temperature, respectively; *Psu*, summer precipitation; CCI, Conrad–Pollak Continuity Index) and topographical (*Lat*, latitude; *Lon*, longitude; *Ele*, elevation) variables (see Table S1 for more details on the sampled sites and their codes) [Colour figure can be viewed at wileyonlinelibrary.com]

mainly on nutrient-poor acidic soils (Abad Viñas, Caudullo, Oliveira, & de Rigo, 2016). Its strong local differentiation and patchy distribution have led to the search for adaptive phenotypic traits (Alía et al., 1997), and molecular analyses have allowed the delineation of geographically structured provenances (Burban & Petit, 2003).

Forty-eight *P. pinaster* forests were sampled along contrasting ecological and climate gradients and include six distinct provenances: Atlantic (12 sites), Northern Iberian (2 sites), Central Iberian (7 sites), Eastern Iberian (6 sites), Southern Iberian (19 sites) and Moroccan (2 sites) (Figure 1a, Table S1). At each site, at least 12 dominant or codominant trees were cored at 1.3 m using Pressler increment borers on the cross-slope sides of the trunk, resulting in 836 sampled

trees. For each study site, latitude, longitude and mean elevation were recorded (Table S1). Wood samples were sanded until rings were visible and then visually cross-dated. Tree-ring width was measured to the nearest 0.01 mm using 2–3 cores per tree with a binocular microscope and measuring devices (LINTAB, Rinntech, Heidelberg, Germany and Velmex Inc., Bloomfield, NY, USA). The accuracy of the visual cross-dating and ring-width measurements was checked using the COFECHA program (Holmes, 1983).

2.2 | Tree-growth responses to climate and drought

The homogenized and quality-checked climate dataset E-OBS 14.0 was used, considering the period 1950–2014 (Haylock et al., 2008). This dataset contains monthly mean, maximum and minimum temperature and precipitation data gridded at a 0.25° spatial resolution and has been checked for homogeneity. Since previous studies showed the effects of aridity, oceanicity and continentality on *P. pinaster* growth (Bogino & Bravo, 2008; Campelo et al., 2013; Rozas, Zas, et al., 2011), we calculated three climatic indices based on the annual range of the monthly mean air temperatures and site latitude: the De Martonne Aridity Index (AI), Marsz Oceanicity Index (MOI) and Conrad–Pollak Continuity Index (CCI; see Andrade & Corte-Real, 2017 for details).

To quantify climate–growth associations, we first calculated site chronologies from mean tree-ring width (TRW) series at the site scale (Table S3). Tree-ring width indices (TRWi) were obtained by adjusting negative exponential or linear functions to the TRW series, which eliminates growth trends as trees become older and larger. This method allowed high-frequency (annual to decadal) growth variability to be retained. We obtained standard TRWi series for each tree as the ratios between the measured (TRW) and fitted values. Lastly, we averaged the individual TRWi series into site-level chronologies following a hierarchical approach from tree to site and using biweight robust means. We did not remove the first-order autocorrelation of the TRWi data to maintain the year-to-year growth variation, which could be meaningful to correctly assess the post-drought resilience. To assess the quality of these site TRWi chronologies, we also calculated several dendrochronological statistics (Table S3). To characterize the geographical variation in the growth patterns of the different provenances across space and time, we conducted a Principal Component Analysis (PCA) using the correlation matrix of site TRWi chronologies. The PCA was applied to the entire network of tree-ring chronologies for the common 1950–2006 period (Figure 1b).

The relationships between the monthly climate series (mean, maximum and minimum temperatures and precipitation) and individual TRWi series were assessed by calculating bootstrapped Pearson correlation coefficients for the common period 1950–2006. The temporal window of growth–climate comparisons included the previous August to the current October. We also calculated correlations based on seasonal and annual values. We associated the correlation coefficients between monthly climate data and TRWi with the latitude, longitude and altitude to detect geographical patterns in



climate–growth relationships. Chronology building and climate–growth associations were performed using the packages *dpIR* (Bunn, 2010) and *treeclim* (Zang & Biondi, 2015) respectively.

2.3 | Forward process-based modelling of tree growth

We used the VS-Lite model and a Bayesian parameter estimation approach to simulate TRWi as a function of climate for each specific site period (see Table S1; Tolwinski-Ward, Tingley, Evans, Hughes, & Nychka, 2015; Tolwinski-Ward et al., 2011, 2013). The model uses the Leaky Bucket Model of hydrology (Huang, van den Dool, & Georgakakos, 1996) to estimate the monthly soil moisture from monthly temperature and total precipitation data. For each year, the model simulates standardized TRW anomalies from the minimum of the monthly growth responses to temperature (gT) and moisture (gM), modulated by insolation (gE). For each study site, day length is determined from site latitude. The gT and gM in the VS-Lite involve only two parameters. The first represents the temperature (T_1) or moisture (M_1) threshold below which growth will not occur, while the second is the optimal temperature (T_2) or moisture (M_2) above which growth is not limited by climate. The growth function parameters were estimated for each site via Bayesian calibration. This scheme assumes uniform priors for the growth response parameters, and independent, normally distributed errors for the modelled TRWi values. The posterior median for each parameter was used to obtain the calibrated growth response for a given site. Finally, the model was run over the entire period for each site using the calibrated parameters to produce a simulated site chronology of tree-ring width indices ($TRWi_{VSL}$), representing an estimate of the site climate signal of forest growth. A more detailed description of the procedure can be found in Tolwinski-Ward et al. (2013).

For each site, temperature (T_i) and soil moisture (M_i) growth parameters were distributed uniformly across intervals, and the growth parameter set producing the simulation that was most significantly correlated with the observed TRWi series was then used in the simulations. In addition, other parameters (e.g. soil moisture, water runoff and root depth) were taken from the literature (Corcuera, Gil-Pelegrin, & Notivol, 2010; Evans et al., 2006; Huang et al., 1996; Mina et al., 2016; Sánchez-Salguero, Camarero, Carrer, et al., 2017; Sánchez-Salguero, Camarero, Gutiérrez, et al., 2017; Tolwinski-Ward et al., 2011; Vaganov et al., 2006). Every model for each site was evaluated 13,000 times using three parallel Markov chain Monte Carlo chains with a uniform prior distribution for each parameter and a white Gaussian noise model error (Tolwinski-Ward et al., 2013). To compute the annual TRWi values, we integrated the overall simulated growth rates (i.e. the pointwise minimum of monthly gT , gM and gE) over the time window from August of the prior year of growth to October of the year of tree-ring formation. This period was determined following previously available information on the xylogenesis and dendroecology of *P. pinaster* (e.g. Bogino & Bravo, 2008; Camarero et al., 2015; Campelo et al., 2013, 2015; Génova, Caminero, & Dochoa, 2014; Rozas, Lamas, & García-González, 2009;

Rozas, Zas, et al., 2011; Vieira, Campelo, & Nabais, 2010; Vieira, Rossi, Campelo, & Nabais, 2014; Vieira et al., 2015). To evaluate the temporal stability of the calibrated growth response functions, we divided the site period into two partially overlapped 35-year intervals (e.g. for the 1950–2014 period: 1950–1985 and 1980–2014) and held the second interval for the validation of the parameters estimated in the first one. Since several studies have demonstrated that radial growth and response to drought in *P. pinaster* are mainly influenced by spring and early summer climatic conditions (Bogino & Bravo, 2008; Rozas, Zas, et al., 2011) and that cambial activity is still ongoing in September (Campelo et al., 2013; Vieira et al., 2010, 2015), we selected the growth response to soil moisture (gMs) from April to September to simulate the physiological mechanism under long-term drought effects and quantified the seasonal variation of growth resilience in relation to genetic provenance and across its distributional range.

