



Differences in temperature sensitivity and drought recovery between natural stands and plantations of conifers are species-specific

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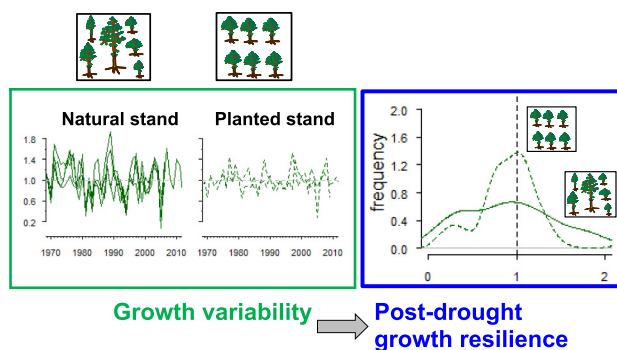
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HIGHLIGHTS

- Plantations are expected to be more impacted by drought than natural stands.
- We compare climate and drought impacts on growth in natural vs. planted forests.
- Growth was constrained by drought in planted and natural stands.
- Plantations were not more sensitivity to climate than natural stands.
- Post-drought growth resilience of plantations and natural stands was similar.

GRAPHICAL ABSTRACT



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ABSTRACT

Forests are being impacted by climate and land-use changes which have altered their productivity and growth. Understanding how tree growth responds to climate in natural and planted stands may provide valuable information to prepare management in sight of climate change. Plantations are expected to show higher sensitivity to climate and lower post-drought resilience than natural stands, due to their lower compositional and structural diversity. We reconstructed and compared the radial growth of six conifers with contrasting ecological and climatic niches (*Abies pinsapo*, *Cedrus atlantica*, *Pinus sylvestris*, *Pinus nigra*, *Pinus pinea*, *Pinus pinaster*) in natural and planted stands subjected to seasonal drought in 40 sites. We quantified the relationships between individual growth variability and climate variables (temperature, precipitation and the SPEI drought index), as well as post-drought resilience. Elevated precipitation during the previous autumn-winter and current spring to early summer enhanced growth in both natural and planted stands of all species. Temperature effects on growth were less consistent: only plantations of *A. pinsapo*, *C. atlantica*, *P. nigra*, *P. pinea*, *P. sylvestris* and a natural stand of *P. nigra* showed negative impacts of summer temperature on growth. Drought reduced growth of all species in both plantations and natural stands, with variations in the temporal scale of the response. Drought constrained growth more severely in natural stands than in plantations of *C. atlantica*, *P. pinaster* and *P. nigra*, whereas the inverse pattern was found for *A. pinsapo*. Resilience to drought varied between species: natural stands of *A. pinsapo*, *C. atlantica* and *P. pinaster* recovered faster than plantations, while *P. pinea* plantations recovered faster than

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natural stands. Overall, plantations did not consistently show a higher sensitivity to climate and a lower capacity to recover after drought. Therefore, plantations are potential tools for mitigating climate warming.

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1. Introduction

Forests cover 31% of land surface and store a large amount of the global terrestrial carbon pool with woody biomass accounting for 15% of the uptake of annual anthropogenic CO₂ emissions (FAO, 2020). The potential of forests to mitigate climate change is promoting an expansion of afforested areas (Payn et al., 2015) while encouraging some governments and administrations to enthusiastically embrace nature-based solutions (Domke et al., 2020), as an alternative to the more urgent need to decarbonize their economies. However, climate change alters forest ecosystem functioning and the provision of the services forests provide for human well-being, including carbon uptake and storage (Gamfeldt et al., 2013). Consequently, the social concern about the necessity of more sustainable forest management practices to reduce the negative consequences of climate change has increased (Allen et al., 2015).

Growth and climate models suggest that forests will face shifting environmental conditions due to ongoing climate change (Huang et al., 2017), and that the higher recurrence of extreme climate events such as droughts will negatively affect forest productivity and growth resilience (Pretzsch et al., 2013; Gazol et al., 2018). Furthermore, simulations suggest that stands located near the species' dry distribution limit may be severely affected by warmer and drier conditions reducing growth rates (Sánchez-Salguero et al., 2017). Future tree plantations need to be resistant and resilient to climatic change and extreme events, including warmer temperatures and reduced water availability, and this will require a shift towards selecting those species or genotypes less affected by dry spells, particularly in drought-prone regions (Resco de Dios et al., 2007). A quantification of climate responsiveness and post-drought growth recovery of planted trees in relation to those growing in natural forests across wide climatic and environmental gradients can provide information on species or sites with higher resistance and resilience which could be selected for planting.

The last IPCC report highlighted the vulnerability of European forests to climate-change threats (Kovats and Kovats, 2014). This is particularly relevant in drought-prone regions where noticeable dieback and mortality events have been reported over the last decades (e.g., Camarero et al., 2015a). Forested areas in this region, and many others around the world, consist of a mix of natural forests, either unmanaged or subjected to a sustainable management regime, and tree plantations established for productive purposes. In the drought-prone Mediterranean Basin, tree plantations represent around 10% of the total forested area (Allard et al., 2013) and are mainly composed of pioneer pine species and other conifer species, which usually deploy fast growth rate in mesic sites or under favourable climatic conditions (Navarro-Cerrillo et al., 2018). Yet, a poorly addressed question so far is whether growth and productivity in plantations would be more or less vulnerable to climate change. This comparison is relevant since a higher vulnerability would lead to more dieback and mortality in planted than in natural stands.

Some studies have reported different tree growth responses to climate in natural vs. planted stands and higher mortality rates in plantations (e.g. Sánchez-Salguero et al., 2012; Navarro-Cerrillo et al., 2018; Rodríguez-Vallejo et al., 2020). Natural stands are uneven-aged and present more structural, compositional and genetic diversity than comparable, even-aged planted stands, formed by one or few tree species of similar genetic origin and planted in regular blocks (Sánchez-Salguero et al., 2013; Navarro-Cerrillo et al., 2016, 2019; Santini et al., 2020). A higher compositional and structural diversity can reduce the negative impacts of drought on tree performance, by alleviating competition or herbivory, due to complementarity effects (Mori et al., 2013; Forrester

and Pretzsch, 2015; Gazol and Camarero, 2016; Grossiord, 2020). And yet, natural stands have shown conspicuous examples of dieback and tree mortality following drought events in Europe and elsewhere (Allen et al., 2010).

Tree plantations are usually managed to maximise productivity, by selecting fast-growing species or genotypes and by reducing competition by thinning (Navarro-Cerrillo et al., 2019); however, some studies have shown that this management can increase drought stress by exposing dominant, released trees to higher evaporative demand (Mausolf et al., 2018). Site characteristics such as stand structure or management history also play an important role on modulating the individual responses to climate (De Luis et al., 2009; Bose et al., 2020). Furthermore, in many cases, the species selected to be planted have been artificially selected for productivity, which may increase their vulnerability to drought stress in such homogeneous, productive stands. Since plantations are structurally less complex and show less complementarity effects than natural stands, we expect planted stands to be less resilient. Nonetheless, there has not been an attempt to assess drought-induced tree growth response in natural and planted stands of the same species.

Radial growth is a valuable proxy which allows reconstructing the impacts of climate variability on forests (Sass-Klaassen et al., 2016). In this sense, dendroecology (Fritts, 1976) provides a retrospective framework to quantify past forest growth response to climatic events and to forecast its response to future climate events (Andreu et al., 2007; Camarero et al., 2015a; Sánchez-Salguero et al., 2017). In addition, the negative effects of drought on tree growth can last for several years resulting in carryover or legacy effects (Anderegg et al., 2015), which might constrain the resilience or capacity to recover pre-drought growth levels (Lloret et al., 2011). Adaptive forest management strategies may thus benefit from the knowledge generated by studying the relationships between growth and climate (Hoffmann et al., 2018).

Here we study the response to climate and in particular to drought of growth from trees in planted and natural stands of six conifers with diverse ecological and geographical ranges, naturally occurring in the Mediterranean Basin (*Abies pinsapo*, *Cedrus atlantica*, *Pinus pinea*, *Pinus pinaster*) and central and northern Europe (*Pinus nigra*, *Pinus sylvestris*). We selected widely distributed tree species whose plantations are commercially important such as *P. sylvestris* (FAO, 2020) with other species showing small distribution areas but with a high potential for climate change mitigation given their drought tolerance such as *C. atlantica* (e.g., Guillemot et al., 2015). We compiled information on tree growth in 20 natural and 20 planted stands. Dendrochronology was used to reconstruct growth variability. Further, we investigated the relationship between growth and climate as well as the impact of drought. We hypothesized that natural stands would display more tightly coupled climate-growth relationships than planted stands and a lower vulnerability to drought. We aimed to determine if: (i) the relationship between growth and climate differs between natural and planted stands; (ii) natural forests are less responsive to drought than plantations of the same species, and (iii) tree growth is more resilient (faster recovery) in than in planted stands.

2. Material and methods

2.1. Study sites and species

In this study, we sampled trees from 20 natural and 20 planted stands, located in Spain, Chile, Australia and Morocco (Fig. S1, Table S1). A

variable number of natural and planted stands, from two to five sites per species and stand type (natural vs. planted stand), were studied (Table 1). Only plantations without recent management (e.g., thinning) were selected. We tried to sample planted and natural stands in similar successional stages considering mature and dominant individuals, but planted trees were usually younger than natural conspecifics (Table 1).

