Linkages between Climate, Radial Growth and Defoliation in *Abies pinsapo* Forests from Southern Spain

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Abstract: Systematic forest networks of health monitoring have been established to follow changes in tree vigor and mortality. These networks often lack long-term growth data, but they could be complemented with tree ring data, since both defoliation and radial growth are proxies of changes in tree vigor. For instance, a severe water shortage should reduce growth and increase tree defoliation in drought-prone areas. However, the effects of climatic stress and drought on growth and defoliation could also depend on tree age. To address these issues, we compared growth and defoliation data with recent climate variability and drought severity in *Abies pinsapo* old and young trees sampled in Southern Spain, where a systematic health network (Andalucía Permanent Plot Network) was established. Our aims were: (i) to assess the growth sensitivity of old and young *A. pinsapo* trees and (ii) to test if relative changes in radial growth were related with recent defoliation, for instance, after severe droughts. We also computed the resilience indices to quantify how old and young trees recovered growth after recent droughts. Wet-cool conditions during the prior autumn and the current early summer improved the growth of old trees, whereas late-spring wet conditions enhanced the growth of young trees. Old trees were more sensitive to wet and sunny conditions in the early summer than young trees. Old and young trees were more responsive to the Standardized Precipitation-Evapotranspiration Index drought index of June–July and July–August calculated at short (one–three months) and mid (three–six months) time scales, respectively. Old trees presented a higher resistance to a severe drought in 1995 than young trees. A positive association was found between stand defoliation and relative growth. Combining monitoring and tree ring networks is useful for the detection of early warning signals of dieback in similar drought-prone forests.

Keywords: climate change; drought; growth resilience; Standardized Precipitation-Evapotranspiration Index (SPEI); forest decline; Mediterranean forests

1. Introduction

Biotic and abiotic stressors (climatic events, insect outbreaks or fungal leaf diseases) have increased during the last decades, leading to changes in tree ring growth responses [1]. Since the late 1970s, recurrent and more severe episodes of forest dieback have been observed in European forests, particularly in drought-prone southern countries [2,3]. Systematic forest health information is

crucial to monitor dieback dynamics and how they affect forest structure and composition. Forest health data has mainly been obtained based on national data networks under the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests). ICP Forests plots characterize tree conditions by descriptors, including defoliation (e.g., leaf deficit relative to a so-called reference tree), among others [4], in an attempt to integrate the physiological mechanisms by which biotic and abiotic stressors affect tree vigor and are translated into radial growth variations, although this process is complex [5,6].

It is unclear how coupled are defoliation and growth, because this relationship may be species- and site-dependent and co-vary with other climatic parameters and physiological responses [7]. In mountain conifers, several authors have found that growth performance depends on tree age and size [8]. Meanwhile, the negative impact of drought events on tree growth and the sensitivity of some tree species to current and previous unfavorable climatic conditions is well-established [9]. However, how these two factors (tree age and climate change response) will interact is still uncertain, prompting calls to explicitly incorporate tree age into forest responses to the changing climate (e.g., [10]). However, defoliation data have been still little-explored as related to interannual variations in radial growth (see [11]). Combining defoliation data from forest health networks could help to better understand the complex relationship between drought, crown condition and growth variability [12,13].

In 2001, the Environmental Department of the Regional Andalusia Government created a Forest Health Network for the monitoring of pinsapo fir (*Abies pinsapo*) forests [14]. The main objective of this network was to quantify long-term changes in the vigor of *A. pinsapo* forests and to detect potential biotic and abiotic drivers affecting *A. pinsapo* forests. It was set up on a 1 × 1-km grid, consisting of 44 permanent plots, which were monitored annually [14]. The network followed the transnational systematic plot protocols of the Level I-ICP network [4]. In *A. pinsapo*, climate-growth relationships vary considerably depending on topographic and local climatic conditions [15,16], with the most consistent response being a radial growth under wet-cool conditions in late-spring to early summer (April–June) [17,18]. However, little research has been performed to quantify growth-climate relationships in coexisting young and old tree of this species (see [13]). It can be expected that older trees, established before the post-70s rapid temperature shift, will be less plastic and more sensitive to climate warming and drier conditions than younger trees, which have germinated and established under warmer conditions and will better tolerate droughts. Tree vulnerability may be modulated by age, which may change growth resiliency and recovery after drought [19]. Age influences physiological processes such as hydraulic conductivity and gas exchange rates [20], which thus determine growth rates and drought legacies [21].

Understanding the climate-change responses of *A. pinsapo* forests requires disentangling the influences of climate, age and species distributions on tree growth. In this study, we contribute new data on the relationships between climate and *A. pinsapo* growth for different age classes based on trees collected in the permanent plots of the Level I ICP Forests network located in Andalusia, Southern Spain. We addressed the following objectives: (i) to assess the growth responses to climatic variability and tree age by comparing old vs. young trees and (ii) to relate growth and defoliation variability. Finding linkages between growth and defoliation will reinforce the use of tree ring data to detect early warning signals in forestry by allowing the identification of stands more vulnerable to climate warming facilitating their management and promoting their conservation.

2. Materials and Methods

2.1. Study Site

The study site is located in Sierra de las Nieves, at the southeastern tip of Andalusia, Spain (Figure 1, 36°41′ N, 4°52′ W), spanning the natural distribution of *A. pinsapo* [22,23]. The total study area is about 2871 ha, with a Mediterranean climate and strong small-scale heterogeneity due to the complex topography of the area [24]. *Abies pinsapo* is an endemic fir species native to Southern Spain and Northern Morocco, where it is limited to altitudes between 1100–2000 m. This Mediterranean fir