2.4 | Growth stability, resilience and vulnerability to drought

To assess the impact of drought on growth stability, we calculated pointer years, that is years with extremely low values of annual growth in a large proportion of trees within a site, to determine which climatic factors were responsible for conspicuously smaller tree rings as described by Schweingruber, Eckstein, Bachet, and Bräker (1990). We calculated the annual percentage of growth change (GC, in %) for each tree by calculating the ratio of TRW in year i and the average TRW in the three preceding years. Site- and provenance-specific pointer years were calculated based on the TRW data for each tree. When more than 50% of all trees within a chronology and provenance exceeded the defined ratio threshold (i.e. 50% of GC), the year was considered to be a negative pointer year (Schweingruber et al., 1990).

We also estimated the effect of drought intensity and duration on TRWi by using the Standardized Precipitation Evapotranspiration Index (SPEI), which is a multiscalar drought index calculated using precipitation and evapotranspiration to estimate the water balance (Vicente-Serrano, Beguería, & López-Moreno, 2010). The SPEI varies from negative to positive values corresponding to dry and wet conditions respectively. Monthly SPEI values for the study sites were calculated considering the period 1950–2014 with an 8-month temporal lag (cf. Camarero et al., 2015; Figure S1).

To quantify the response of tree growth to drought, we calculated the indices proposed by Lloret et al. (2011): resistance (R_t), recovery (R_c), resilience (R_s) and relative resilience ($rRs = R_s - R_t$). They were calculated using both (1) TRW data and (2) the growth response to soil moisture during the growing season (hereafter gMs). The R_t index quantifies the difference between TRW or gMs during the dry year and the preceding years (i.e. it quantifies the capacity of trees to buffer drought stress and continue growing during drought), whereas the R_c index accounts for the growth reaction following the drought period (i.e. it quantifies the difference in TRW or gMs between the dry year and the subsequent period). The R_s index

quantifies the difference in TRW or gMs before and after the dry year (i.e. it measures the capacity of trees to recover in terms of growth rates and the gMs observed before the drought event). Lastly, the rRs index is the difference between R_s and R_t , i.e. the net balance between buffering (during) and recovering (after) an extreme drought (cf. Sánchez-Salguero et al., 2013). To quantify these indices, we defined a period of 3 years before and after drought occurrence according to the previously applied criterion (Gazol, Ribas, et al., 2017). We also calculated the drought impact as the inverse of R_t . To calculate the pointer years and the resilience indices, we used the *pointRes* package (Van der Maaten-Theunissen, van der Maaten, & Bouriaud, 2015).

Finally, we used Generalized Least Square models (GLS, Pinheiro & Bates, 2000) to study the influence of site characteristics on the R_t , R_c and rRs indices calculated at the tree level for gMs . Topographical (latitude, longitude, elevation), and climatic (mean annual and minimum temperature, growing-season precipitation, continentality and oceanity indices) variables were included as predictors in the GLS models. The R_t , R_c and rRs indices were log-transformed prior to the analyses to adhere to the assumption of normality. We used the R 'MuMIn' package (Barton, 2012) to select the most parsimonious models (i.e. those showing the lowest Akaike information criterion [AIC] values). We also evaluated the fit of the models through graphical examination of the residual and fitted values (Zuur, Ieno, Walker, Saveliev, & Smith, 2009). The models were fitted using the 'gls' function in the R 'nlme' package (Pinheiro, Bates, DebRoy, & Sarkar, 2014). Differences between sites and provenances were computed using one-way ANOVA. All analyses were performed in the R 3.3.3 environment (R Development Core Team, 2017).

3 | RESULTS

3.1 | Climate–growth relationships

We detected high variability in the climate–growth relationships within each *P. pinaster* site and among provenances (Figure S2). Wet May and June conditions significantly ($p < .05$) enhanced growth in the Atlantic and Northern Iberian *P. pinaster* provenances, and this positive association increased with latitude ($r = .35$) and elevation ($r = .27$) but decreased with longitude ($r = -.37$), that is approaching the Mediterranean coast. Previous autumn temperatures were negatively related to growth in the Atlantic provenance sites, with this relationship increasing with latitude ($r = .33$) and decreasing with elevation ($r = -.48$, $p < .01$).

Tree growth in the Central Iberian provenance was positively related to winter and spring precipitation, increasing northwards ($r = .40$, $p < .01$), westwards ($r = .27$, $p < .05$) and upwards ($r = .51$, $p < .01$), whereas warm summer conditions were associated with lower growth values, particularly at low-elevation sites. We found a common influence of winter climate conditions on growth in Mediterranean locations (Eastern and Southern Iberian provenances) because wet and warm conditions enhanced growth at these sites. These effects decreased with longitude in Eastern provenance sites,

but followed the opposite pattern in Southern provenance sites. Growth in the Eastern and Southern provenances was improved by wet–cool May to June conditions, with contrasting effects of latitude and longitude in Eastern and Southern provenances (Figure S2). Lastly, the Moroccan provenance sites showed high growth rates in response to the wet summer conditions.

3.2 | Drought-induced negative pointer years

We observed similar patterns of drought-induced negative pointer years within each provenance (Figure 2 and Figure S1). The Eastern provenance sites showed the highest number of negative pointer years (45%), followed by the Southern, Central and Northern provenances respectively (Figure 2). We selected the following negative extreme growth events for resilience index calculation: 1996 and 2003–2004 (Atlantic provenance); 2011–2012 (Northern provenance); 1995 and 2005 (Eastern, Central and Southern Iberian provenances) and 1995 and 2007 (Moroccan provenance) (Figures 2 and 3 and Figure S1).