Six conifers were sampled: *Abies pinsapo* Boiss., *Cedrus atlantica* (Endl.) Manetti ex Carrière, *Pinus nigra* Arnold, *Pinus pinea* L., *Pinus pinaster* Ait, and *Pinus sylvestris* L. *Abies pinsapo* is a circum-Mediterranean fir endemic to mountains of southern Spain and northern Morocco. *A. pinsapo* growth is enhanced by wet springs and responds negatively to warm temperature of the previous autumn. *C. atlantica* is distributed mainly in the mountain ranges of Morocco and Algeria, where high elevation favours rainfall (>500 mm year⁻¹, Benabid, 1994). *C. atlantica* has been planted successfully in several sites in southern Europe with productivity purposes (e.g., Guillemot et al., 2015). *P. nigra* is a drought sensitive species widely distributed in central and southern Europe (Andreu et al., 2007; Martín-Benito et al., 2008). We compared two subspecies dominant in planted (*Pinus nigra* subsp. *nigra*) and natural (*Pinus nigra* subsp. *salzmannii*) stands across Spain. Both subspecies showed similar growth sensitivity to climate (Sangüesa-Barreda et al., 2019). *P. pinea* is native to the Mediterranean Basin where it forms forests on sites with sandy, acid soils. *P. pinea* has been planted for commercial purposes in different regions around the

globe with Mediterranean climate such as Chile (Loewe Muñoz et al., 2015). The radial growth of *P. pinea* is enhanced by the occurrence of warm winters and humid conditions from autumn to spring (Natalini et al., 2015, 2016; Shestakova et al., 2020). *P. pinaster* is a species widely distributed in the western Mediterranean basin linked to disturbances (fire) in sites with acid soils (Fernandes and Rigolot, 2007), and it has been successfully planted in different regions. *P. pinaster* growth responds positively to spring precipitation and negatively to summer drought (Caminero et al., 2018) with Atlantic and Mediterranean provenances being less or more limited by drought, respectively (Rozas et al., 2011; Camarero et al., 2015b; Sánchez-Salguero et al., 2018). All studied *P. pinaster* stands corresponded to inland, Mediterranean provenances excepting one (a stand located near the Cantabrian Sea, Liencres; Table 1). *P. sylvestris* is widely distributed across Eurasia from southwestern Spain to Siberia (Bose et al., 2020). The growth of *P. sylvestris* is constrained by summer drought and cold springs (Andreu et al., 2007).

The studied sites presented marked differences in climate conditions (Fig. 1; Table S1). For instance, the natural *P. nigra* stands were located in the semi-arid south-eastern Spain (Sierra María, Almería) and in the more humid Pre-Pyrenees in north-eastern Spain (Villalangua, Huesca). In contrast, planted *P. nigra* stands were located in humid (Paco Cenera, Los Pintanos, Urriés) and dry (Alcubierre) sites of north-eastern Spain but also included trees from Bendora (ACT, Australia).

Table 1

Site and tree-ring characteristics of the study natural (N) and planted (P) stands. The location of each site is shown together with the mean tree-ring width (Mean) and its standard deviation (SD), the first-order autocorrelation of the ring-width series (AR1) as well as the start and the end of well-replicated site series, and the number of trees and cores sampled and processed. Age was estimated at 1.3 m (values are means ± SE). The effective inter-series correlation (Rbar) and the Expressed Population Signal (EPS) for the periods referred are also shown. The EPS measures how well replicated is a chronology with values above 0.85 indicating adequately replicated chronologies (cf. Wigley et al., 1984).

Species	Type	Site	Country	Longitude (+E, -W)	Latitude (+N, -S)	Elevation (m a.s.l.)	Mean (mm)	SD (mm)	AR1	Start	End	No. trees	No. Cores	Age (yrs.)	Rbar	EPS
<i>Abies pinsapo</i>	N	Cañada del Cuerno	Spain	-5.01	36.69	1420	0.69	0.21	0.41	1970	2005	17	35	204 ± 16	0.42	0.92
	N	La Torrecilla	Spain	-5.00	36.68	1746	2.97	1.20	0.55	1970	2005	10	22	66 ± 10	0.27	0.77
	N	Cañada de las Ánimas	Spain	-5.01	36.69	1650	0.79	0.30	0.49	1970	2005	25	57	195 ± 10	0.46	0.95
	P	Bendora	Australia	149.07	-35.53	1280	3.20	1.02	0.55	1970	2005	8	12	41 ± 3	0.26	0.72
	P	Orcajo	Spain	-1.51	41.09	1152	2.33	1.01	0.46	1970	2005	17	35	51 ± 3	0.76	0.98
<i>Cedrus atlantica</i>	N	Azrou	Morocco	-5.22	33.33	1930	0.31	0.21	0.09	1986	2009	11	19	210 ± 16	0.72	0.97
	N	Azrou	Morocco	-5.22	33.33	1860	1.06	0.41	0.48	1986	2009	20	39	151 ± 19	0.58	0.96
	N	Col du Zad	Morocco	-4.67	32.64	2250	0.74	0.30	0.22	1986	2009	14	28	213 ± 30	0.71	0.97
	N	Col du Zad	Morocco	-4.67	32.64	2232	1.17	0.38	0.31	1986	2009	10	21	134 ± 19	0.64	0.95
	P	Bañón	Spain	-1.19	40.84	1358	2.63	1.07	0.18	1986	2009	15	27	46 ± 2	0.80	0.98
	P	Sierra de las Nieves	Spain	-4.98	36.73	1400	5.06	1.54	0.51	1986	2009	14	26	26 ± 1	0.52	0.94
	P	Sierra Nevada-low	Spain	-3.42	37.13	1767	4.57	1.84	0.58	1986	2009	10	19	30 ± 2	0.65	0.95
	P	Sierra Nevada-high	Spain	-3.42	37.13	1837	5.65	1.92	0.46	1986	2009	12	24	31 ± 1	0.53	0.93
<i>Pinus nigra</i>	P	Fiñana	Spain	-2.88	37.13	1572	3.31	1.43	0.62	1986	2009	16	31	24 ± 1	0.69	0.97
	N	Corbalán	Spain	-0.99	40.40	1210	0.42	0.32	0.59	1974	2006	14	27	113 ± 8	0.72	0.97
	N	Sierra María	Spain	-2.17	37.67	995	0.87	0.39	0.35	1974	2006	30	58	98 ± 6	0.58	0.98
	N	Villalangua	Spain	-0.80	42.41	620	2.11	0.83	0.41	1974	2006	30	50	46 ± 3	0.46	0.96
	N	Gúdar	Spain	-0.72	40.33	1510	0.65	0.29	0.47	1974	2006	20	39	95 ± 5	0.59	0.97
	P	Paco Cenera	Spain	-1.20	42.48	840	2.17	1.12	0.74	1974	2006	10	20	50 ± 1	0.52	0.91
	P	Los Pintanos	Spain	-1.02	42.53	799	1.87	1.14	0.66	1974	2006	10	20	43 ± 1	0.49	0.90
	P	Urriés	Spain	-1.07	42.25	565	1.86	1.15	0.68	1974	2006	10	20	44 ± 1	0.58	0.93
	P	Bendora	Australia	149.07	-35.53	1280	2.62	0.94	0.73	1974	2006	14	18	51 ± 3	0.25	0.81
	P	Alcubierre	Spain	-0.45	41.81	566	1.04	0.59	0.64	1974	2006	10	18	60 ± 4	0.41	0.87
<i>Pinus pinea</i>	N	Viloria	Spain	-4.39	41.45	879	3.23	1.29	0.48	1973	2006	17	32	56 ± 4	0.58	0.96
	N	Oristà	Spain	2.05	41.92	475	1.70	0.73	0.47	1973	2006	15	30	69 ± 3	0.54	0.95
	P	Bubierca	Spain	-1.85	41.31	708	3.21	1.76	0.44	1973	2006	18	35	38 ± 3	0.64	0.96
	P	Doñana	Spain	-6.24	37.00	35	3.09	1.15	0.29	1973	2006	16	31	35 ± 2	0.66	0.96
	P	Valbona	Spain	-0.81	40.23	1050	0.95	0.50	0.38	1973	2006	8	8	57 ± 2	0.71	0.95
<i>Pinus pinaster</i>	N	Valbona	Spain	-0.81	40.27	1075	1.28	0.71	0.53	1973	2006	25	50	105 ± 4	0.79	0.99
	N	Valle de Cabra	Spain	-0.78	40.28	1165	1.22	0.64	0.58	1970	2006	15	30	78 ± 3	0.71	0.97
	N	Mina Amparo	Spain	-1.32	40.22	1345	0.66	0.31	0.50	1970	2006	26	49	126 ± 4	0.62	0.98
	N	Miedes	Spain	-1.43	41.27	963	0.58	0.31	0.58	1970	2009	15	28	90 ± 2	0.71	0.97
	P	Liencres	Spain	-3.93	43.46	75	2.41	0.98	0.69	1970	2009	15	29	40 ± 1	0.35	0.85
	P	Valonsadero	Spain	-2.53	41.78	1097	2.69	1.43	0.65	1970	2009	15	30	47 ± 3	0.69	0.97
	N	Corbalán	Spain	-0.99	40.40	1218	0.48	0.23	0.19	1983	2009	10	20	105 ± 5	0.51	0.91
<i>Pinus sylvestris</i>	N	Las Eras	Spain	-0.80	42.88	1361	4.80	1.33	0.35	1983	2009	30	44	41 ± 8	0.33	0.92
	N	Pico del Águila	Spain	-0.40	42.30	1612	1.54	0.62	0.36	1983	2009	30	56	79 ± 9	0.26	0.91
	P	Coyhaique	Chile	-72.07	-45.58	690	4.52	1.59	0.74	1974	2013	24	27	32 ± 1	0.20	0.78
	P	Sierra de las Nieves	Spain	-4.98	36.73	1400	4.08	1.67	0.68	1983	2009	15	33	29 ± 1	0.54	0.95
	P	Valonsadero	Spain	-2.53	41.78	1097	2.05	0.88	0.43	1983	2009	15	30	48 ± 1	0.64	0.96