occurs on north-facing slopes in wet climates (annual precipitation 2000–3000 mm) and dry summer seasons from June to September [24]. The average rainfall in Sierra de las Nieves ranges from 900 to 1600 mm year^{-1} at lower and higher elevations, respectively. January and July are the wettest (225 mm) and driest (3.5 mm) months, respectively. Summer temperatures are relatively colder than surrounding areas (monthly mean air temperature of 25 °C), while winter can reach minimum air temperatures of −1.5 °C during the coldest month. The topography in the study area is highly heterogenous, resulting in similarly heterogenous microclimatic conditions. Although *A. pinsapo* tolerates a range of soils, the best stands develop on southern brown soils (on peridotites) and forest brown soils (on limestones and dolomites). *A. pinsapo* takes a dominant canopy role in these forests, appearing either as monospecific or mixed forests with a complex community (including *Quercus ilex* subsp. *ballota*, *Q. faginea*, *Q. suber*, *Pinus halepensis* or *P. pinaster*) and highly diverse understory [25].
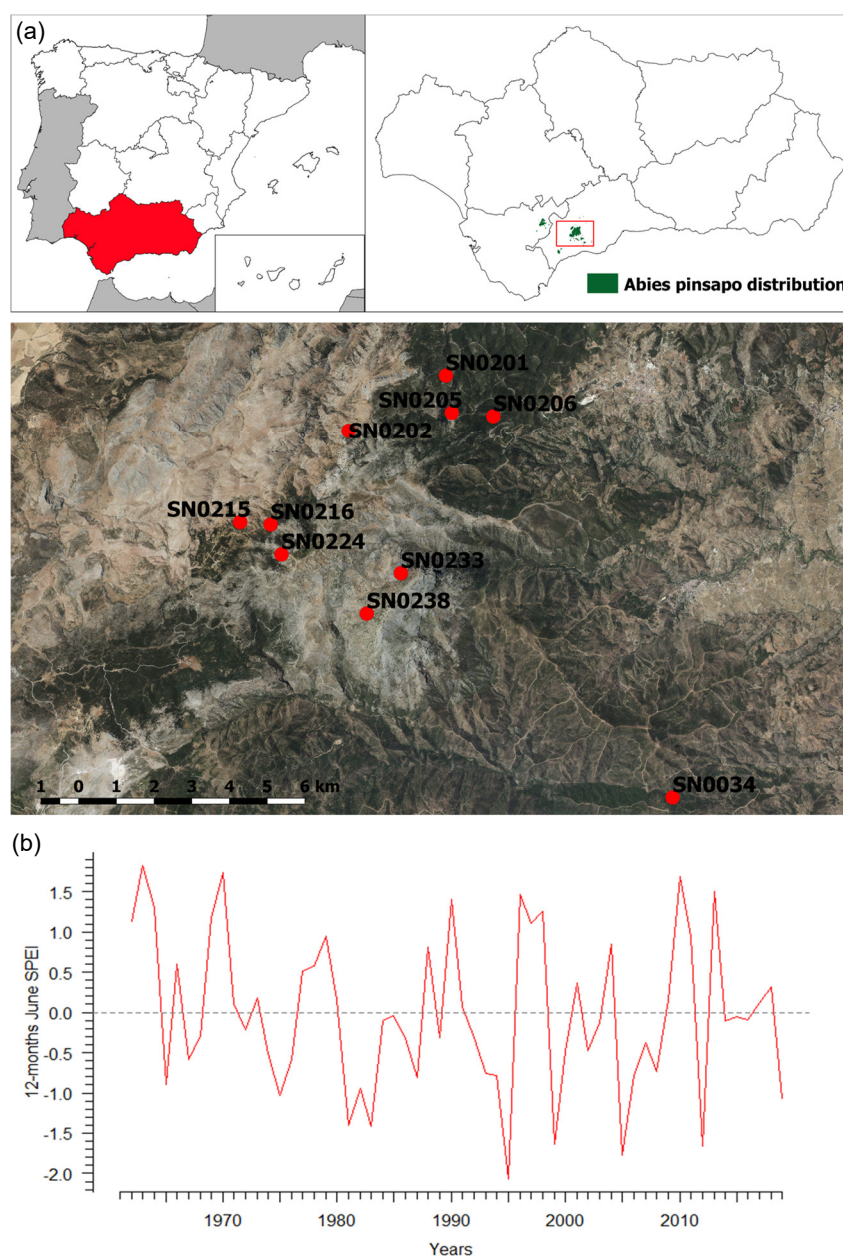

Figure 1. (**a**) Spatial distribution of *Abies pinsapo* ICP-Forests plots in Sierra de las Nieves (Málaga, South Spain). (**b**) Climate trends considering the Standardized Precipitation Evapotranspiration Index (SPEI) calculated at 12-month-long scales for the 1960–2019 period.

2.2. Field Sampling

A. pinsapo ICP Forest Level I network is complementary to the Andalusia ICP Forest Level I network covering the whole *A. pinsapo* species distribution. Level I sampling design followed a 1-km × 1-km systematic grid design, including a wide set of sites and stand variables to be measured [14]. Since 2001, a total of 44 plots have been repeatedly monitored to follow the presence and health status of *A. pinsapo* trees. Due to the protection status of the study areas, our sampling was limited within each site. Ten plots, with a total of 55 *A. pinsapo* trees, were selected based on four criteria: (i) including a wide range of age classes (young and old trees), (ii) showing consistent good crown between 2001 and 2017, (iii) showing no sign of pest and diseases damages and (iv) having similar micro topographical conditions (Figure 1 and Table S1, Supplementary Materials). For each tree, we measured geographical (location) and topographical variables (elevation, slope and aspect); size (dbh: diameter at 1.3 m, height and total height) and age (number of rings at 1.3 m). From 2001 onwards, defoliation and mortality data collection were conducted annually during the summer months on all the trees present in each of the intensive monitoring plots. The crown defoliation was estimated by expert visual assignation of different defoliation levels on the basis of the quantification of the condition of the canopy; i.e., the percentage crown decline and transparency, following ICP forest protocols [4]. Additionally, one core per tree was extracted at 1.3 m height, using a Pressler increment borer, aiming at having a comparable sample size of two age groups established based on previous analyses and considering young (age ≤ 67 years) and old individuals (age > 67 years) (Table 1).

Table 1. Dendrochronological statistics of old and young *Abies pinsapo* trees. Values are means ± SE. Different letters indicate significant ($p < 0.05$) differences between old and young trees according to Mann-Whitney tests.

	No. Trees/No. Radii	Interval	Tree Ring Width (mm)	First-Order Autocorrelation	Correlation with Mean Series
Old trees	12/24	1744–2007	1.52 ± 0.09a	0.80 ± 0.03	0.52 ± 0.02
Young trees	43/86	1940–2007	2.65 ± 0.08b	0.77 ± 0.02	0.55 ± 0.02

2.3. Tree Ring Methods

The cores were air dried and polished using sandpaper of progressively finer grains until tree rings were clearly visible and then scanned at 3200 dpi using an Epson Perfection V750 Pro scanner© (Seiko Epson Corp., Nagano, Japan). Ring widths were measured with a LINTABII measuring system with a resolution of 0.01 mm, and all cores were visually cross-dated using characteristic narrow tree-rings (1909, 1924, 1932, 1943, 1955, 1965, 1974, 1980, 1987, 1995 and 2005). Dendrochronological statistics (first-order autocorrelation, mean sensitivity and mean correlation of all series with the site mean chronology) were also calculated to compare radial-growth variability among sites and species [26].