3.3 | Assessment of drought extremes using a process-based growth model

The VS-Lite model accurately predicted the year-to-year variability in growth (TRWi) during the 1950–2014 period (Table S4). The mean growth response to temperature (gT) peaked from April to October in Mediterranean *P. pinaster* forests (Central, Eastern and Southern provenances), while the growth response to moisture (gM) dropped during summer, as expected in response to lower summer growth rates due to the soil moisture deficit (Figure 3). The Atlantic provenance sites were less limited by low temperature and water availability than the Mediterranean provenance sites. Tree growth was limited by low temperatures ($gT < gM$) at the beginning and end of the growing seasons and by reduced soil moisture availability ($gM < gT$) during late spring, summer and autumn (from April to October, except in the Atlantic and Moroccan provenances; see Figure 3). There were exceptions to these patterns such as the growth limitation caused by low temperatures at the coldest sites in the Central and Eastern provenances (Table S2) or the low growth limitation caused by reduced soil moisture in the populations more subjected to oceanic influence (Figure 3).

The estimated minimum and optimal temperature and soil-moisture thresholds (T_1 , T_2 and M_1 , M_2) for growth showed the highest sensitivity of growth on average to low soil moisture in the Central and Northern provenances, followed by the Atlantic provenance (Table S5). Eastern provenance sites were susceptible to cold temperatures (T_2 value) in low-elevation sites subjected to continental conditions (see Table S2), whereas the Atlantic and Northern provenances were the least sensitive (Table S5). The Eastern and Southern provenances presented the highest percentage of soil moisture below which growth is limited (M_1), which suggests that spring–early summer water deficits constrain growth in those areas. A comparison of the observed mean growth response (gT , gM) during the

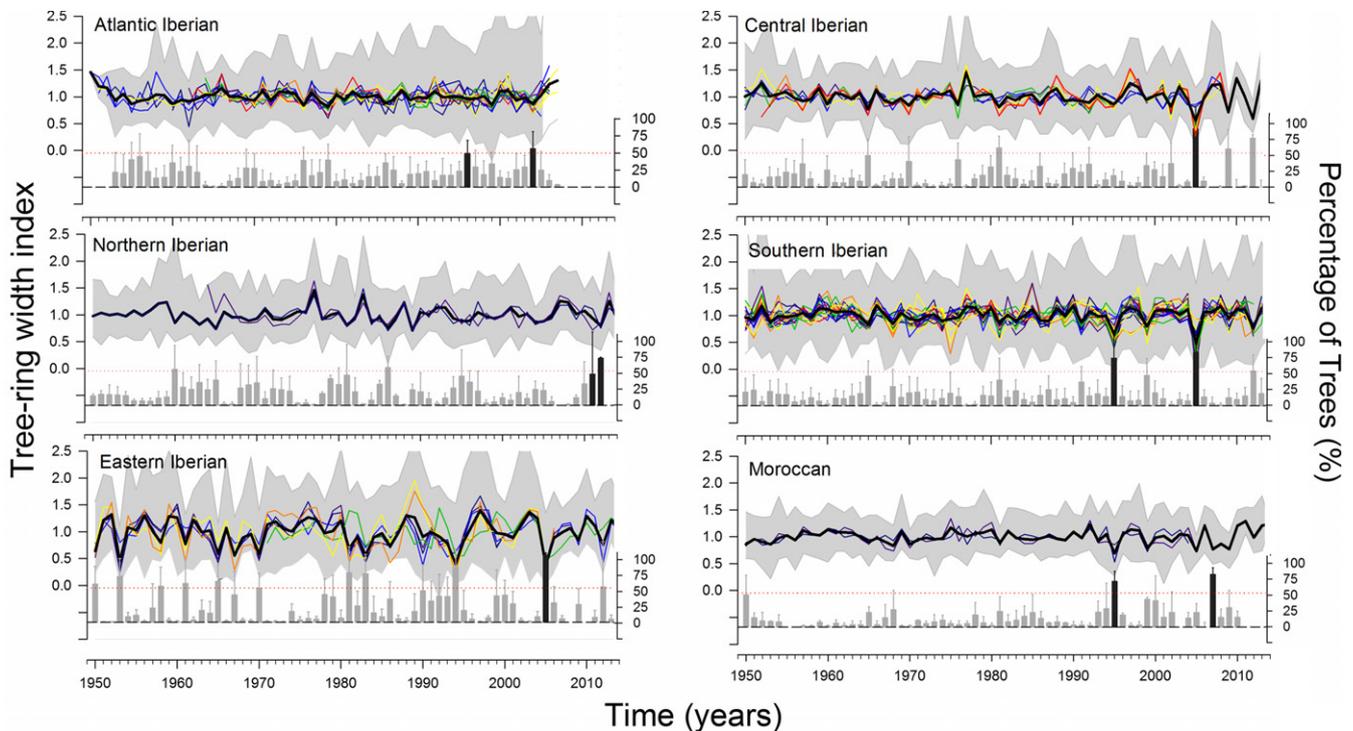


FIGURE 2 Tree-ring width indices (TRWi, left y axis) for *Pinus pinaster* calculated for each provenance and extreme growth years (percentage of trees showing a growth reduction with respect to mean growth of the previous 3 years, right y axis) for the period 1950–2014. Mean TRWi are shown as black lines and grey areas represent the maximum and minimum TRWi values considering all studied trees per provenance. Mean site chronologies are shown (coloured lines). The lower plots show negative pointer years (bars) expressed as percentage of trees showing a growth reduction as compared to the growth of the previous 3 years. The black bars indicate selected climatically extreme years causing a sharp growth reduction (see Figure S1 for further details) [Colour figure can be viewed at wileyonlinelibrary.com]

growing season with the growth responses in selected drought extreme years indicates strong variation in each provenance and site (Figure 3, Table 1). The highest deviations of mean growth conditions were recorded for the Moroccan, Southern and Eastern provenances respectively. Furthermore, there was a strong impact of extremely dry years on the TRWi of inland sites in the Atlantic provenance sites (Figure 3).

3.4 | Growth stability and resilience components in response to drought

We found that the impact of drought on growth (i.e. the inverse of the growth resistance index) varied among sites and provenances (Figures 3 and 4, Table 1). Populations from the driest region (see Table S2) showed a greater reduction in TRWi and *gMs* than those from the north-western Iberian area (Figure 4). Growth stability components varied among provenances (Table 1), and also within populations (Figures 4 and 5). Resistance indices (calculated for TRW and *gMs*) revealed a stronger growth decline in the Southern and Eastern provenances, except for coastal sites (Figures 3 and 4). Growth resistance to drought increased (both TRW and *gMs*) to the east, and summer water availability increased, whereas the post-drought recovery decreased with increasing latitude and annual precipitation (Figures 4 and 5, Table 2). Resilience indices for forest growth and *gMs* were geographically structured, with high variation among and

within some provenances (Figure 4, Tables 1 and 2). Relative resilience to drought (for TRW and *gMs*) increased with increasing elevation and longitude (i.e. Mediterranean climate influence) but decreased with increasing spring precipitation, with higher effects in the southern inland forests (Figures 4 and 5).