2.2. Field sampling and age estimation

In each site, between eight and 30 dominant or co-dominant trees were selected. Two cores per tree were extracted at 1.3 m using 5.15-mm increment borers (Haglöf, Sweden), and perpendicular to the slope. In the laboratory the wood samples were air-dried, glued, and polished using sandpaper until ring boundaries were visible. Each core was visually cross-dated and measured to the nearest 0.01 mm using a LINTAB measuring device (Rinntech, Heidelberg, Germany). The software COFECHA was used to check for cross-dating accuracy (Holmes, 1983).

Tree age was estimated as the number of rings in cores with pith. In those cases where samples had no pith, pith-offset estimates were calculated by fitting a geometric pith locator to the innermost rings and converting this distance to the theoretical pith into the number of missing rings (Duncan, 1989). We estimated tree age as the maximum number of rings measured or estimated in each individual.

2.3. Climate data and drought index

Monthly values of average temperature and total precipitation for the period 1901-2019 were obtained from the CRU TS v4.01 database (Harris et al., 2014). The CRU dataset is derived by the interpolation of monthly climate anomalies from extensive networks of weather station observations on a 0.5° grid. We downloaded monthly average temperature and total precipitation for each site using the Climate Explorer webpage (<https://climexp.knmi.nl/>).

We used the Standardized Evapotranspiration Precipitation Index (SPEI; Vicente-Serrano et al., 2010) to quantify drought impact for each species in each site. The SPEI is a multi-scalar index that quantifies drought intensity according to the difference between the atmospheric evaporative demand and precipitation for different temporal periods. Negative values of the SPEI indicate water scarcity. We calculated monthly SPEI values at temporal scales of one, three, six, nine and 12 months using the spei package (Beguería et al., 2014) in the R environment (R Development Core Team, 2020).

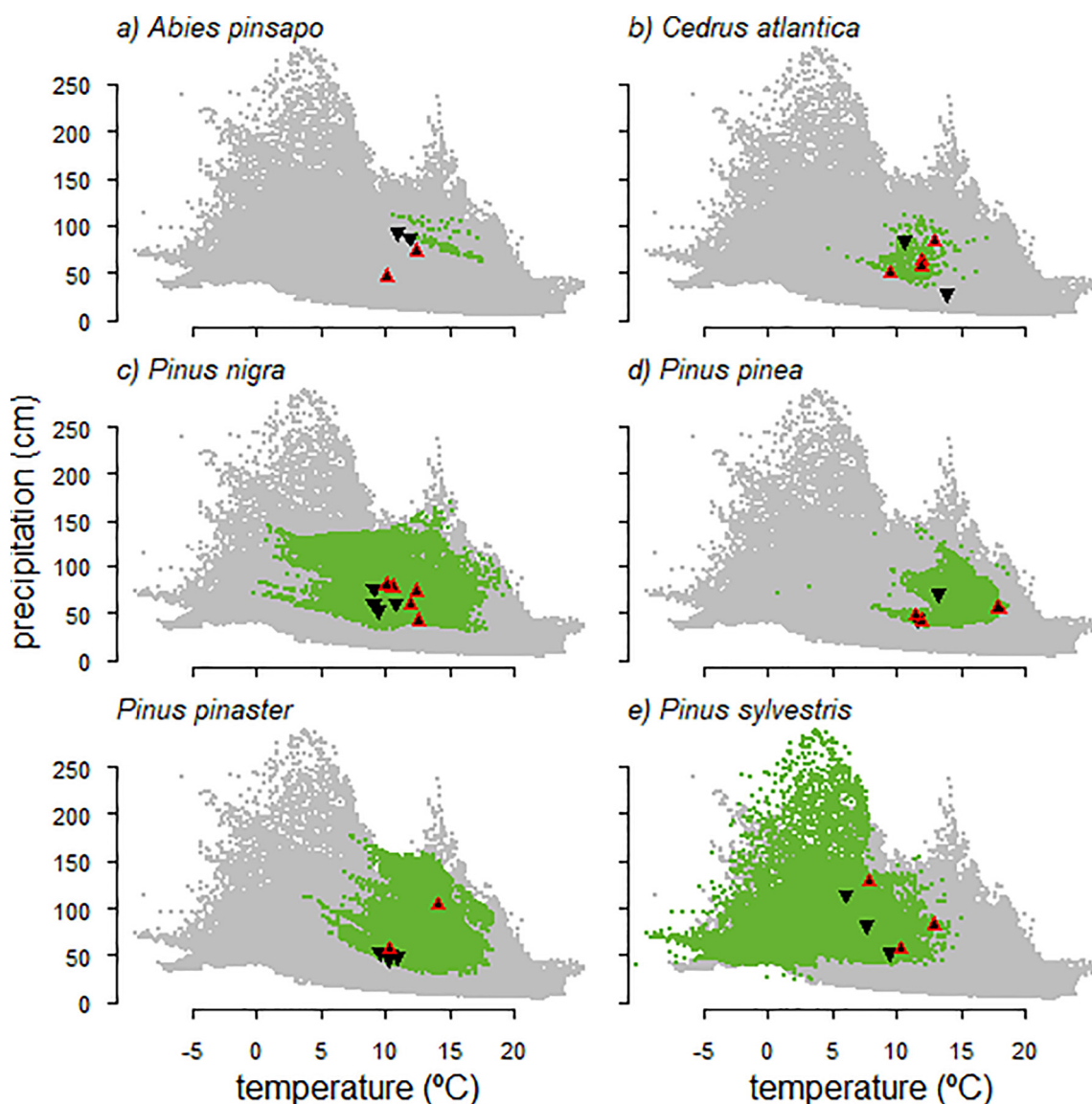


Fig. 1. Climate space of studied species, natural and planted stands. Grey dots indicate the climate space in which the species occurs (latitude: from 32° to 72° N or S; longitude: from 12° W to 60° E), whereas green dots correspond to the natural distribution of each species. The upward and downward triangles indicate natural and planted stands, respectively. For each species, distribution maps were downloaded (De Vries et al., 2015) and completed using recent distribution maps (Caudullo et al., 2017). Maps of mean annual temperature (MAT) and mean annual precipitation (MAP) were downloaded from the worldClim database (Fick and Hijmans, 2017). These maps represent annual sums or averages over the period 1970–2000. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.4. Dendrochronological processing of samples

To obtain ring-width indices (RWI), individual tree-ring width series were detrended using a cubic regression spline with a frequency response of 0.5 at a wavelength of 2/3 of the series length. The resulting standardized RWI tree-level series (RWIstd) were pre-whitened (fitting an autoregressive model to the time series) to remove the temporal autocorrelation and produce residual series (RWIres). The RWIstd and RWIres individual series were averaged year-by-year using a biweight robust mean to obtain a standard and residual site chronology, respectively. We calculated the Expressed Population Signal (EPS) to assess the internal coherence of each chronology (Wigley et al., 1984). Detrending and chronology computation were performed using the package dplR (Bunn, 2008, 2010) in R.

We quantified the vulnerability of tree growth (RWIstd) to drought as the resilience capacity for each tree of each species in each site. We compared the resilience indices defined by Lloret et al. (2011) between trees in natural and planted stands. Resilience of tree growth can be quantified according to three indices: (i) the resistance index (R_t), which compares the growth in the pre-drought and drought period; (ii) the recovery index (R_c), which compares the growth in the drought and post-drought period; and (iii) the resilience index (R_s), which compares the growth in the pre- and post-drought periods. These two periods were both 3-year long.

For each species in each site, we estimated the number of drought years as those in which the 12-month June SPEI (calculated from July of the previous year to June of the growth year) was lower than -1.5. We focused on the 12-month long SPEI for June (December in the southern Hemisphere) as it reflects the drought conditions from July (January) in the prior year to June (December) in the growth year (Pasho et al., 2012). For those drought years, we calculated the growth reduction of the series of each individual tree in each site as compared

to the preceding four years. The R_t , R_c and R_s indices were calculated for each drought event in the common period 1986–2005. The R package pointRes was used to calculate resilience components (van der Maaten-Theunissen et al., 2015).