To quantify the climate-growth relationships, tree ring width chronologies were standardized, applying linear regressions using ARSTAN [27]. The tree ring widths were converted into indices by dividing the observed values by the expected values estimated using negative linear or exponential functions. Autoregressive modeling was performed to remove the first-order temporal autocorrelation. Finally, a bi-weight robust mean was computed to average the standardized individual series and to produce residual chronologies of prewhitened tree ring width indices. For each age class, statistics were calculated considering the common interval 1970–2007 to compare growth features between the two age groups in both study sites [26], including the first-order autocorrelation of tree ring width raw data and the mean between-trees correlation of residual series (Table 1).

Mean basal area increment (BAI) series for each age class were obtained by averaging the annual values of the measured series. Converting tree ring width into BAI ameliorates the problem of declining ring widths in larger trees was done using the formula:

$$\text{BAI} = \pi \, (R^2_t - R^2_{t-1}) \tag{1}$$

where R is the radius of the tree, and t is the year of tree ring formation. Since any measurement of tree growth, including BAI, varies with tree size and age, we first modeled specific changes in BAI as a function of tree diameter. We focused on BAI trends for the period 1970–2007 when trees have surpassed their early BAI release phase. Relative growth rates (RGR$_{2007}$) for each age group were calculated following the formula RGR = (dbh$_f$ − dbh$_i$)/(t$_f$ − t$_i$), where t is the year of growth, and the subscripts f and i are final (2007) and initial (2001) values, respectively.

2.4. Climate and Drought Data

Meteorological stations in this region are sparse and generally located at lower elevations. Therefore, we used interpolated weekly and monthly climatic data (Figure S1, Supplementary Materials). Specifically, we obtained the following data from the 1.1-km^2 gridded dataset available for Spain [28]: tg, mean temperature; tx, mean maximum temperature; tn, mean minimum temperature; rr, precipitation and qq, radiation. We also obtained weekly series of the Standardized Precipitation-Evapotranspiration Index (SPEI) for 1-, 3-, 6-, 9- and 12-month timescales. The SPEI is a drought index that accounts for the effects of temperature on evapotranspiration and estimates climatic water balances for different time scales [29].

2.5. Growth Resilience Indices

To quantify the effects of droughts on growth recovery, we calculated the three resilience indices (Rt, resistance; Rc, recovery and Rs, resilience) developed by [19]. These resilience components are constructed by comparing the growth before, during and after the occurrence of drought events. Thus, high resistance (Rt) indicates a small reduction in growth during the drought years. Recovery (Rc) quantifies post-drought growth increases. Finally, resilience (Rs) expresses the persistent effects of the drought on mean growth after the event [18]. We calculated the resilience components using the standard ring width index (RWI) on the 1995 and 2005 droughts:

- The resistance index (Rt): this index quantifies the growth of the tree during the drought (D$_r$) with respect to the previous growth (PreD$_r$):

$$(Rt = D_r/PreD_r) \tag{2}$$

- The recovery index (Rs): this is the response of the growth after the drought (PostD$_r$) compared with D$_r$:

$$(Rs = PostD_r/D_r) \tag{3}$$

- The resilience index (Rc): this is the ratio of the growth values after (PostD$_r$) and before (PreD$_r$) the drought:

$$(Rc = PostD_r/PreD_r) \tag{4}$$

where D$_r$ is the RWI in the year of the drought, PreD$_r$ is the mean RWI calculated for the previous period of up to n years before the drought and PostD$_r$ is the mean RWI calculated for the period spanning n years after the drought. The periods that we considered for calculations of drought effects (n) were 1 and 2 years, consistent with previous works indicating the legacy effects on growth are stronger up to 2 years after a drought [30].

2.6. Statistical Analyses

To assess the differences in growth between the two age classes (old vs. young trees), we used the Student's *t*-test for independent samples and repeated measures for analysis of variance (ANOVAs). Prior to the statistical analysis, variables were tested for normality and homoscedasticity, and non-normal variables were log-transformed. We assessed differences in the three resilience indices (Rt, Rs and R$_c$) calculated for the two selected droughts (1995 and 2005) of old

and young trees using a nonparametric Mann-Whitney's test. Differences among treatments were considered significant at a level of $p = 0.05$.

We quantified growth responses to the climate and SPEI drought index using Pearson correlations based on weekly or monthly data and using the two residual chronologies of old and young trees as response variables. Correlations with monthly climate variables (mean temperature, total precipitation) were calculated from the previous September until current August for the common period (1970–2007).

Relationships between defoliation in 2017 and relative growth (RGR_{2007}) were determined using lineal regression models. We performed linear regression analyses to evaluate the growth-defoliation associations by relating the average plot defoliation in 2017 (D_{2017}), considering either young or old trees, with RGR_{2007}.

All analyses were performed using R software version 3.4.0 (R Foundation for Statistical Computing, Vienna, Austria). The *dplR* and *Treeclim* libraries were used to calculate tree ring statistics and climate-growth correlations [31]. The *lm* and *glm* libraries [32] were used for Pearson, ANOVA and Mann-Whitney´s tests and the *yisreg* R package for the regression [33].

3. Results

3.1. Growth and Chronology Statistics

The chronology of the old trees covered the last 250 years, with a mean age of 263 years, whereas the mean age of young trees was 67 years (Table 1 and Figure S2, Supplementary Materials). We found a marked decrease in the BAI during two principal droughts (1994 to 1995 and 2005); nevertheless, both the BAI and the impact of drought on growth varied between tree age (Figure 2a).