Growth stability models explained over 50% of the variance in drought resilience components (54%, 52% and 50% in the *R_t*, *R_c* and *r_S* indices respectively). Tree growth resistance to drought increased in Northern provenance sites, and with increasing elevation and oceanic influence, whereas the *R_c* decreased with latitude and mean annual temperature (Figures 4 and 5, Table 2). The model for *r_S* revealed positive effects of longitude and precipitation, which were stronger in Southern provenance sites, whereas latitude and mean temperature negatively influenced *r_S*.

Growth resilience responses to soil moisture (*gMs*) revealed that pre-drought growth levels were achieved 3 years after the drought, and such growth recovery improved in the Atlantic and Northern provenances (Figure 6a) and at the high-elevation or coastal sites in the Southern provenance; however, this did not occur in the semi-arid Eastern area (Figure 6a). Mean growth responses during critical periods of the growing season, under extremely dry conditions (i.e. spring–summer–*gMs*), showed that the Moroccan and Eastern provenances experienced the highest drought impact, followed by the Southern and Central Iberian provenances (Figure 6b). On the other hand, Atlantic and Northern forests were less vulnerable to severe

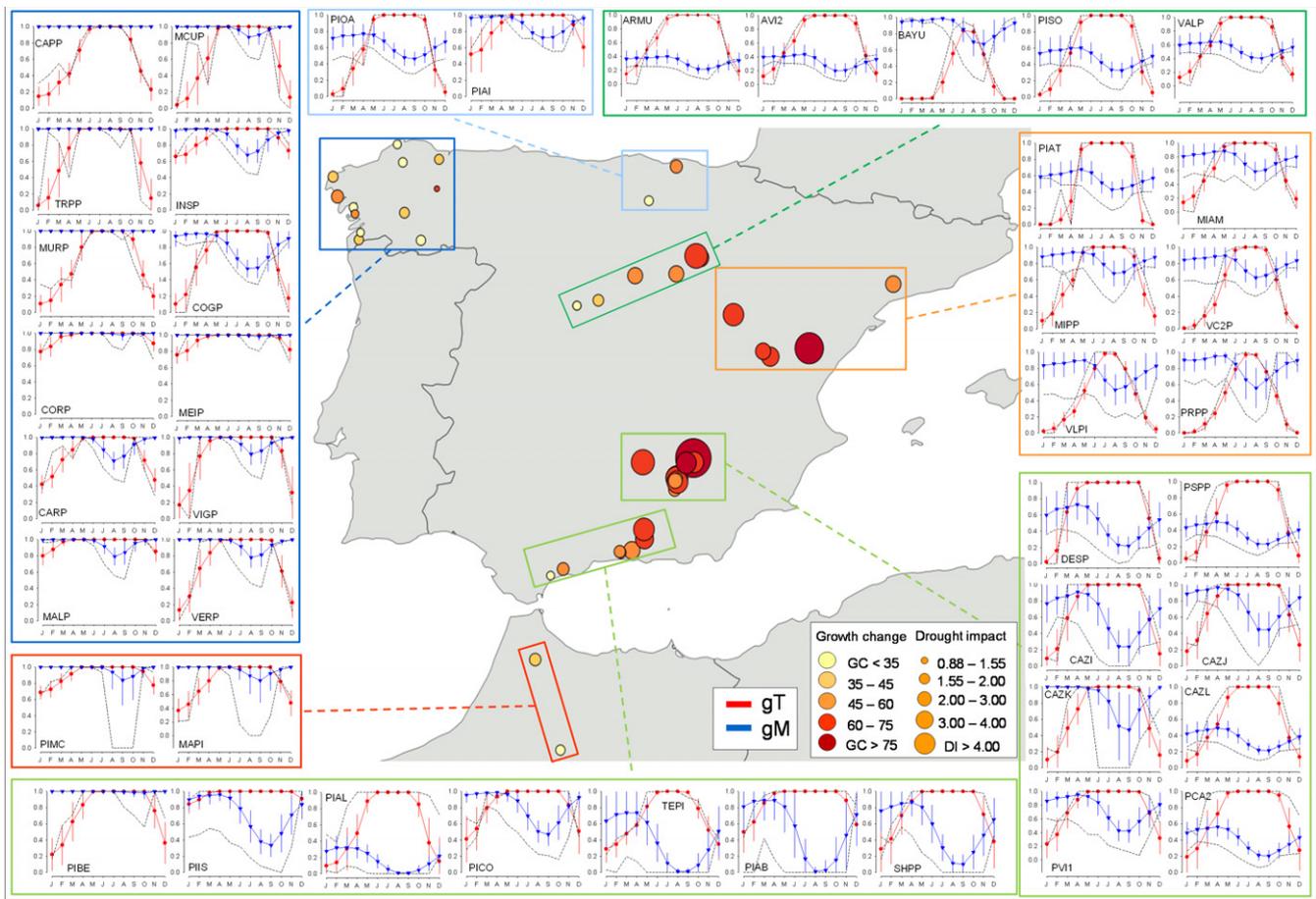


FIGURE 3 Simulated monthly growth response curves (gT , gM) for *Pinus pinaster* using the VS-Lite model of tree growth and considering the period 1950–2014. The growth responses are based on temperature (gT , red lines-mean and error line-SD) and soil moisture limitations (gM , blue lines-mean and error line-SD) for each site (see Figure 1 and Table S1 for site codes). Note that high and low values of either gT or gM indicate low and high growth limitations respectively. Selected extreme low growth years are indicated by dashed black lines (see Figure 2). The map displays site-level drought impact: different colours represent the percentage of growth change (GC) (%) for the selected extreme years and size represents the inverse of tree resistance (DI): $1/R_t$ for the same selected year (see Gazol, Ribas, et al., 2017). Different colours of squares correspond to the classification of sites shown in Figure 1a [Colour figure can be viewed at wileyonlinelibrary.com]

droughts, which suggests more stable growth performance in these areas (Figure 6b).

4 | DISCUSSION

Hypotheses concerning the adaptability of tree species across biogeographical gradients to global warming have been difficult to test due to the long life cycle of tree species, their high reproductive age and their slow speciation (Petit & Hampe, 2006). However, understanding the temporal and spatial growth variability among contrasting provenances in response to extreme drought is fundamental to assess long-term changes in forest productivity, tree growth and the adaptability of tree species to climate warming. Here, for the first time, we demonstrate that the impacts of severe droughts and the plasticity of *P. pinaster* growth in response to them greatly differ among provenance regions and are strongly influenced by site conditions (Figures 2 and 3). We disentangled the relationships between

local adaptive variability and resilience to drought, assessing the importance of growth adaptation and plasticity to cope with drought across the WM *P. pinaster* distributional area.