2.5. Statistical analyses

We studied the relationship between growth and climate by calculating bootstrapped correlations of tree-ring width chronologies (RWIres) and air temperature and precipitation. For each species in each site, the analyses were performed from September of the year before the tree-ring was formed to October of the growth year. Bootstrapped correlations were also used to test for the relationship between RWIres and the SPEI calculated at resolutions of one, three, six, nine and 12 months. The exact bootstrapping method was used to assess significance by resampling 1000 times (Meko et al., 2011). The temporal period for which the relationships were calculated varied between species due to differences in the length of the chronologies (see Table 1). The analyses were performed using the Seacorr package (Meko et al., 2011).

Linear mixed-effects models (Pinheiro and Bates, 2000) were used to evaluate whether the relationship between tree-ring width series (RWIstd) and drought depend on stand type (natural vs. planted stands) at the individual tree level. We modelled RWIstd as function of the 12-month long SPEI, forest type (i.e. natural or planted) and their interaction. Tree identity, nested within site identity, was included as random factor. A first-order autocorrelation structure was introduced in the model to control the dependency of tree growth in year t for that in year $t-1$. We selected the most parsimonious model based on information theory (Burnham and Anderson, 2002) and according to the corrected Akaike Information Criterion (AICc) values (i.e. the model with the lowest number of fixed factors among those with a difference

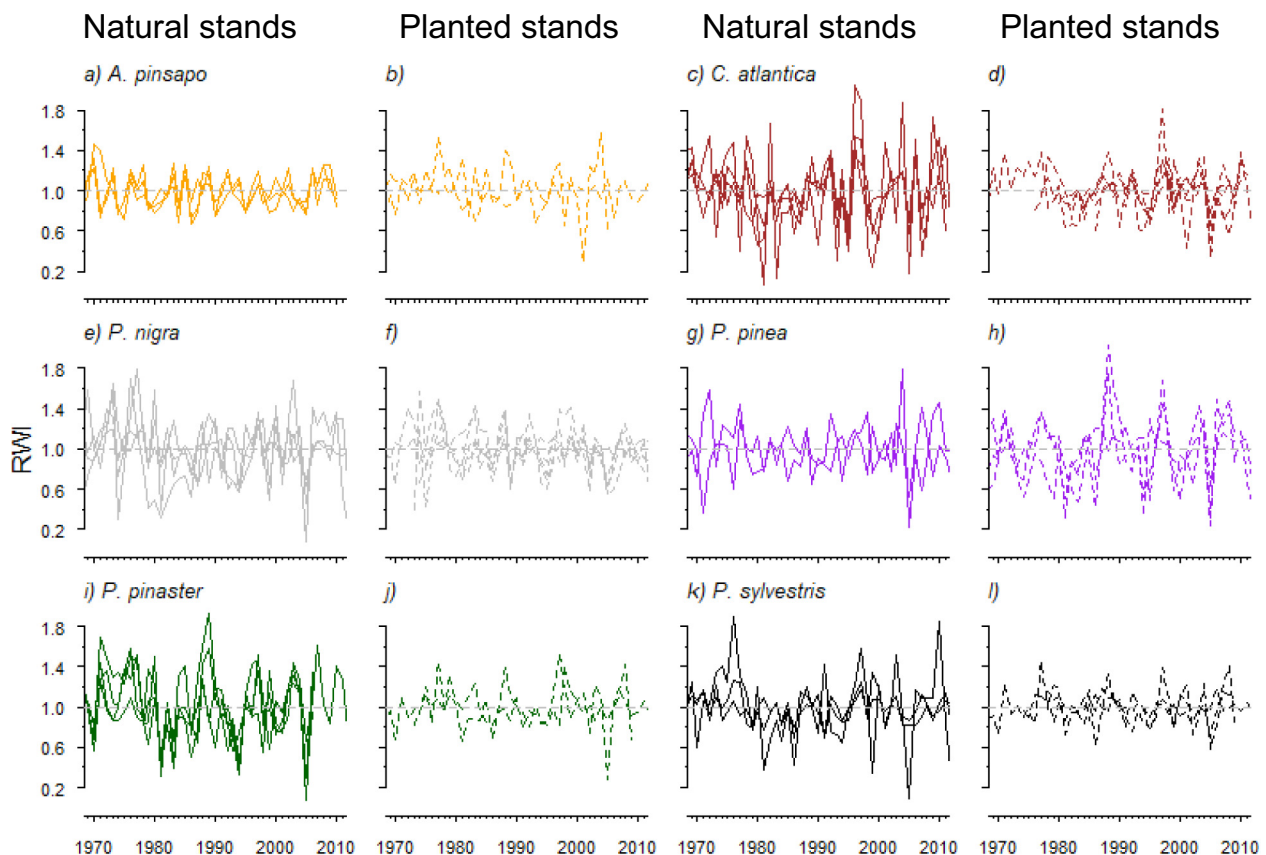


Fig. 2. Site chronologies (standardized ring-width indices, RWIstd) considered for each species in natural (solid lines; a, c, e, g, i and k plots) and planted (dashed lines; b, d, f, h, j and l plots) stands.

lower than 2 AICc). The final selected model was evaluated graphically, and its fit was quantified with the conditional (R^2_c) and marginal (R^2_m) coefficients of determination which account for the effects of fixed and fixed plus random effects, respectively (Nakagawa et al., 2017). The nlme package (Pinheiro et al., 2020) was used to fit these models. All statistical analyses were performed in the R environment (R Development Core Team, 2020).

Linear mixed-effects models were also used to evaluate whether resilience indices (R_t , R_c and R_s) during drought years differed between natural and planted stands of each species. Stand type (i.e. natural or planted) and SPEI were used as fixed factors while tree identity, nested within site, was included as random factor. Again, we selected the most parsimonious model based on its lowest AICc. The selected model was graphically evaluated, and its fit was quantified with the R^2_c and R^2_m coefficients.

3. Results

3.1. Growth patterns

Growth variability differed between species and between natural and planted stands (Fig. 2; Table 1). Plantations presented larger and more variable growth rates (mean \pm SD, 2.97 ± 1.24 vs. 1.36 ± 0.55 mm) and higher first-order autocorrelation values (0.56 vs. 0.42) than their natural counterparts ($t = 2.90\text{--}5.71$, $p < 0.01$ in all cases). Natural stands were formed by older trees than planted stands (114 vs. 41 years; $t = 5.82$, $p < 0.0001$), and tended to show higher inter-series correlation (\bar{r}) and EPS values, but differences were not significant. No sign of growth release was detected in the growth series of planted stands, which further confirmed lack of management intervention at least for the past 20 years for the selected study sites.