As expected, older stands have lower mean growth rates (Table 1). This difference was highly significant ($p < 0.001$) during the best-replicated period (1970–2007), when the mean ring widths (±SE) of old and young trees were 1.09 ± 0.04 and 2.37 ± 0.12 mm, respectively (Figure 2b). During this period, the standard chronologies of old and young trees were significantly correlated with each other (r = 0.66, $p < 0.001$). Other dendrochronological statistics, such as autocorrelation or correlation with mean series, showed no significant differences between old and young (Table 1). The overall high first-order autocorrelations in *A. pinsapo* trees reflects a high persistence of the ring width chronologies, likely suggesting carry-over effects from previous year's climate on the current year's ring width (Figure S3, Supplementary Materials).
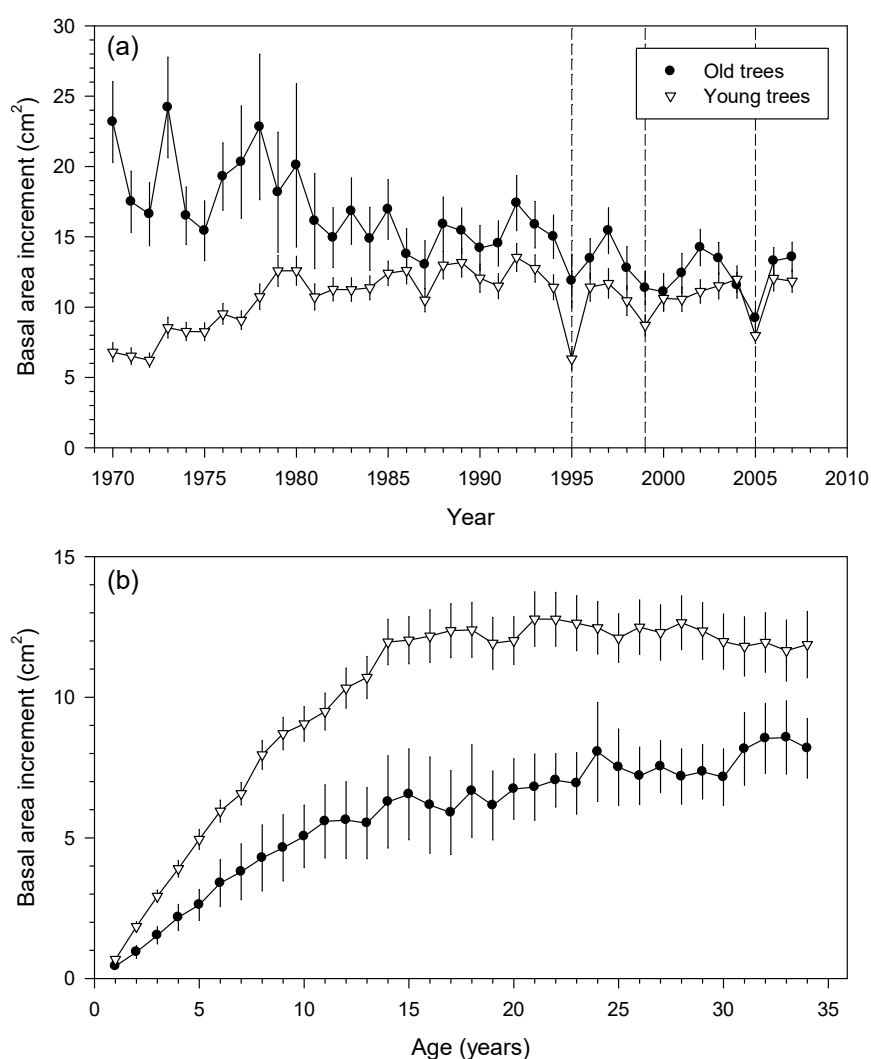
Figure 2. Basal area increments of old and young trees as a function of the calendar year (**a**) and cambial age (**b**). The vertical dashed lines in plot (**a**) correspond to the 1995, 1999 and 2005 droughts (see Figure S1 in the Supplementary Materials). Values are means ± SE.

3.2. Age-Dependent Growth-Climate Associations

Older trees showed a stronger response to temperature and precipitation than younger ones (Figure 3). Low mean temperatures and high precipitation levels in the previous September (i.e., warm and wet autumns) and high precipitation during the current June enhanced *A. pinsapo* growth in old trees. Younger trees showed a stronger response to wet earlier conditions, responding positively to precipitation in May, rather than in June. The temperature in September in the year prior to ring formation was the most relevant climatic factor limiting the radial growth of old trees, while younger trees had very little influence of prior years' conditions (Figure 3). Old trees were also more negatively correlated with temperatures in the early summer (June). Overall, young trees showed limited influences of temperature on their growth.