In addition to detecting geographical and altitudinal trends in growth responses to climate (Figure S2), relevant site-to-site variability modulating growth stability components was found (see also Gazol, Camarero, et al., 2017). Our novel methodological framework, based on the use of a process-based growth model coupled with climate-growth associations, could complement findings from niche-based models and allow the quantification of this within-site variability (Sánchez-Salguero, Camarero, Carrer, et al., 2017; Serra-Varela et al., 2015).

4.1 | Provenance of *P. pinaster* and growth responses to drought

The impact of drought on the response of the growth to soil moisture (gMs) varied among provenances (Figure 3). Populations from



the south-eastern Iberian Peninsula, that is the driest region (Table S2), showed more severe growth reductions than those from the wet North region (Figure 3), in agreement with other studies performed in *P. pinaster* and other Mediterranean pine species (De Luis et al., 2013; Gazol, Ribas, et al., 2017; Rozas, García-González, et al., 2011; Rozas, Zas, et al., 2011).

Furthermore, we found strong geographical variation in growth resilience indices based on the growth response to soil moisture (*gMs*) (Figure 3). Our results indicate that site climatic differences, mainly precipitation and mean annual temperature during the growing season, are the main factors explaining growth responses to drought among *P. pinaster* provenances (Figure 4, Table 2). Specifically, resistance to drought was linked to the annual water

TABLE 1 ANOVA results showing significant differences in resilience indices based on the growth response to the soil moisture during the growing-season (*gMs*) among all the *Pinus pinaster* provenances (see also Figures 4 and 5). In all cases the *p* values are lower than .001

Variable	Sum of squares	Mean squares	F-value
Rt	2.037	0.407	12.771
Rc	71.859	14.372	6.277
Rs	1.293	0.259	3.305
rRs	5.388	1.078	11.682
Pre	2.200	0.440	11.186
Dro.	2.871	0.574	17.672
Pos.	1.674	0.335	7.940

Variables' abbreviations: resistance (Rt), recovery (Rc), resilience (Rs) and relative resilience (*rRs*) indices; before (Pre.), during (Dro.) and after (Pos.) drought values of *gMs*.

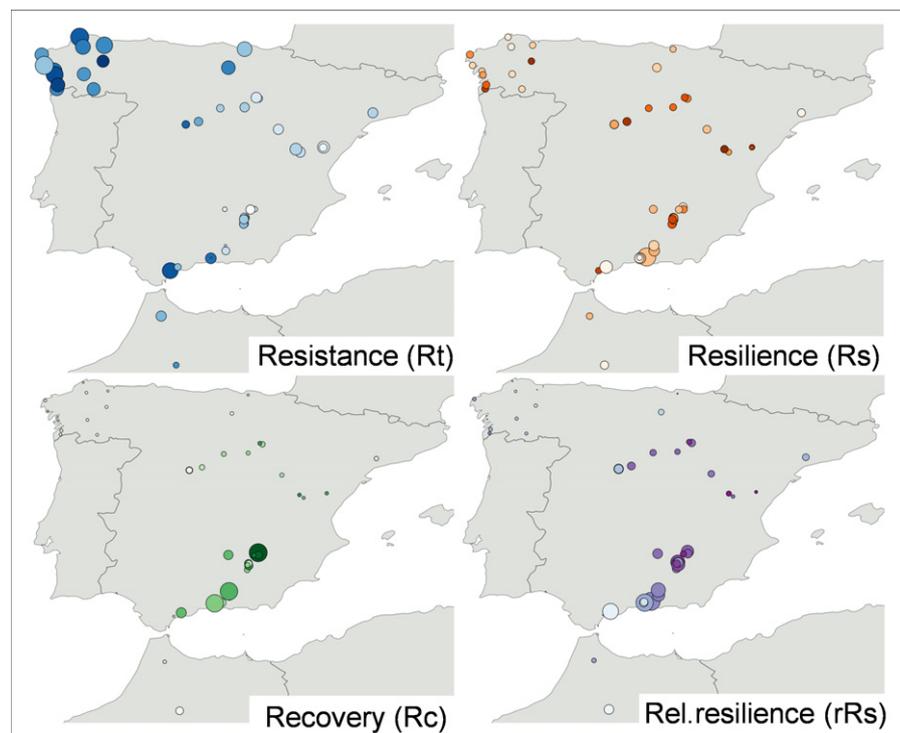
availability, which is higher in the northern area (Table 2). Conversely, post-drought recovery increased in Mediterranean sites with low water availability (Figure 3), while the lowest recovery rates were observed at the wettest sites. These results suggest a trade-off between growth resistance to drought and post-drought recovery, that is higher resistance implies lower recovery. This trade-off is likely modulated by site conditions, because growth recovery was more conspicuous in the semi-arid Mediterranean areas (Figure 6). In addition to southern locations, the forests in Atlantic provenance sites will also withstand harsh conditions if they have to cope with severe and prolonged droughts, which may be amplified by further climate warming (Gazol, Ribas, et al., 2017). Thus, *P. pinaster* shows high phenotypic growth plasticity across the WM range (Alía et al., 1997; but see Lamy et al., 2014), in agreement with the variability in growth–drought responses among provenances (Figures 3 and 4).

Our study would have benefited from a more refined delineation of provenances based on genetic and palaeoecological analysis, as it is possible that in some of the studied *P. pinaster* provenances, some stands originated from seeds brought from other regions or provenances, given the long history of exploitation and use of *P. pinaster* (Abad Viñas et al., 2016). Nevertheless, our research focused on natural stands from areas where *P. pinaster* has been dominant and is considered native (Bucci et al., 2007).