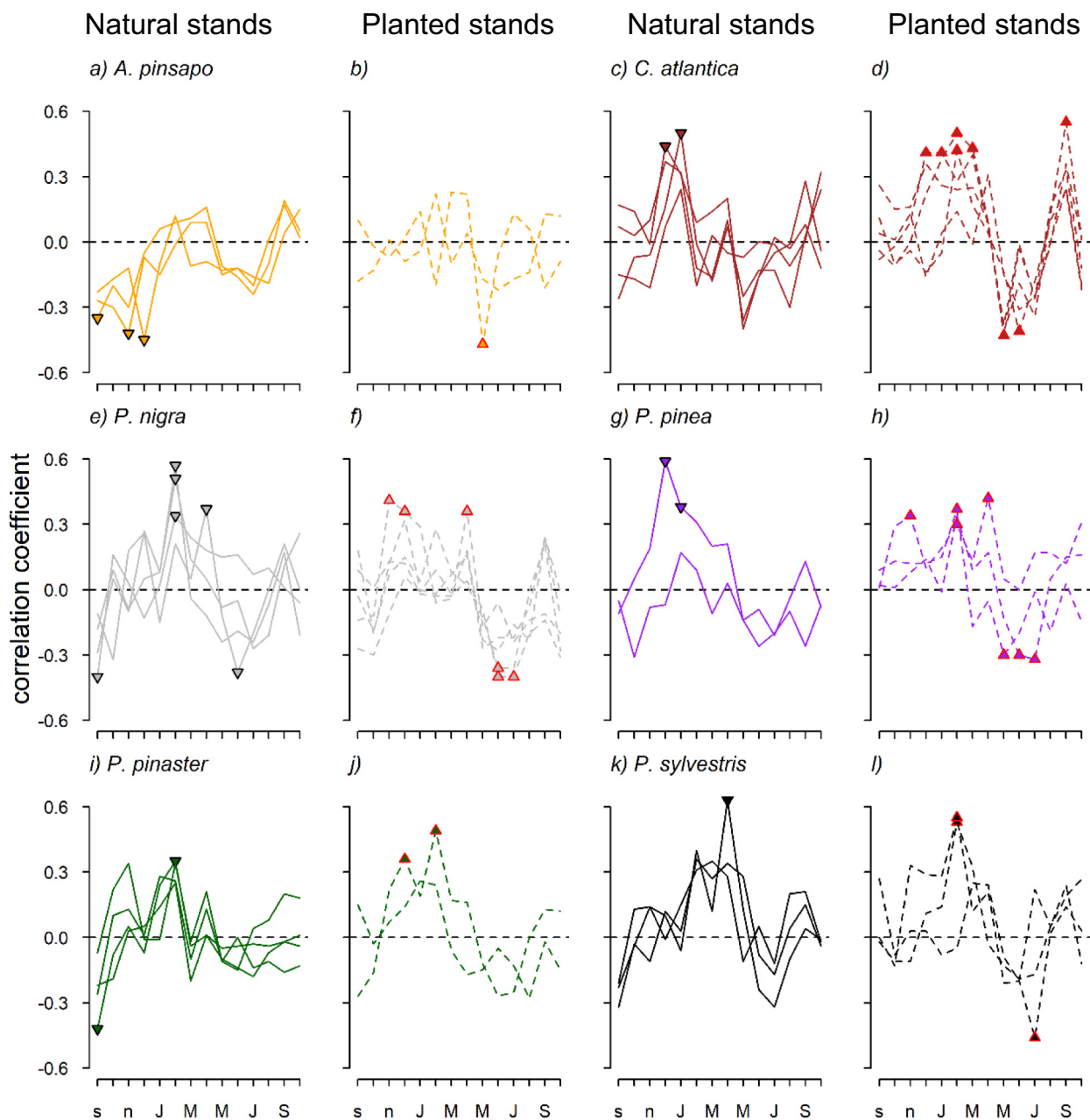


Fig. 3. Bootstrapped correlation coefficients between monthly temperature data and the residual site chronologies (RWires) in natural (solid lines; a, c, e, g, i and k plots) and planted (dashed lines; b, d, f, h, j and l plots) stands. Significant relationships are indicated with downward or upward triangles in natural and planted stands, respectively. The y axes shows the months of the prior (abbreviated by lowercase letters) and current (abbreviated by uppercase letters) years considering the northern Hemisphere notation.

3.2. Growth responses to climate

The relationship of growth rate (RWIres) with temperature and precipitation varied considerably between stand types and among species (Figs. 3 and 4). For example, high temperatures during the previous autumn and winter constrained growth in natural *A. pinsapo* stands. In several other species (*C. atlantica*, *P. nigra*, *P. pinea*) summer temperatures negatively impacted growth more in planted than in natural stands. In planted *P. pinaster* stands, growth positively responded to winter temperatures, whereas in one natural stand growth was constrained by warm prior-autumn temperature. In *P. sylvestris* we also observed negative relationships between growth and summer temperature in one planted site.

In *A. pinsapo*, significant positive correlations between growth and precipitation were restricted to previous autumn conditions and January (natural stands), May (planted stands) and June (Fig. 4). In *C. atlantica*, growth was very sensitive to precipitation, with natural stands being

more sensitive to summer precipitation than planted stands. In *P. nigra* and *P. pinea* the relationships between growth and precipitation during winter were stronger in natural than in planted stands. Planted stands of *P. pinaster* were more sensitive to prior winter and spring-summer precipitation than natural stands. In both planted and natural *P. sylvestris* stands, growth responded positively to spring-summer precipitation with some wet sites showing negative associations to elevated precipitation in September (Fig. 4).

3.3. Growth responses to drought

We found significant relationships between ring-width indices (RWIres) and the SPEI drought index for 33 out of 40 stands. Most significant correlations were found for the 12-month SPEI, but some differences were found between stand types and the different SPEI temporal scales (Fig. 5). For the SPEI calculated at the 12-month scale, we found

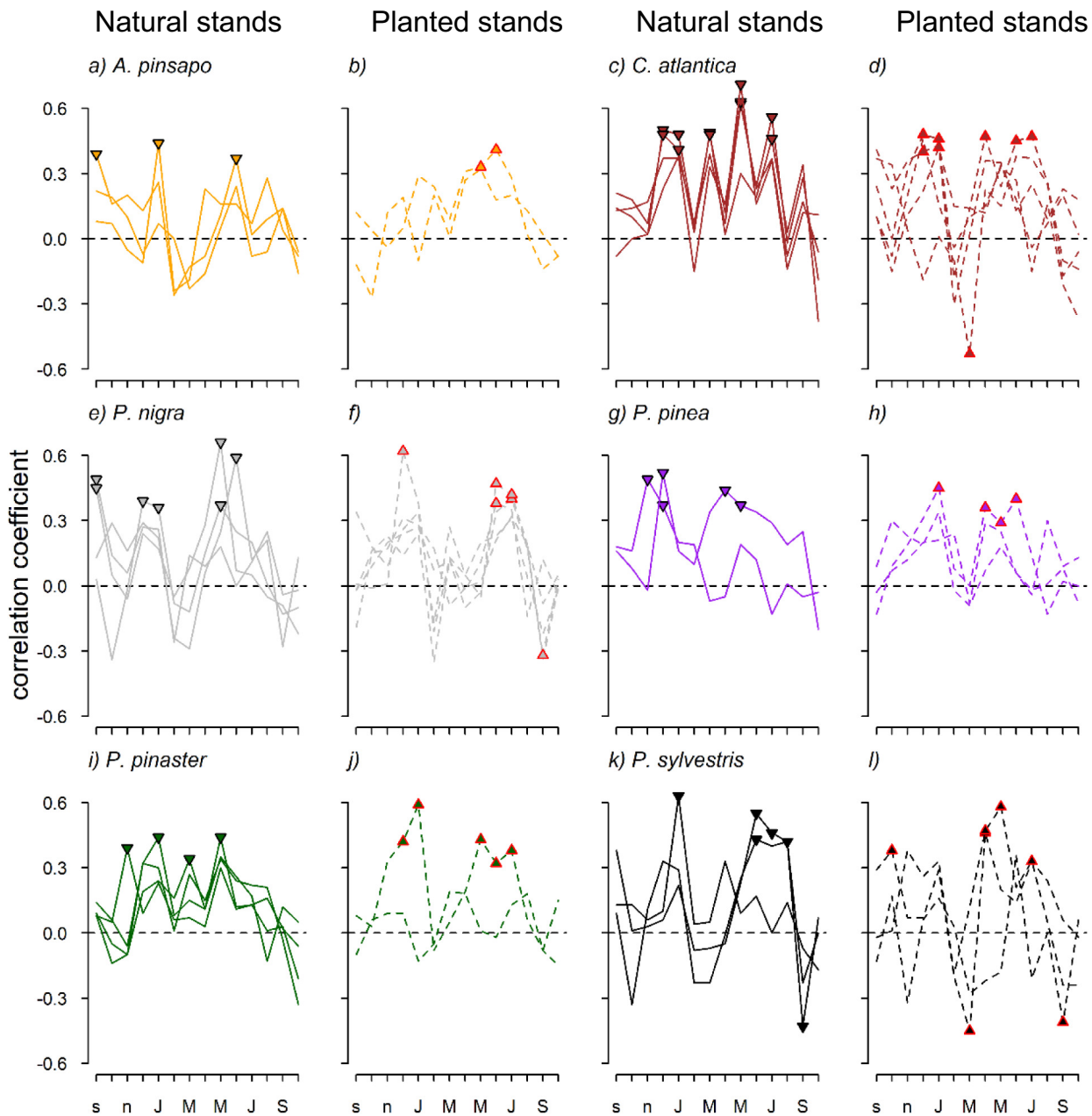


Fig. 4. Bootstrapped correlation coefficients between monthly precipitation data and the residual site chronologies (RWIres) in natural (solid lines; a, c, e, g, i and k plots) and planted (dashed lines; b, d, f, h, j and l plots) stands. Significant relationships are indicated with downward or upward triangles in natural and planted stands, respectively. The y axes shows the months of the prior (abbreviated by lowercase letters) and current (abbreviated by uppercase letters) years considering the northern Hemisphere notation.