Using a weekly scale showed consistent results (Figure 4), although with different correlation coefficients as a function of tree age. Old trees showed significant positive effects of spring and summer precipitations (June and August) and summer radiation (July and August) Young trees' growth was negatively correlated with radiation (June and September), late spring precipitation (June) and mean minimum temperature (August and December).
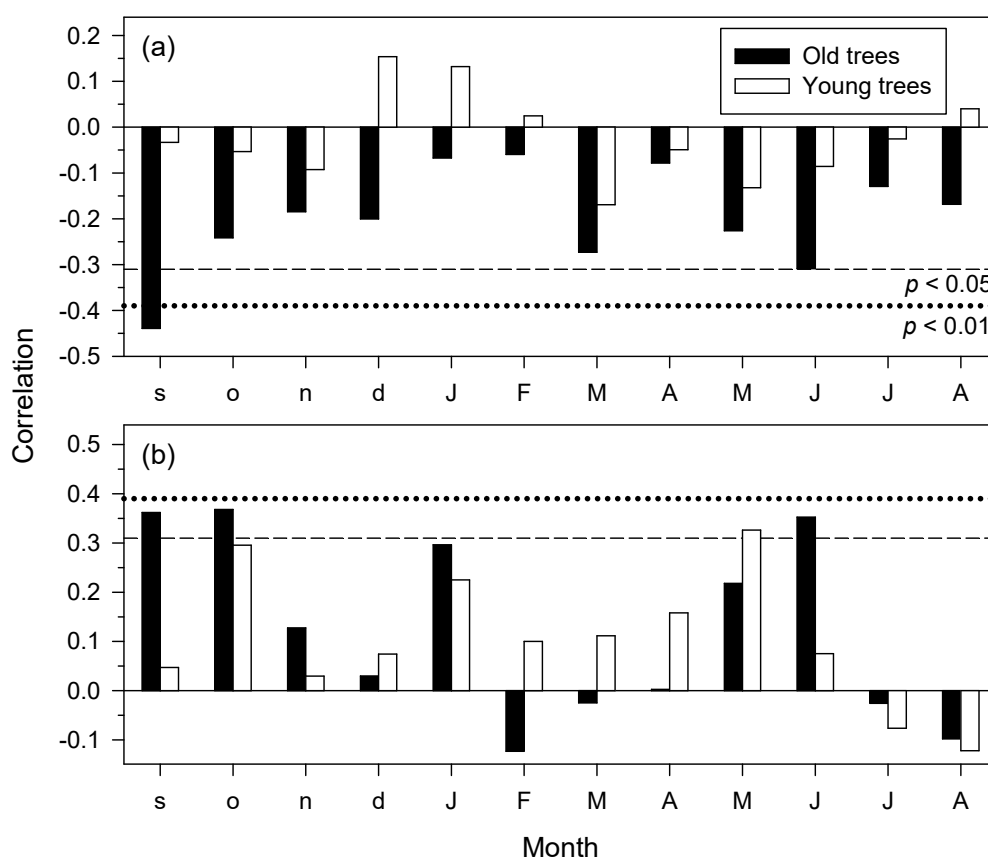
Figure 3. Correlations calculated between the chronologies of old and young trees and (**a**) mean monthly temperatures or (**b**) monthly precipitation. Horizontal dashed and dotted lines show the 0.05 and 0.01 significance levels, respectively. The prior- and current-year months were abbreviated using lowercase and uppercase letters, respectively.
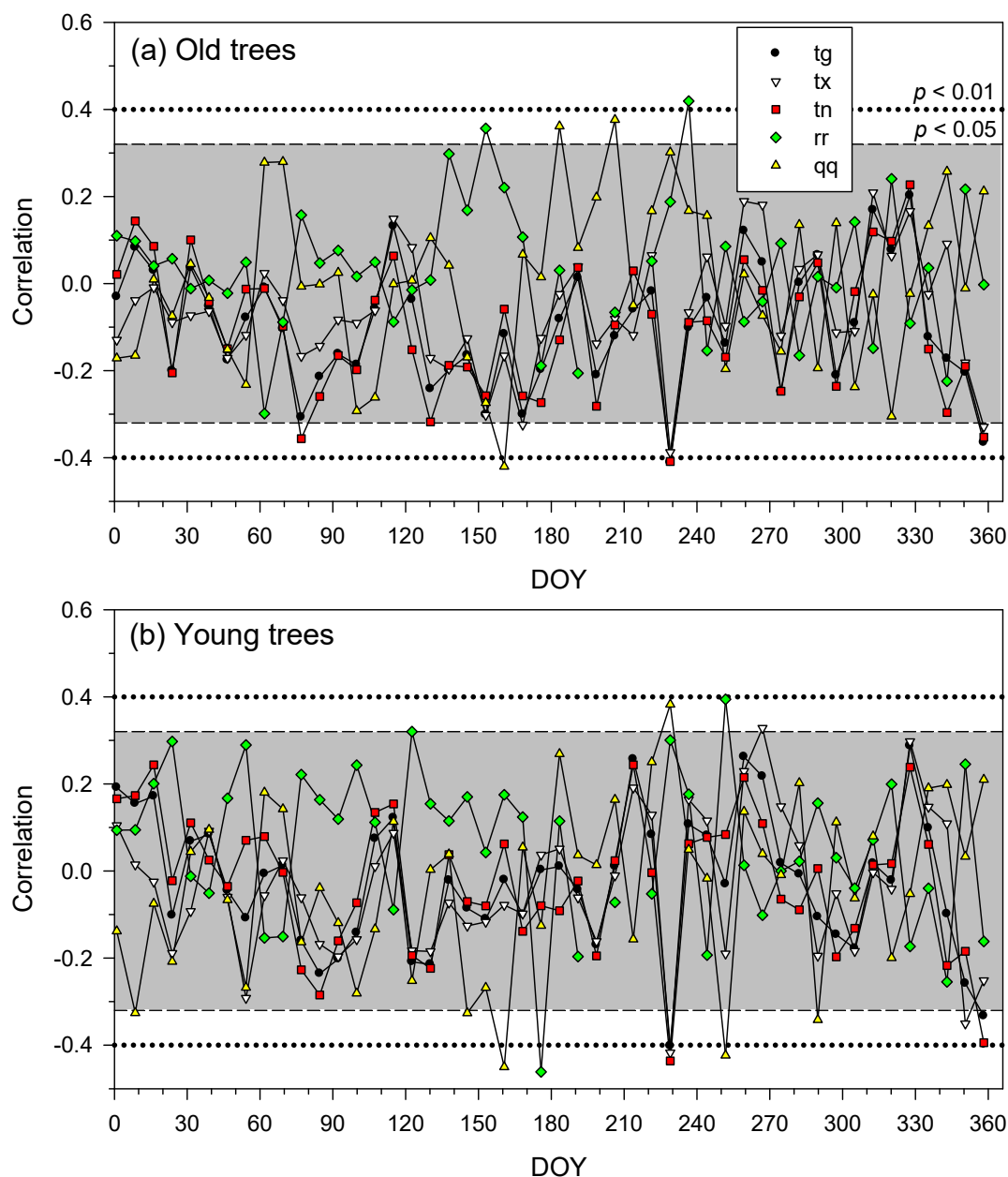
Figure 4. Correlations between the ring width indices of old (**a**) and young (**b**) trees and weekly climate variables (tg, mean temperature; tx, mean maximum temperature; tn, mean minimum temperature; rr, precipitation and qq, radiation) calculated at the weekly scale. The x-axis indicates the day of the year (DOY). Horizontal dashed and dotted lines show the 0.05 and 0.01 significance levels, respectively. Significant values are those located outside the grey area.