4.2 | Phenotypic adaptation of resilience components

The variability in growth resilience indices highlights the wide growth plasticity of *P. pinaster* across its WM range (Figure 4). The contrasting patterns in growth resistance and recovery suggest the

FIGURE 4 Components of tree resilience (standardized to values between 0 and 1) of *Pinus pinaster* growth in response to selected extreme droughts (see Figures 2 and 3) based on the tree-ring width (size) and the simulated growing-season response to the soil moisture (*gMs*) based on VS-Lite model (colours) for each site. Values are fitted for the period 1950–2014 and the dates of selected drought events for every provenance (see Figure 2). The size and the colour intensity are proportional to the represented index (the larger the index, i.e. the better the performance during/after drought, the darker the colour and the larger symbol) [Colour figure can be viewed at wileyonlinelibrary.com]



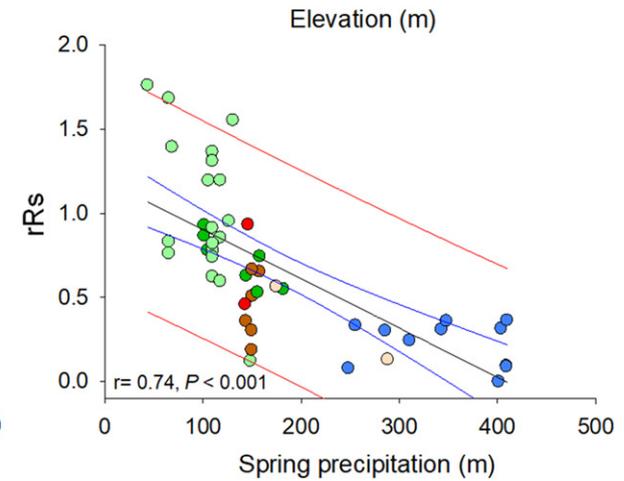
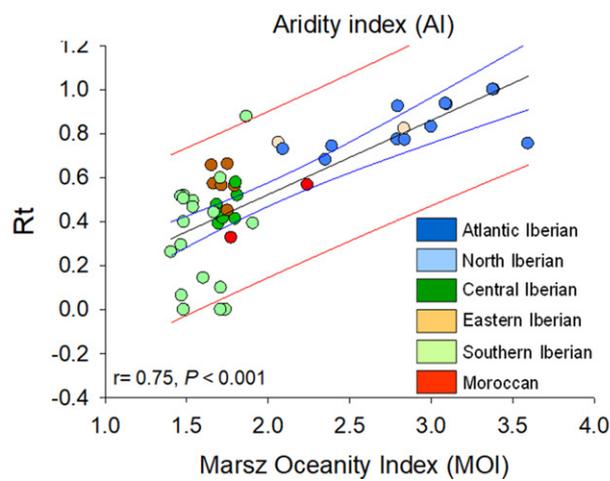
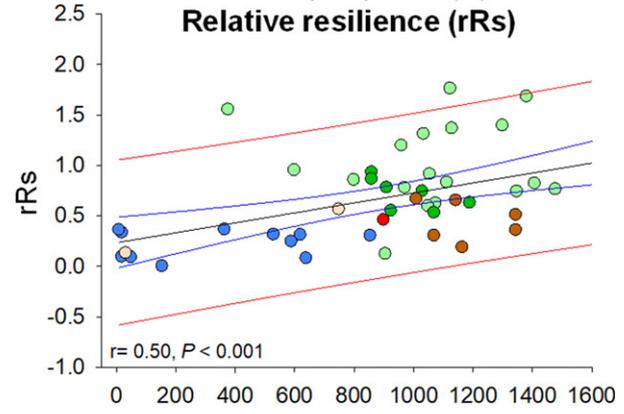
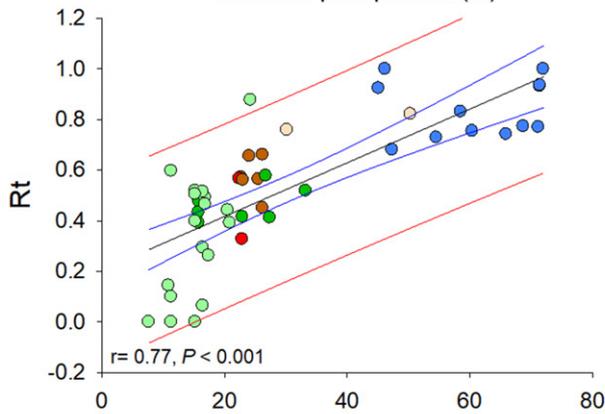
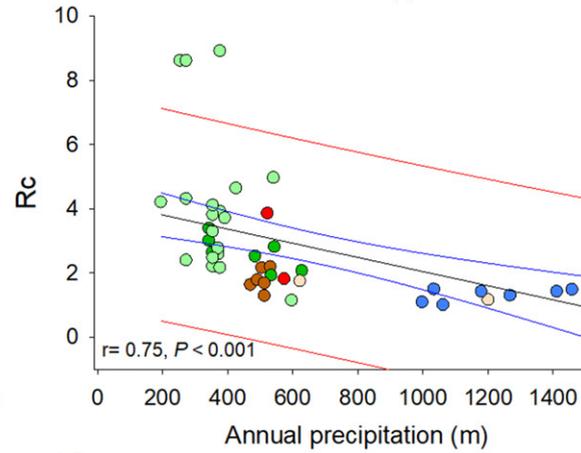
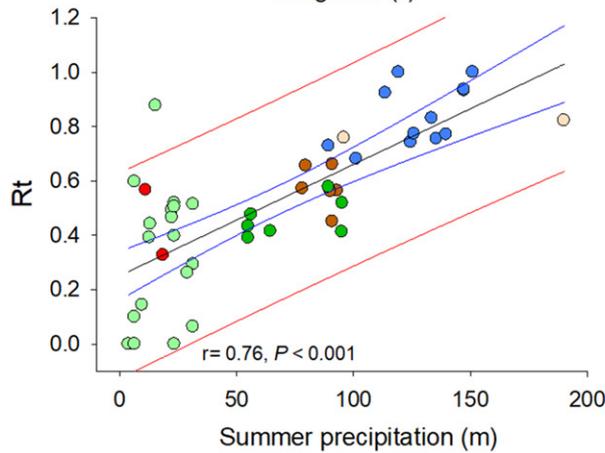
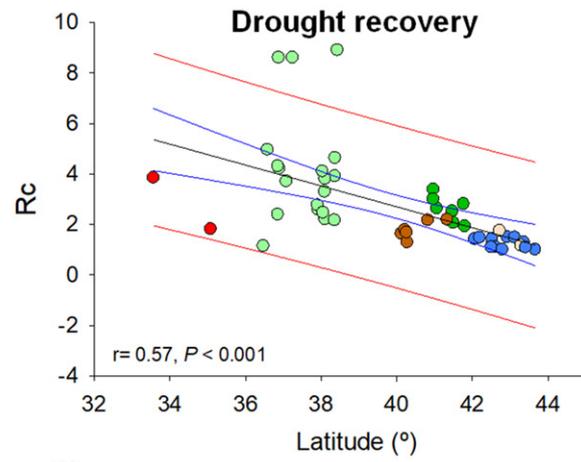
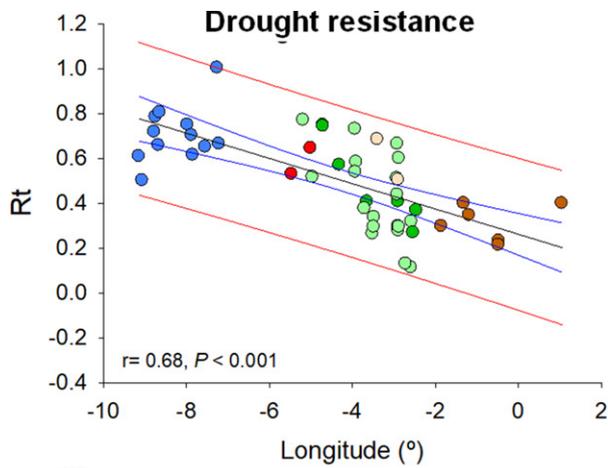