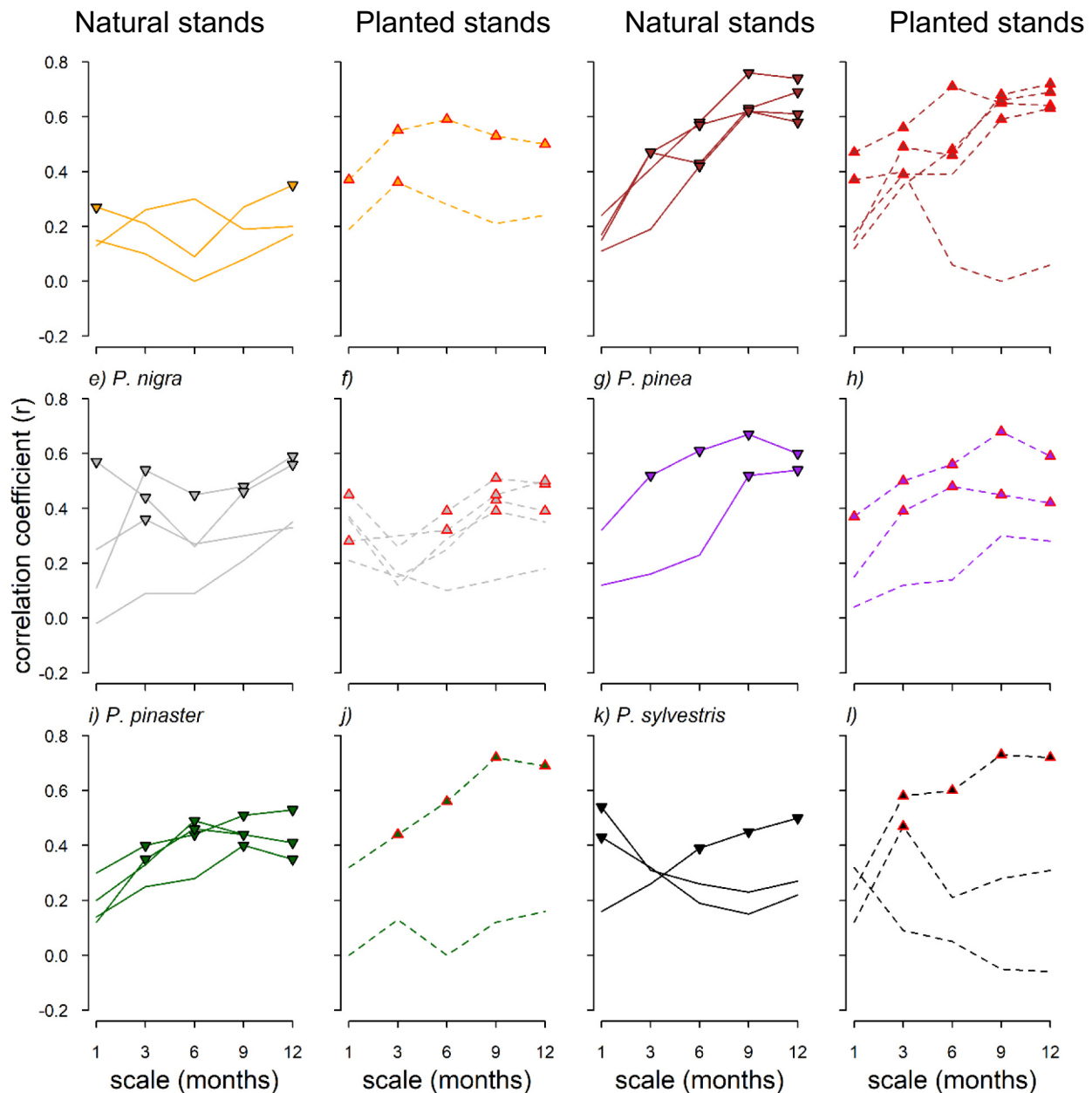


Fig. 5. Bootstrapped correlation coefficients between the 12-month SPEI in June (Northern Hemisphere) or December (Southern Hemisphere) at different scales and the residual site chronologies (RWIres) in natural (solid lines; a, c, e, g, i and k plots) and planted (dashed lines; b, d, f, h, j and l plots) stands. Significant relationships are indicated with downward or upward triangles in natural and planted stands, respectively. The y axes show the temporal scale of the SPEI drought index.

Table 2

Results of the linear mixed-effects models showing how the impact of SPEI on growth rates (RWIres) varied between planted and natural stands. For each tree species, the period studied is shown together with the t-statistic of the variables included in the model: natural vs. planted (Type), 12-month long SPEI in June (Northern Hemisphere) or December (Southern Hemisphere) and the interaction between the two variables (Type x SPEI). Significant (**; $p < 0.01$) interactions between type and SPEI indicates that trees in planted and natural forests differ in the response to drought. The $\Delta AICc$ and the Akaike weight (relative importance of each model) associated with the selected model are shown together with the marginal and conditional R^2 values (R^2_m and R^2_c , respectively).

Species	Period	Type	SPEI	Type x SPEI	$\Delta AICc$	Akaike weight	R^2_m	R^2_c
<i>A. pinsapo</i>	1970–2005	1.40	5.88**	6.28**	34.65	1.00	0.06	0.06
<i>C. atlantica</i>	1986–2009	0.13	22.82**	-4.40**	16.34	1.00	0.20	0.22
<i>P. nigra</i>	1974–2006	-0.77	26.50**	-7.65**	54.12	1.00	0.12	0.13
<i>P. pinea</i>	1970–2009	-	27.86**	-	0.87	0.52	0.19	0.19
<i>P. pinaster</i>	1973–2006	-1.06	24.03**	-4.22**	13.85	1.00	0.13	0.13
<i>P. sylvestris</i>	1984–2009	2.43	12.51**	-	1.93	0.66	0.04	0.04

that all species and stands types showed significant positive growth-SPEI relationships, for at least one stand.

When the analyses between growth (RWires) and 12-month long SPEI were carried out at the tree scale, we found significant relationships for all tree species (Table 2). Furthermore, we found significant differences in the response to drought between natural and planted stands for four (*A. pinsapo*, *C. atlantica*, *P. nigra* and *P. pinaster*) out of the six species studied (Fig. 6). If we only considered sites located in Spain, we also found significant differences between natural and planted *P. sylvestris* stands (results not presented). Natural populations were more sensitive to SPEI than their planted counterparts in three species while planted populations were more sensitive to drought in the case of *A. pinsapo*.

3.4. Growth recovery after drought: resilience indices

The occurrence of drought years varied between sites from 0 (in Coyhaique, Chile, *P. sylvestris* planted stand) to 6 (Col du Zad, Morocco, *C. atlantica* forests) events in the 1983–2005 period (Table S1). Resilience components during drought years (12-month June SPEI < -1.5) varied between natural and planted stands (Table 3). Most trees presented low resistance values ($R_t < 1$) in response to drought (Fig. 7), particularly in *C. atlantica*, *P. nigra* and *P. sylvestris*. No patterns were observed in recovery (R_c) and resilience (R_s) indices (Figs. S2 and S3). In *A. pinsapo* and *C. atlantica*, natural stands had lower resistance (lower R_t ; Fig. 7) and higher recovery (higher R_c) than planted stands (Fig. S3). Conversely, natural *P. pinea*

stands had higher resistance (R_t) and lower recovery capacity (R_c) than planted stands (Table 3). Recovery and resilience indices of natural *P. nigra* and *P. pinaster* stands were higher than in planted stands (Figs. S2 and S3). The stronger the drought, the lower the resilience and the higher the recovery in *C. atlantica*, *P. nigra* and *P. pinea*, while opposite results were found in *P. pinaster* (Table 3). In *P. sylvestris* we found higher resilience (R_s) in planted than in natural stands.

4. Discussion

Our results show that both natural and planted stands of these six conifers are vulnerable to drought and that the more intense the drought the greater the growth reduction. We found that tree growth responses to climate varied among species and between stand types, as can be expected considering the multiple factors involved (stand structure, tree age, management, soils, microclimate, etc.) that influence tree growth. This variability challenges our ability to assess drought vulnerability of plantations in comparison to their conspecific natural stands under current climate change scenario. Our results do not agree with our initial hypothesis that natural stands would be less vulnerable to drought than planted stands of the same species. Instead, our results indicate that projected climate warming will likely exacerbate growth reductions in drought-prone regions sites threatening productivity and the carbon sink capacity of both natural and planted stands. Our results from sensitivity analyses of tree-ring series to historic climate can be combined with information on management type and

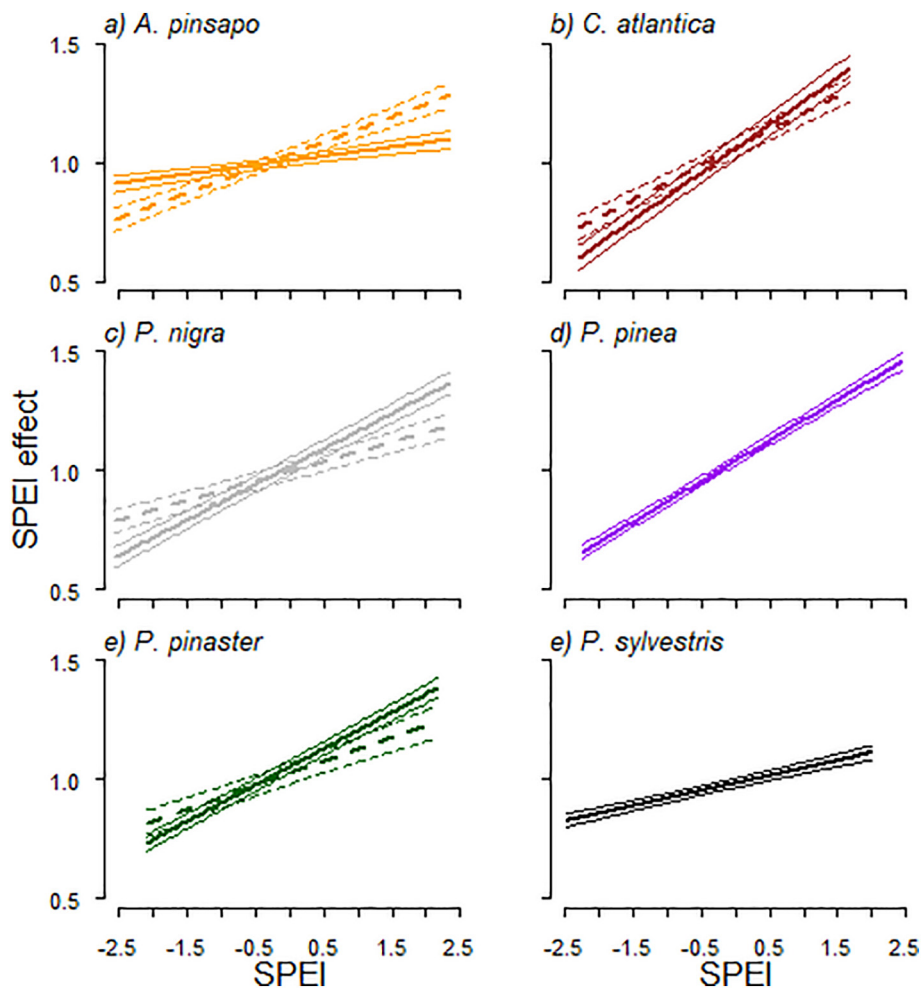


Fig. 6. Effect of drought severity (12-month SPEI in June (Northern Hemisphere) or December (Southern Hemisphere), abbreviated as SPEI) on growth (standardized ring-width indices) according to linear mixed-effects models for the different tree species. Distinct lines are drawn for natural (solid lines) and planted (dashed lines) stands when significant interactions between site type (i.e. natural and planted) and SPEI were found.