The year-to-year variability of ring width indices of old and young *A. pinsapo* trees related to the SPEI drought index was similar (Figure 5), but there were differences between age classes. Old trees showed a higher correlation of growth with SEPI calculated at three months, while young trees responded more strongly to longer drought spells (six months SPEI). In old trees, correlations between weekly SPEI and growth indices peaked in June for three months SPEI and, for July, August and September, in the case of six months SPEI (Figure 5 and Figure S4, Supplementary Materials). In young trees, the highest correlations between weekly SPEI values and growth indices were found for June and July and considered short-term droughts (one- to three-month SPEI). Overall, drought seemed to be a more consistent limiting factor for young trees' growth during the dry season at almost all SPEI resolutions.
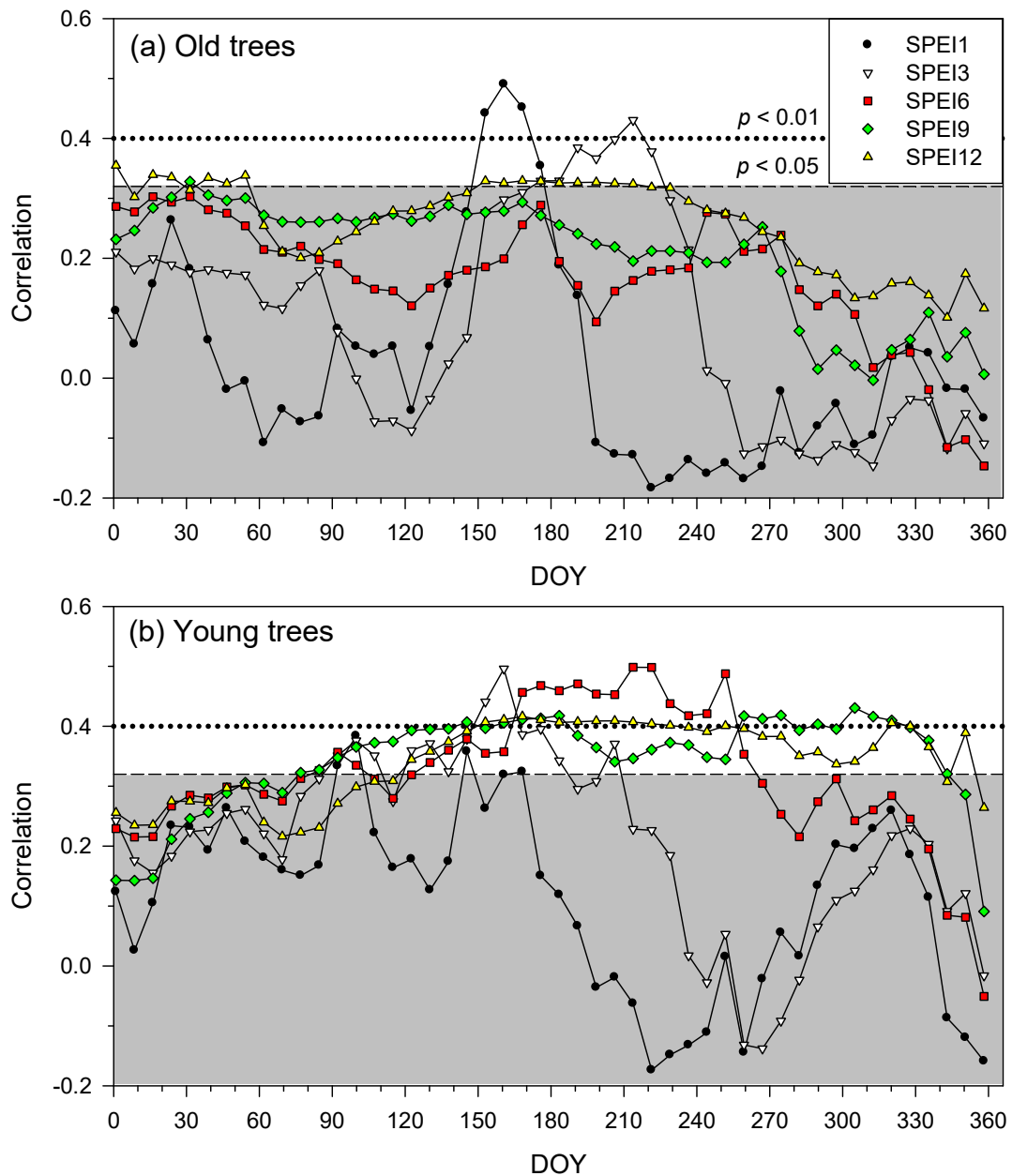
Figure 5. Correlations between the ring width indices of old (**a**) and young (**b**) trees and the weekly Standardized Precipitation-Evapotranspiration Index (SPEI) drought index calculated at 1- (SPEI1), 3- (SPEI3), 6- (SPEI6), 9- (SPEI9) and 12-month (SPEI12) resolutions. The x-axis indicates the day of the year (DOY). Horizontal dashed and dotted lines show the 0.05 and 0.01 significance levels, respectively. Significant values are those located outside the grey area.

3.3. Resilience Indices

Regarding the resilience indices, we found smaller-than-expected differences between old and young trees. Old trees presented higher resistance and lower recovery than young trees in the 1995 drought at both one- and two-year-long intervals, but these differences were not consistent for the 2005 drought (Table 2). Resilience values were not significantly different between old and young trees at any temporal scale or for any of the droughts studied.

Table 2. Resilience indices (Rt, resistance; Rc, recovery and Rs, resilience) calculated for the 1995 and 2005 severe droughts on individual series of standard ring width indices (RWI) or on a series of basal area increments (BAI) for old and young trees. The indices were obtained for 1- and 2-year periods. Values are means ± SE. Different letters indicate significant ($p < 0.05$) differences between old and young trees according to Mann-Whitney tests.

RWI	1995 Drought						2005 Drought					
	Rt		Rc		Rs		Rt		Rc		Rs	
	1 Year	2 Yrs.	1 Year	2 Yrs.	1 Year	2 Yrs.	1 Year	2 Yrs.	1 Year	2 Yrs.	1 Year	2 Yrs.
Old trees	0.76 ± 0.06b	0.74 ± 0.06b	1.38 ± 0.11a	1.47 ± 0.11a	0.92 ± 0.03	0.97 ± 0.04	0.86 ± 0.07	0.80 ± 0.06	1.53 ± 0.07	1.28 ± 0.07	1.25 ± 0.06	1.20 ± 0.07
Young trees	0.52 ± 0.02a	0.50 ± 0.02a	2.58 ± 0.20b	2.49 ± 0.16b	1.03 ± 0.05	0.96 ± 0.03	0.76 ± 0.03	0.78 ± 0.03	1.55 ± 0.04	1.18 ± 0.04	1.15 ± 0.04	1.20 ± 0.04
BAI	1995 Drought						2005 Drought					
	Rt		Rc		Rs		Rt		Rc		Rs	
	1 Year	2 Yrs.	1 Year	2 Yrs.	1 Year	2 Yrs.	1 Year	2 Yrs.	1 Year	2 Yrs.	1 Year	2 Yrs.
Old trees	0.75 ± 0.06b	0.73 ± 0.06b	1.36 ± 0.11a	1.45 ± 0.10a	0.90 ± 0.03	0.95 ± 0.03	0.85 ± 0.07	0.78 ± 0.06	1.49 ± 0.06	1.21 ± 0.07	1.20 ± 0.06	1.12 ± 0.06
Young trees	0.52 ± 0.02a	0.49 ± 0.02a	2.54 ± 0.20b	2.45 ± 0.16b	1.00 ± 0.05	0.94 ± 0.03	0.73 ± 0.03	0.73 ± 0.02	1.53 ± 0.04	1.09 ± 0.03	1.09 ± 0.04	1.09 ± 0.03