FIGURE 5 Relationship between resistance (R_t), recovery (R_c) and relative resilience (rRs) indices based on the growth responses to soil moisture (gMs) by VS-Lite model of *Pinus pinaster* trees in response to selected extreme droughts (see Figures 2 and 3), and site variables (longitude, latitude, elevation; annual, spring and winter precipitation; aridity (AI) and Marsz Oceanity Index (MOI)). Different colours correspond to the classification of sites provenances (see Figure 1). The regression lines (black), 95% confidence bands (blue), 95% prediction bands (red) and correlation coefficients with their significance levels, are also shown [Colour figure can be viewed at wileyonlinelibrary.com]

presence of different strategies to cope with severe drought (Figure 3). The adaptive potential with regard to the drier conditions experienced by the Southern and Eastern *P. pinaster* populations (i.e. through phenotypic plasticity—great recovery capacity) could significantly buffer these forests against future warmer and drier conditions (Benito-Garzón, Alía, Robson, & Zavala, 2011). However, the trees in the Atlantic and Northern provenances, growing under wet and temperate conditions, seem to be more vulnerable to more intense droughts since they are less able to recover after them because they tend to grow more and produce more juvenile needles than those from dry sites in the Mediterranean provenances (De la Mata, Voltas, & Zas, 2012; Rozas, Zas, et al., 2011). Aridification trends in those wet sites could threaten some populations or favour the northward expansion of provenances from drought-prone sites (Serra-Varela et al., 2015).

Our results agree with other studies that found little variation in anatomical and functional traits (e.g. leaf features, stomatal conductance) among pine species' provenances but large variation in growth-related adaptations (e.g. wood anatomy, cambial phenology; e.g. Carvalho, Nabais, Vieira, Rossi, & Campelo, 2015; Lamy et al., 2014; Martínez-Vilalta et al., 2009; Paiva et al., 2008; Plomion et al., 2016; Rozas, Zas, et al., 2011). We hypothesize that, on average, trees from drier sites have a great capacity to cope with drought by forming more drought-tolerant xylem, that is with a low vulnerability

to embolism, or by adjusting their needle production (De la Mata et al., 2012). This is also consistent with studies of *P. pinaster* (Carvalho et al., 2015; Paiva et al., 2008), which found that tracheid diameter was optimized to achieve the greatest hydraulic efficiency for a given tracheid length (Delzon, Douthe, Sala, & Cochard, 2010). In particular, some traits may provide a better adaptive capacity to withstand drought stress by allowing more integrated adjustment of the hydraulic system (e.g. leaf area-to-sapwood area ratio; Martínez-Vilalta et al., 2009). Our results based on growth suggest that these features could operate in the drier *P. pinaster* provenances, but this idea should be tested.

Our quantification of growth responses to drought across the species area is crucial to reveal differences among and within tree provenances. Interestingly, our findings are supported by previous dendroecological studies (Bogino & Bravo, 2008; Campelo et al., 2013; Rozas, Zas, et al., 2011), molecular and quantitative analyses of materials from different provenances (Alía et al., 1997; De la Mata et al., 2012; González-Martínez, Alía, & Gil, 2002) and species distribution models (Serra-Varela et al., 2015, 2017). However, other local site factors that were not considered in this study, such as topography and soil properties, could also influence local species adaptation (Gazol, Ribas, et al., 2017).

TABLE 2 Summary of the generalized least square (GLS) models fitted to the resilience growth indices (R_t , resistance; R_c , recovery; and rRs , relative resilience) in response to the selected droughts by the VS-Lite growth model for *Pinus pinaster*. We show the variables included in the best model and the adjusted R^2 of the selected models. The selected variables are all significant at $p < .05$ level

Variable	R_t	R_c	rRs
Intercept	1.707	1.609	0.564
Provenance ^a	−0.027	0.684	0.029
Longitude	−0.031	—	0.028
Latitude	0.032	−0.653	−0.036
Elevation	0.002	−0.003	—
P_g	0.033	0.022	0.022
T_a	0.023	−0.085	−0.013
MOI	0.038	−0.057	−0.029
CCI	−0.003	—	0.005
T_i	0.013	−0.024	−0.015
R^2_{adj}	.54	.52	.50

P_g , growing season precipitation; T_a , mean annual temperature; MOI, Marsz Oceanity Index; CCI, Conrad–Pollak Continentality Index; T_i , mean minimum temperature.

^aProvenances: 1, Atlantic; 2, Northern Iberian; 3, Central Iberian; 4, Eastern Iberian; 5, Moroccan and 6, Southern Iberian.

4.3 | Impacts of climate extremes on forests from the forward growth model

The large inter-site variability in the modelled VS-Lite parameters (Figure 6) may arise from differences in environmental conditions among sites and/or contrasting drought tolerances among tree provenances caused by phenotypic plasticity and possible local adaptation (Valladares et al., 2014). Based on the VS-Lite growth responses to the soil moisture resilience indices, severe droughts could cause *P. pinaster* populations from wet sites to shift from reduced temperature constraints to increased soil moisture limitations (Figure 3). This would correspond to higher growth sensitivity to weather conditions during the early growing season, especially at the northernmost species limits (cf. Benito-Garzón et al., 2011), when the functional thresholds for optimum growth responses (gT and gM) would be exceeded. A longer dry season during extreme drought years also negatively affects growth in the wet Atlantic and continental Central provenances, as they have the lowest percentage of soil moisture under which growth is not limited (M_2) (Table S5). This suggests a prominent role of spring water deficit in *P. pinaster* growth (Rozas, Zas, et al., 2011), which is in line with studies emphasizing the dependence of wood formation on the rate of cell production in the early growing period, when drought stress is lower than in summer (Vieira et al., 2015).