Table 3

Results of the linear mixed effects models showing how resistance (*Rt*), recovery (*Rc*) and Resilience (*Rs*) indices vary between planted and natural stands ('Type') and the 12-month long SPEI in June (Northern Hemisphere) or December (Southern Hemisphere). For each species, the *t* statistics of the variables included in the model are shown considering natural vs. planted stands (type). Significant effects of stand type and SPEI are indicated (**p* < 0.05, ***p* < 0.01). The ΔAICc and the Akaike weight associated with the selected model are shown together with the marginal and conditional R² values (R²m and R²c, respectively).

Resilience indices	Species	Type	SPEI	ΔAICc	Akaike weight	R ² m	R ² c
Resistance (<i>Rt</i>)	<i>A. pinsapo</i>	5.46**	–	2.04	0.73	0.14	0.22
	<i>C. atlantica</i>	4.57**	4.94**	18.40	1.00	0.06	0.06
	<i>P. nigra</i>	–	2.70**	1.41	0.63	0.02	0.02
	<i>P. pinea</i>	–2.97**	8.42**	6.70	0.97	0.22	0.22
	<i>P. pinaster</i>	–	–4.57**	1.68	0.70	0.06	0.06
	<i>P. sylvestris</i>	–	–	1.53	0.49	<0.01	<0.01
Recovery (<i>Rc</i>)	<i>A. pinsapo</i>	–5.79**	3.16**	7.78	0.98	0.17	0.17
	<i>C. atlantica</i>	–3.29**	–4.03**	8.63	0.99	0.04	0.13
	<i>P. nigra</i>	–4.82**	–3.07**	7.14	0.97	0.08	0.14
	<i>P. pinea</i>	4.57**	–6.98**	18.31	1.00	0.20	0.20
	<i>P. pinaster</i>	–2.43*	–	2.00	0.64	0.02	0.02
	<i>P. sylvestris</i>	–	–2.42*	2.07	0.63	0.02	0.18
Resilience (<i>Rs</i>)	<i>A. pinsapo</i>	–3.20*	3.36**	7.55	0.95	0.05	0.05
	<i>C. atlantica</i>	–	–2.97**	2.03	0.42	0.02	0.02
	<i>P. nigra</i>	–3.99**	–	0.41	0.55	0.05	0.16
	<i>P. pinea</i>	–	–	–0.17	0.27	0.01	0.01
	<i>P. pinaster</i>	–4.09**	–9.85**	14.43	1.00	0.23	0.23
	<i>P. sylvestris</i>	2.80**	–	–0.64	0.40	0.03	0.03

intensity and other local factors to help develop more sustainable forest management practices in sight of climate change. The plantations studied here did not present dieback or mortality episodes linked to drought and showed high growth rates, therefore we can infer that they represent suitable sites for our study species, beyond their natural range, but still comparable to natural forests. Overall, our findings agree with previous studies showing a minor impact of stand structure on tree growth (e.g., Long and Shaw, 2010).

We found that potential differences between planted and natural stands were strongly dependant on species identity. In the case of *A. pinsapo*, abundant rainfall in late spring and early autumn might alleviate the water stress caused by summer drought typical of the Mediterranean climate (Linares et al., 2009b). Firs are also sensitive to temperature of the year before tree-ring formation: for example, warm autumn and winter conditions during the year prior to ring formation have been found to negatively impact the growth of sub-Mediterranean silver fir forests (Camarero et al., 2011). Another question is why planted *A. pinsapo* stands are more responsive to drought, less resistant and more resilient than natural stands (Figs. 6, 7, S2 and S3). This pattern is partially driven by the stronger response to SPEI found in one of our sites, an old plantation which had previously shown reduced water-use efficiency (Santini et al., 2020) and increased sensitivity to drought (Fig. 5, Orcajo, Spain). Plantations of this species are located in drier sites than natural stands, and microclimate conditions of natural forests (e.g., wet-cool site conditions) are not reflected by annual climate data (Fig. 1). Natural *A. pinsapo* forests form relict populations that in the past were subject to management, and drought impact on them can be influenced by their management history, structure and composition (Navarro-Cerrillo et al., 2016, 2020). This, together with sufficient rainfall registered in the natural Sierra de las Nieves stands (Table S1) would make *A. pinsapo* natural forests less impacted by drought than the Orcajo plantation (Fig. 1). The results from this old *A. pinsapo* plantation contrasts with observations from those from Australian *A. pinsapo* planted stand (Bendora) where drought impacts occurred at shorter time scales and were less intense (Fig. 5). Overall, we found that for *A. pinsapo*, the negative impact of drought was buffered more in natural forests than in plantations (which were less resistant; Fig. 7). This latter result suggests that marginal and relictual populations might not always be at greater extinction risk in comparison to those in the central part of their climatic distribution range (Vilà-Cabrera and Jump, 2019). Also, extreme climatic events, and their interaction with compositional and structural attributes, have an important impact on the growth of these isolated relict stands

(Linares et al., 2010). The observed growth and response to climate observed here suggest that plantations may be a feasible alternative to aid conservation of this endangered species whose natural distribution is restricted to isolated and fragmented patches, provided that drought episodes do not increase in length and severity.

Our analyses also confirmed the strong dependency of *C. atlantica* growth on winter to summer precipitation, in line with prior research (Linares et al., 2013; Touchan et al., 2017). We found negative relationships between March precipitation and growth in the *C. atlantica* and also *P. sylvestris* plantations located in the wet Sierra de las Nieves site (Spain). This pattern can be explained by the exceptionally wet conditions found in that mountain range (Navarro-Cerrillo et al., 2016). Overall, we found positive relationships of previous autumn-winter and spring precipitation with growth in some forests of Mediterranean pines confirming the importance of previous autumn-winter and spring water stress affecting growth of these species (Andreu et al., 2007; Rozas et al., 2011; Pasho et al., 2012; Camarero et al., 2015b). This pattern was clear in natural stands, but it was also evident in plantations (Figs. 3 and 4). However, we cannot obviate the existence of differences among sites in the growth response to climate pointing to the importance of different local factors. In this respect, natural forests tend to be uneven aged with size- and age factors modulating growth response to climate (De Luis et al., 2009). Along with this, management type and intensity, through the impacts in structural and compositional attributes, can strongly modify growth variability in both natural and planted stands (Pretzsch et al., 2013; Navarro-Cerrillo et al., 2016). Thus, further studies are required to advance in the understanding on whether and why natural forests respond differently to climate than plantations with a special focus on the potential impact of drought in sight of climate change. One potential explanation for the different growth sensitivity to climate in planted vs. natural stands has to do with the degree of artificial selection planted species have experienced. One of the main purposes for planting is to obtain revenues as a result of high yield. Thus, special attention has been given to select high growth genotypes that, in many cases, have been further genetically improved through genetic programs (e.g., seed orchards). It is likely that some of the sampled plantations were composed of individuals that had undergone improvement (e.g., *P. sylvestris*), and therefore best-growth stands would have been overrepresented in our study. Other species from less productive, dry sites were often planted for restoration (e.g., *P. pinaster*). These sampling biases could also explain some of our results.