3.4. Effects of Growth on Defoliation

The regression analyses between the relative growth rate (RGR_{2007}) and the defoliation in 2017 (D_{2017}) showed that defoliation increased linearly with RGR_{2007} for both age groups and followed a positive linear relationship (Figure 6). Considering age as a factor, defoliation was significantly different between young and old trees ($t = 8.154$, $p = 0.009$) but not the RGR ($t = 0.251$, $p = 0.622$). In old trees, the R^2 value was higher (0.72) than considered young trees (0.41). However, the relationship between growth and defoliation was stronger for younger than older trees.
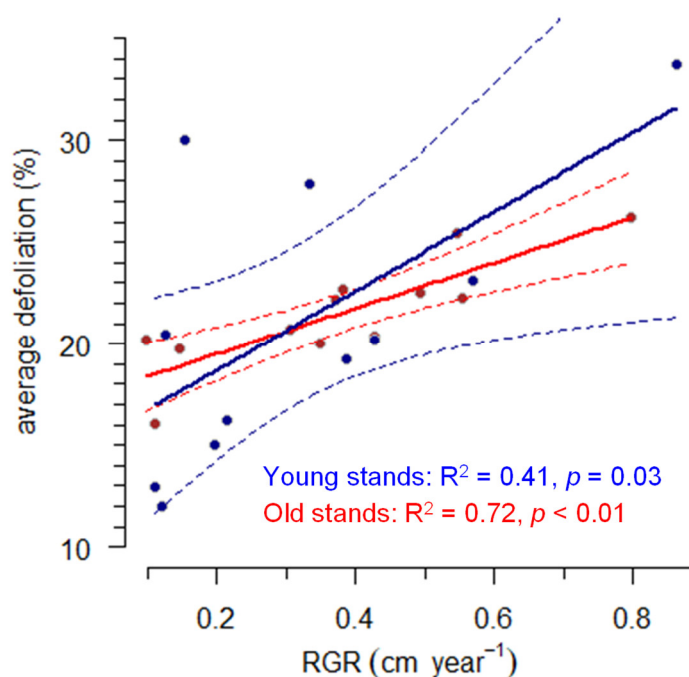

Figure 6. Lineal regression between the relative growth rate (RGR, calculated for the period 2001–2007) and average defoliation in 2017 of young (blue lines and symbols) and old (red lines and symbols) *Abies pinsapo* trees. The dashed lines show the 95% prediction intervals.

4. Discussion

The dendroclimatic potential of *A. pinsapo* to detect the effects of climatic conditions on growth has been illustrated before, albeit usually using a limited number of sites and samples [15–18]. We fill this gap by comparing the climate-growth associations using dendrochronological data from a systematic ICP forest network of *A. pinsapo* and including the potential different responses between old and younger individuals. Thus, this study represents a novel dendrochronological approach to growth variations of *A. pinsapo* across a climatic gradient and the relationships between growth and climate at the southern endemic geographical distribution in the Western Mediterranean Basin. We found marked differences in growth responses between young and old trees. Further, we explored the linkages between defoliation and secondary growth, two proxies that have been proposed for monitoring forest health and the impact of climate change. We found delayed impacts of growth on defoliation, pointing to the potential of tree ring growth to anticipate the impacts of climate warming on forest health, thus reinforcing the idea of using dendrochronological tools for the identification of early warning signals to better manage and conserve climate change vulnerable forests.

4.1. Growth and Climatic Response

Descriptive statistics of the *A. pinsapo* series agreed with previous studies on *A. pinsapo* [15,16,34]. We found, however, clear significant growth differences related to tree age. As expected, old trees had lower growths than younger ones, although this difference has decreased in the last decades. We did find clear similarities in the variability of the standard chronologies of old and young trees, which is consistent with the strong climate limitation on tree ring growth across tree developmental stages observed in other Mediterranean species [35–37]. However, the clear decrease in growth in the older trees in comparison with the rather stable growth trends of younger trees indicated similar drought-induced sensitivity during the last decades, when *A. pinsapo* experienced a decrease on the annual TRW growth. The growth decrease during this recent period coincided with increasing drought anomalies, i.e., increasingly dry conditions [38] that may lead to the local extinction of *A. pinsapo* from part of its current distribution and its substitution by more tolerant species [39].

A. pinsapo growth seems to benefit from warm and wet autumn conditions in the previous year, and high precipitation in the late spring of the current year, while high temperatures in the early summer were associated with reduced tree growth. This supports previous dendroclimatological studies on nearby *A. pinsapo* populations [15–17]. However, we show here that these factors have different importances between trees developmental stages, suggesting that old trees are substantially more limited by temperature conditions than young trees [36]. Young trees were sensitive to earlier growing season conditions. Spring conditions are particularly important for Mediterranean mountain conifers, as it many times strongly influences the length of the growing season and, consequently, tree ring width [35,40]. Consequently, wet and mild conditions in the spring may increase the production of earlywood and hydraulic conductivity [40]. These findings confirm that a water supply during the spring season is crucial for tree growth at low elevations. Previous autumn precipitation also seems to be an important factor; likely, it can contribute to replenishing the soil water, promoting early spring growth. By contrast, warm and dry late autumns can reduce the accumulation of carbohydrate reserves by limiting photosynthesis through drought stress, increasing the respiration rate and diverting energy reserves to the current year growth [40].