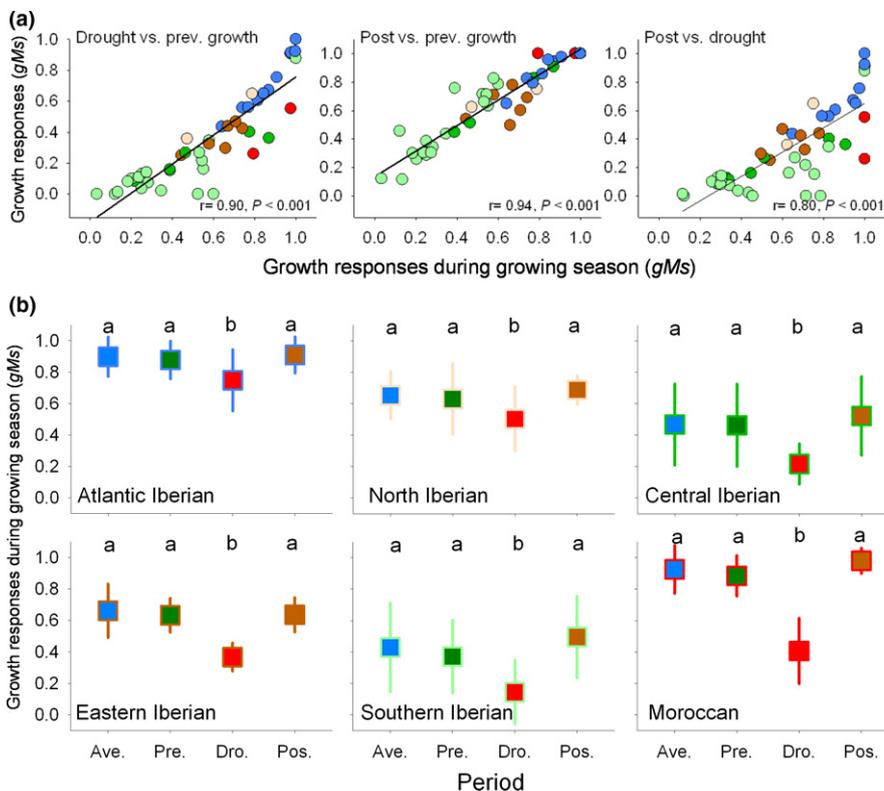


FIGURE 6 (a) Relationship between growth responses in *Pinus pinaster* to soil moisture during the growing season (gMs) before, during and after the selected extreme droughts. The correlation coefficients, associated significance levels and regression lines are shown. Different colours correspond to the provenances classification following Figure 1. (b) Mean growth responses to soil moisture during the growing season (gMs) for the studied provenances. The average (1950–2014) (Ave.), before (Pre.), during (Dro.) and after (Pos.) drought growth responses and SD are shown. We selected the mean growth responses 3 years before (green colour), during (red colour) and 3 years after (brown colour) the selected drought (see Figure 2). Different contours colours correspond to the provenances classification following Figure 1. Different letters indicate significant ($p < .05$) differences between the compared periods based on Tukey's HSD post-hoc tests [Colour figure can be viewed at wileyonlinelibrary.com]

Forest growth responses to climate could also be modulated by rising atmospheric CO₂ concentrations, which could improve water-use efficiency and growth recovery after drought. However, adult *P. pinaster* individuals did not show any long-term growth improvement in response to increasing CO₂ concentrations (Camarero et al., 2015). The high stomatal sensitivity to drought of *P. pinaster* might be an advantage under water shortage, but drought limits net carbon assimilation and growth rates and might constrain post-drought growth recovery. Further research on adult individuals from different *P. pinaster* provenances using C and O isotopes could provide deeper insight on this issue.

Our approach can be useful for the conservation and sustainable use of forest genetic resources because it allows the ecogeographical zonation of forest resilience to be defined based on spatially explicit information (Figure 4). For instance, these results highlight that distinct provenances may be better adapted to recovery after drought and therefore could be used in assisted migration programmes (Moran, Lauder, Musser, Stathos, & Shu, 2017). Finally, we advocate that species distribution models (e.g. Serra-Varela et al., 2017) should be supplemented by dendroecological information and in situ genetic characterization to better adapt forest management strategies.

In conclusion, the use of a process-based growth model and tree-ring data allowed growth reactions to drought to be quantified within the framework of differentiated provenances. High phenotypic plasticity in drought tolerance allows *P. pinaster* to resist and recover after severe droughts, displaying strong variation across the species distribution range but common patterns within each provenance. This study is one of the first attempts to illuminate aspects of

forest resilience to drought based on long-term growth data by identifying provenances with different vulnerability levels. Both the high growth resilience variation in the phenotypic plasticity of *P. pinaster* provenances and the high sensitivity of this species to spring–summer drought suggest divergent impacts of predicted climate warming on different regions.

ACKNOWLEDGEMENTS

We acknowledge the use of the E-OBS climate dataset (EU-project ENSEMBLES) and the data providers in the ECA&D project (<http://www.ecad.eu>) and Dr. Geert Jan van Oldenborgh for his assistance. We also thank A. Hevia for help with statistical analysis. This study was supported by projects: Xunta de Galicia (PGIDIT06P-XIB502262PR), Spanish Ministry of Economy, Industry and Competitiveness with the projects FunDiver (CGL2015-69186-C2-1-R), CoMo-ReAdapt (CGL2013-48843-C2-1-R), (CGL2015-69985); Senscom (CGL2008-06005), Dendro-Avenidas (CGL2007-62063) and Dinecofor (CGL2011-27229), CANOPEE (Interreg V-A POCTEFA 2014-2020-FEDER funds) and 'Historia y dinámica del paisaje vegetal' Research Group. RSS, AG and AA are supported by Postdoctoral grants (RSS and AG, IJCI-2015-25845, MINECO-FPDI 2013-16600, FEDER funds; AA, Russian Ministry of Education, Project '5-100', Grant N° M 2.2., and the Russian Science Foundation, Grant 14-14-00219-P).

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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DATA ACCESSIBILITY

The datasets reported in this paper have been deposited in the Pangaea repository <https://doi.pangaea.de/10.1594/PANGAEA.885924>

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

How to cite this article: Sánchez-Salguero R, Camarero JJ, Rozas V, et al. Resist, recover or both? Growth plasticity in response to drought is geographically structured and linked to intraspecific variability in *Pinus pinaster*. *J Biogeogr*. 2018;45:1126–1139. <https://doi.org/10.1111/jbi.13202>

BIOSKETCH

The research team leads projects on forest dynamics and the effects of climate and land use in a global change scenario. The main challenge of our research has been to disentangle the interacting effects of long-term climate trends, climate variability and land use changes on forest ecosystems. The group is experienced in studying biotic and abiotic interactions governing forest growth, forest-decline and mortality processes, and species dynamics, using tools such as dendroecology, spatial statistics and forest-dynamics modelling, involving responses to global change at several scales, from the landscape to individual process-based approaches and tree ecophysiology.

Author contributions: R.S.-S. and J.J.C. designed the study and conceived the ideas. All authors performed the sampling, collected and processed the data. R.S.-S and J.J.C. analysed the data and led the writing. All the authors contributed to the discussion, read and approved the final draft.