Negative associations between late-spring to early-summer temperatures and growth were common in *C. atlantica*, *P. nigra*, *P. pinea* and

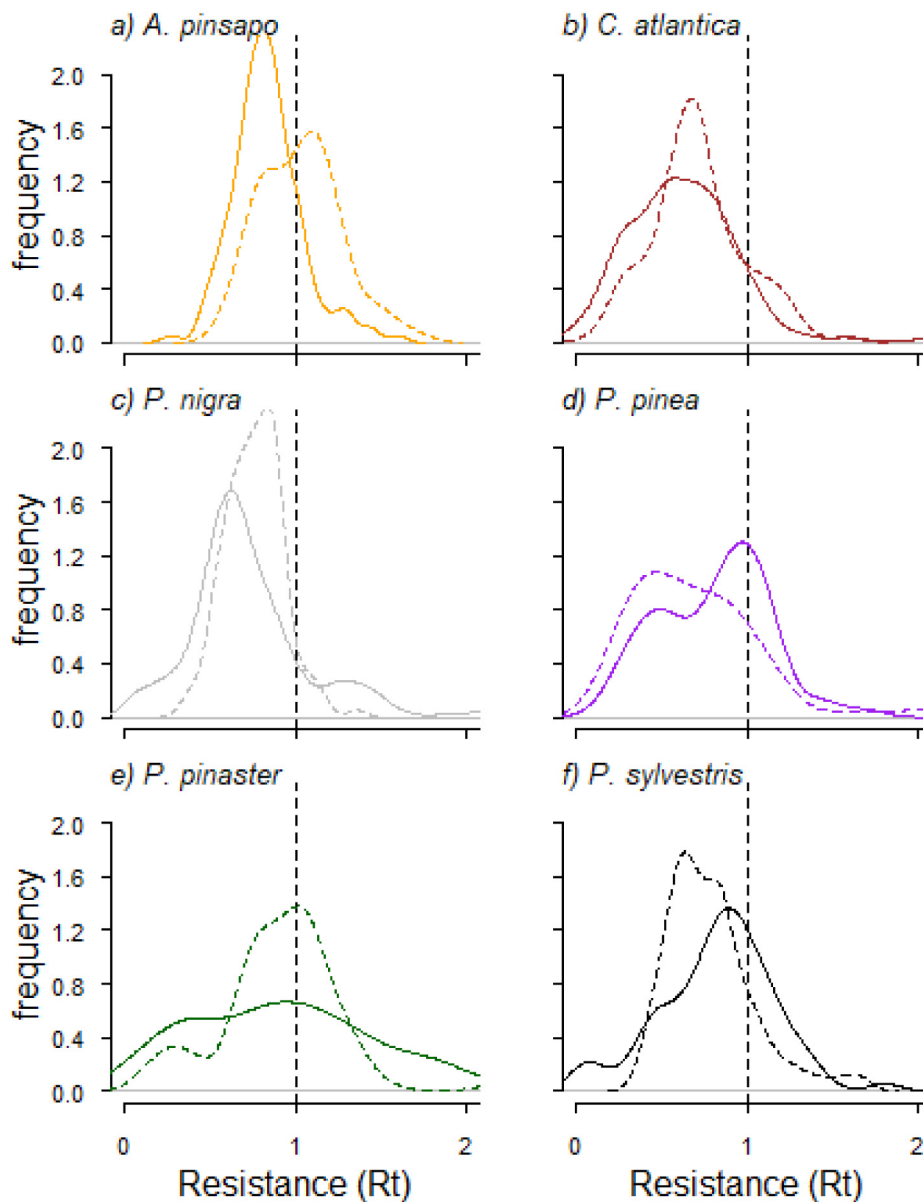


Fig. 7. Distribution of resistance indices (R_t) to drought (years with 12-month June SPEI < -1.5) of trees in natural (solid line) and planted (dashed line) stands for each species.

P. sylvestris. Together with the positive associations with precipitation, the negative correlations point to the vulnerability of such stands to high evaporative demand and water scarcity experienced during the late part of the growing season (Bogino and Bravo, 2008; Sánchez-Salguero et al., 2010). Not surprisingly, we found that drought was an important factor limiting the growth of most of the species studied in both natural forests and plantations, as observed before in natural forests (Gazol et al., 2018). Indeed, all species responded negatively to drought, despite variations in the temporal scale (Fig. 5). Species adapted to xeric conditions, such as *C. atlantica* and *P. pinaster*, showed a strong dependency of growth on SPEI at long temporal scales (from 6 to 12 months) in natural stands. In fact, three species (*C. atlantica*, *P. nigra* and *P. pinaster*) showed a more marked response to drought in natural than in planted stands (Figs. 5 and 6). The cessation of growth formation in *P. pinaster* and *Cedrus libani* is strongly dependent on water availability during summer (Vieira et al., 2014; Güney et al., 2015). In the case of *C. atlantica*, the four natural forests were strongly linked to the SPEI and the planted forest in the Sierra de las Nieves was the only one not showing significant relationships with the SPEI. Natural *C. atlantica* stands have displayed growth declines and dieback since

the late 1970s in dry north African sites (Linares et al., 2013), and their survival and distribution are severely threatened in sight of the forecasted drought increase due to climate change. This drought sensitivity can explain the low drought resistance found in both natural and planted stands of this species (Fig. 7). Despite less intense, drought impacts were also evident in cedar plantations located in southern France (Guillemot et al., 2015). Nevertheless, cedars (e.g., *C. atlantica*, *C. libani*) represent valuable species for establishing productive plantations in southern and central Europe under a warmer and drier climate since they tolerate low winter temperatures and severe summer drought (Messinger et al., 2015). Further research is needed to address how thinning may alleviate water competition in planted stands more impacted by severe droughts (Sohn et al., 2016).

Stronger relationships between growth and drought were also found in natural *P. nigra* and *P. pinaster* stands than in plantations (Fig. 6). Similar to other Mediterranean pine species, the growth of *P. nigra* and *P. pinaster* is strongly dependent on summer drought (Andreu et al., 2007; Camarero et al., 2015b). It is also well established that management type and intensity can modulate growth response to drought of these species (Sánchez-Salguero et al., 2013). Particularly,

thinning may alleviate competition with neighbors for water resources thus increasing growth rates and reducing the negative impacts of drought (Navarro-Cerrillo et al., 2016, 2018).

We found no differences in the growth response to drought between natural and planted *P. sylvestris* and *P. pinea* forests (Fig. 6). In the case of *P. sylvestris*, only one natural site showed significant relationships with the 12-month SPEI and the same pattern was observed in planted forests (Fig. 5). Indeed, the slope of the relationship between growth and SPEI was less steep for *P. sylvestris* than for the rest of species. Thus, the inclusion of wet productive sites (sites with fewer drought episodes) where water shortage is rare may explain these results. *P. pinea* is a species that is well adapted to cope with drought and it is capable to pause wood formation during the dry summer months and resume growth in autumn (Nabais et al., 2014). Iberian *P. pinea* populations showed similar growth responses to climate in different regions (Natalini et al., 2015, 2016). It is thus plausible that regional factors, including atmospheric circulation patterns, and inherent adaptation could have buffered growth response to climate of the forests studied here. However, it is important to note that the resistance to droughts was higher in natural than in planted *P. sylvestris* and *P. pinea* stands suggesting that local factors modulate the response to extreme events (Fig. 7; Table 3).

Overall, our results concur with previous findings that drought occurrence and water availability are major drivers of growth variability and resilience in conifers from Mediterranean and continental sites. In relict species with limited distribution range, such as *A. pinsapo*, plantations far from the distribution range can be an alternative to preserve them. Plantations of *C. atlantica* also offer a potential for productive and resilient forestry if European climate continues warming and drying. However, plantations are also likely to suffer from the negative impact of drought, and thus multi-purpose management policies aiming to enhance their resilience, productivity and structural diversity are required (Paquette and Messier, 2010; Nabuurs et al., 2013). It should be noted that some of the current productive plantations (e.g., industrial forests) are the result of extensive field trials, and therefore only those attempts that were successful are nowadays available for a long-term growth sampling and climate sensitivity assessment. Thus, in plantations we should expect biases due to site- and/or individual factors, while natural stands should express the average species performance. Furthermore, more productive sites (e.g., flat areas with deeper and richer soils), and degraded sites (e.g., overgrazed woodlands on steep slopes and thin soils) have long been selected for forestry productive or restoration purposes, respectively.

Making adequate decisions for the adaptive management of plantations would be facilitated by quantifying the resilience of comparable natural and planted stands. Refining these comparisons requires quantitative information on local factors including stand structure, management history or genetic origin, which are often missing. We thus advocate for the study of similar natural and planted conspecific stands to advance in the understanding of forest functioning and assess the real mitigation potential of nature-based solutions under current climate change scenario. Research on mixed stands can also help to elucidate some of the questions resulting from this research.

5. Conclusions

We compared growth patterns and responses to climate and a drought index in natural and planted stands of six conifer species encompassing wide climatic gradients. We found that the main processes accounting for different patterns in growth response to climate between natural and planted trees are mainly related to site-contingent effects, while a species-specific framework prevails in climate-growth sensitivity studies. Growth of the study species is enhanced by wet-cool conditions prior or during the growing season. Plantations did not show higher growth sensitivity to climate variability. The post-drought growth resilience was similar between planted

and natural stands, excepting in three species (*A. pinsapo*, *C. atlantica* and *P. pinaster*) showing better recovery of natural stands, and another one (*P. pinea*) showing a better recovery in plantations.

Consent for publication

Not applicable.

Ethics approval

Not applicable.

CRedit authorship contribution statement

J. Julio Camarero: Conceptualization, Methodology, Software, Data curation, Writing – original draft, Visualization, Investigation, Supervision. **Antonio Gazol:** Conceptualization, Methodology, Software, Data curation, Writing – original draft, Visualization, Investigation, Software, Validation. **Juan Carlos Linares:** Data curation, Writing – original draft. **Alex Fajardo:** Data curation, Writing – original draft. **Michele Colangelo:** Writing – review & editing. **Cristina Valeriano:** Writing – review & editing. **Raúl Sánchez-Salguero:** Writing – review & editing. **Gabriel Sangüesa-Barreda:** Data curation, Writing – original draft. **Elena Granda:** Writing – review & editing. **Teresa E. Gimeno:** Data curation, Writing – original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2021.148930>.

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