Contrary to our expectations, we found no strong radial growth response to summer precipitation. Dry summer conditions are generally considered the most limiting climatic factor on tree growth in Mediterranean coniferous species [38]. We did detect an increasing sensitivity of younger *A. pinsapo* trees to drought stress (SPDI), showing that growth-climate associations were age-dependent in this species, as has been previously discussed for other species [41]. Young trees have a less well-established fine root system, resulting in a reduction of available water than old trees, which is critically linked to the drought susceptibility of trees [42]. Age differences may also be explained by physiological differences in the susceptibility of young and old trees to extreme climatic events (e.g., leaf age, root dieback, xylem cavitation, reduced leaf photosynthetic capacity

and changes in carbon allocation patterns [42–44]), which may provide a comparative advantage for old trees.

4.2. Climate Response Indices

Old and young trees only showed significant differences in their resilience components for the 1995 drought, when old trees presented higher Rt values and lower Rc values than young trees. Our results suggest that age does not play an important role on the growth responses to the extreme drought of *A. pinsapo* [45]. This agrees with previous studies showing that *A. pinsapo* sensitivity to drought is modulated by other physiological features besides age, which makes this species more vulnerable and less resilient in response to drought-induced stress than other Mediterranean coniferous species [15]. This susceptibility to drought is consistent with the well-documented recent decline of growth in this species and the often-abrupt mortality events after severe droughts (e.g., 1995, 1999, 2005 and 2012) [46].

Additionally, the downward trend of the resistance (Rt) and resilience (Rs) in young and old trees is a relevant finding; it indicates a cumulative effect of droughts on their capacity to respond to consecutive droughts. Increasing the sensitivity of *A. pinsapo* stands to drought may suggest that they will become increasingly vulnerable to drought-triggered tree mortality in the coming decades [18,39].

4.3. Effects of Growth on Defoliation

Defoliation was correlated with previous relative growths in young and old trees, although it was stronger for the last age group. Previous studies on drought-induced defoliation have frequently found an inverse relationship between active growth and sensitivity to drought impact [47,48]. However, a positive relationship between growth and defoliation is less commonly encountered, in concordance with other studies showing higher growth rates for declining prior to drought occurrence [49]. *A. pinsapo* is considered a drought-avoiding tree species that may adapt to droughts by diverse physiological responses (e.g., rapid stomatal closures with relatively high values of soil water contents [46]. The current situation of an increasing winter temperature may be causing an increase of winter growth due to the higher photosynthetic rate of *A. pinsapo* [50]. This winter growth expansion may not be maintained during the increasingly hot and dry summers, which leads to an imbalance between higher winter growths and a higher risk of suffering drought stress—and, therefore, the defoliation of drought-sensitive *A. pinsapo*—during the summer. This paradox of the "mediocre forest" where low growth trees may better survive extreme climate events has already been proposed for other species [49]. Our findings indicate that *A. pinsapo* trees showing higher radial growths also tend to have a lower capacity to withstand drought and may be more likely to die. Consequently, under the expected climate scenario, this unbalance between winter expansion growth and summer increasing temperature and declining water availability may exacerbate the defoliation and mortality of *A. pinsapo*.

4.4. Management Implications on A. pinsapo Conservation

Climate changes will impact the endemic *A. pinsapo* forests in Southern Spain, but still, the effect is not clear in the middle term. A positive correlation between growth variation and defoliation was evident in the growth data obtained in a specific forest health network (ICP Pinsapo Network). Therefore, the implementation of these types of networks and long-term assessments may play a critical role on forest ecosystem protections in European forests under high climatic risks. However, one can expect different growth responses along the environmental, silvicultural and age gradients. Although the use of defoliation to detect tree dysfunction has been under question [11], our results indicate a high predictive capacity of growth and defoliation data from the ICP Pinsapo Network. Improving the feasibility and consistency in the ICP monitoring networks will enhance their capacity to anticipate severe defoliation and mortality events [50,51].

5. Conclusions

We compared tree ring width chronology characteristics and climate–growth responses of *A. pinsapo* along a climatic gradient in the endemic populations of Southern Spain. Our results indicate that tree age affects the growth trends of *A. pinsapo* trees in Sierra de las Nieves. In general, the climate–growth relationships found for *A. pinsapo* resemble the growth patterns found in other populations of this species and other conifers at the Mediterranean mountains. *A. pinsapo* growth is enhanced primarily by warm and wet autumn conditions in the previous year and high precipitation during the current and later spring in old and young trees. Young trees showed to be more sensible to limited spring moisture and droughts. In the study area, radial growth has been decreasing significantly since the 1980s, and tree growth anomalies as a response to severe drought are evident. Under the current warming trend, *A. pinsapo* populations may be impacted from increasing temperatures and precipitation reductions in the south limit of the Iberian Mountains, which may threaten some of these stands, triggering dieback and widespread mortality. A way to forecast drought-induced growth decline in *A. pinsapo* is the reinforcement of the ICP Pinsapo Network to compare populations growing under the whole climatic gradient in the species distribution area. Additionally, the study of the buffer effect of the site-specific variables (slope, aspect, soil types, tree density, management, etc.) may help to understand the negative effects of drought on growth and help to prevent severe mortality episodes in *A. pinsapo* forests. Growth indices may be useful for the early detection of forest dieback in *A. pinsapo* forests that need to be analyzed at the local scale. More research is needed incorporating species-specific climate–growth reactions to assess growth patterns to clarify the biogeographic responses of this endemic species on the more vulnerable refuge areas and to refine silvicultural alternatives to contribute to stand acclimations to the regional impacts of climate changes in Mediterranean fir forests.

Supplementary Materials: The following are available online at www.mdpi.com/1999-4907/11/9/1002/s1: Figure S1. Climate variables obtained at weekly resolutions for the study area, including (a) mean maximum and minimum temperatures, (b) precipitation and (c) radiation. Figure S2. Raw tree ring chronologies and ring width index of the *Abies pinsapo* in Sierra de las Nieves (South Spain). Figure S3. Comparison of the standard (STD) and residual (RES) indexed ring width chronologies of old (a) and young (b) trees considering the best-replicated period (1970–2007). The bars show the differences (right y-axes) between the STD and RES chronologies (STD-RES). Figure S4. Mean series of residual ring width indices (chronologies) of old and young trees and 3- (SPEI3) and 6-month SPEI (SPEI6) drought indices for the first week of August. These two scales of the SPEI gave the highest mean correlations with old (SPEI3, r = 0.43) and young (SPEI6, r = 0.50) trees, respectively. Table S1. Site descriptions and characteristics of selected stands. Alt: altitude above sea level and H and DBH: tree height and diameter at breast height, mean values (±SD).

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