ORIGINAL ARTICLE

Age-related tree-ring sensitivity at the dry forest-steppe boundary in northwestern Patagonia

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Abstract

Key message **The association between growth and climate in the forests of *Austrocedrus chilensis* placed at the forest-steppe ecotone was found to be age dependent, with ring widths from the oldest trees providing a better expression of climate variability.**

Abstract Over the course of their lives, trees may undergo changes in sensitivity to climate during their ontogenetic development, i.e., from seedling to maturity. Identifying these age-dependent responses is relevant to minimize under or over estimations of the climatic signal in dendroclimatic reconstructions. It also provides important clues in predicting the reactions of different age-class trees to ongoing climate changes. In this context, the main goal of this study was to determine the sensitivity of radial growth of *Austrocedrus chilensis* (Ciprés de la Cordillera) to climate variability as a function of tree age. Wood cores from 90 trees growing in the forest-steppe ecotone of northwestern Patagonia in Argentina, were sampled. By analyzing their growth rings, trees were classified in two age classes: young (< 93 years) and mature (≥ 93 years). Pearson's and moving correlations revealed that spring-early-summer total precipitation positively correlated with growth regardless of age, particularly during the previous growing season. Mean temperature and standardized precipitation-evapotranspiration index (SPEI-1 month), however, showed a stronger association with the growth of mature trees than with young trees, especially in relation to the previous growing season. The moving correlation analysis showed, moreover, that the associations between climatic variables and radial growth of *A. chilensis* varied between age classes during the last century. The obtained results could help to improve our understanding of the ecology of *A. chilensis* and provide a better interpretation of how Patagonian forests could be influenced by climate change processes.

Keywords *Austrocedrus chilensis* · Age class · Climate sensitivity · Tree growth-climate response · Forest ecology

Introduction

During their ontogeny, trees undergo changes in their structure and interactions with the environment, e.g., photosynthetic rates, hydraulic resistance, competition for resources, timing and duration of xylogenesis (Fritts 1976; Rossi et al.

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2007; Yu et al. 2008). In a climate change context (IPCC 2018), the projected increase in physiological stresses affecting forests may well impact their reproductive performance and yield, particularly for those tree species that reach old ages and acclimatize more slowly to severe environmental changes (e.g., Lindner et al. 2010; Allen et al. 2015; Anderegg et al. 2019; Arco Molina et al. 2019). Therefore, it is relevant to inquire about the age-dependent sensitivity of trees to climate, as relationships that provide clues about how ongoing climatic changes can distinctly affect the growth of both young and mature trees (Primicia et al. 2015). In dendrochronology, it is usually assumed that the relationship between radial growth and climate is not tree-age dependent (Linderholm and Linderholm 2004). However, the existence of such a dependency (age-climate interaction) may lead to uncertainties in climate-reconstruction models. The risk of under- or over estimating the climatic signal in dendroclimatology could vary according to tree species and ecological conditions of the site. Therefore, it is relevant to establish whether the response to climate varies with tree age to avoid sampling biases in the development of tree-ring chronologies for climatic reconstructions (Bunn et al. 2011).

Dendroclimatic studies explore the characteristics of the climatic information contained in tree rings. This knowledge, in turn, may inform sampling strategies and subsequent development of models when aiming to reconstruct the long-term climate history (Esper et al. 2002; D'Arrigo and Wilson 2006). Some dendrochronological studies have indicated that the climatic signal is similar between the age classes of certain tree species (Wilson and Elling 2004; Esper et al. 2008; Liñán et al. 2012). However, numerous studies have reported diverse responses of tree growth to climate (temperature and precipitation), evidencing cases in which trees experience greater sensitivity to climate with increasing age (Szeicz and McDonald 1994; Yu et al. 2008; Copenheaver et al. 2011; Wang et al. 2011; Jiao et al. 2017; Peng et al. 2018), or when they are young (Rozas et al. 2009; Vieira et al. 2009; Wu et al. 2013; Hadad et al. 2015; Pompa-Garcia and Hadad 2016; Sanchez Salguero et al. 2018). Therefore, knowledge of how climate sensitivity is related to tree age becomes relevant in a context of climate change, with its potential impacts on tree physiology (Rahman et al. 2018). In recent decades, northwestern (NW) Patagonia has experienced a sustained decline in precipitation and an increase in air temperature (Pessacg et al. 2020). In the central Andes a persistent drought has occurred from year to year, i.e., during the last ten years (Garreaud et al. 2019; Muñoz et al. 2020), which has been linked to both natural and anthropogenic factors (Cai et al. 2014; Boisier et al. 2016). This long-term drought has strongly affected the growth of forests in these mid-latitudes of South America (Morales et al. 2020; Matskovsky et al. 2021). This phenomenon has also

been evidenced when comparing tree-ring chronologies with the Standardized Precipitation Evapotranspiration Index (SPEI) for species from South America (Serrano-Notivoli et al. 2020; Hadad et al. 2021). SPEI is a multiscalar drought index based on climatic data, which allows detection, monitoring, and analysis of drought events (Vicente-Serrano et al. 2010). Positive values of SPEI correspond to humid conditions, while negative values indicate drought (Vicente-Serrano et al. 2010). Many tree-ring studies have used the SPEI to determine the impact of extreme droughts on tree growth (e.g. Kurz-Besson et al. 2016; Bhandari et al. 2019; Hadad et al. 2022).

A tree species widely used as a climate proxy in NW Patagonia is *Austrocedrus chilensis* (D. Don) Pic. Serm. & Bizzarri, commonly known as Ciprés de la Cordillera (Schulman 1956; Villalba et al. 1998; Roig and Villalba 2008). Previous dendrochronological studies showed that radial growth of *A. chilensis* is negatively correlated with temperature and positively with precipitation, particularly during the austral growing season (Villalba and Veblen 1996; Villalba et al. 1998; Le Quesne et al. 2006; Mundo et al. 2010; Muñoz et al. 2016). Furthermore, *A. chilensis* tree-ring chronologies have been used to reconstruct past climate variability on the eastern and western flanks of the Andes (Le Quesne et al. 2006; Christie et al. 2011; Morales et al. 2020; Serrano-Notivoli et al. 2020; Hadad et al. 2021). However, the possible influence of tree age on the climatic signal contained in *A. chilensis* tree rings has not been explored so far.

Based on the above-mentioned information, the main objective of this study was to identify possible differences in the intensity of tree-ring climate sensitivity with respect to the age of trees growing in xeric sites in NW Patagonia, Argentina. To complete this objective, wood samples were collected from both young and mature trees and their respective tree-ring chronologies compared with climatic variables and the multiscalar SPEI. We hypothesized that the sensitivity of radial growth to climate varies as a function of age in *A. chilensis* trees, and that it is higher in old trees.

Materials and methods

Study area and tree-ring sampling

Two *A. chilensis* monospecific and open forest stands were selected for this study (Fig. 1A, C, D). These sites are referred to as Río Traful (RTN) and Estancia Pilcaniyeu (EPL), which are separated by 73 km. Both stands are located at the eastern and driest edge of the species' natural range in the Argentina Patagonia. These forests are found at relatively low elevations and are mainly associated with well-drained soils and rocky outcrops, conditions that
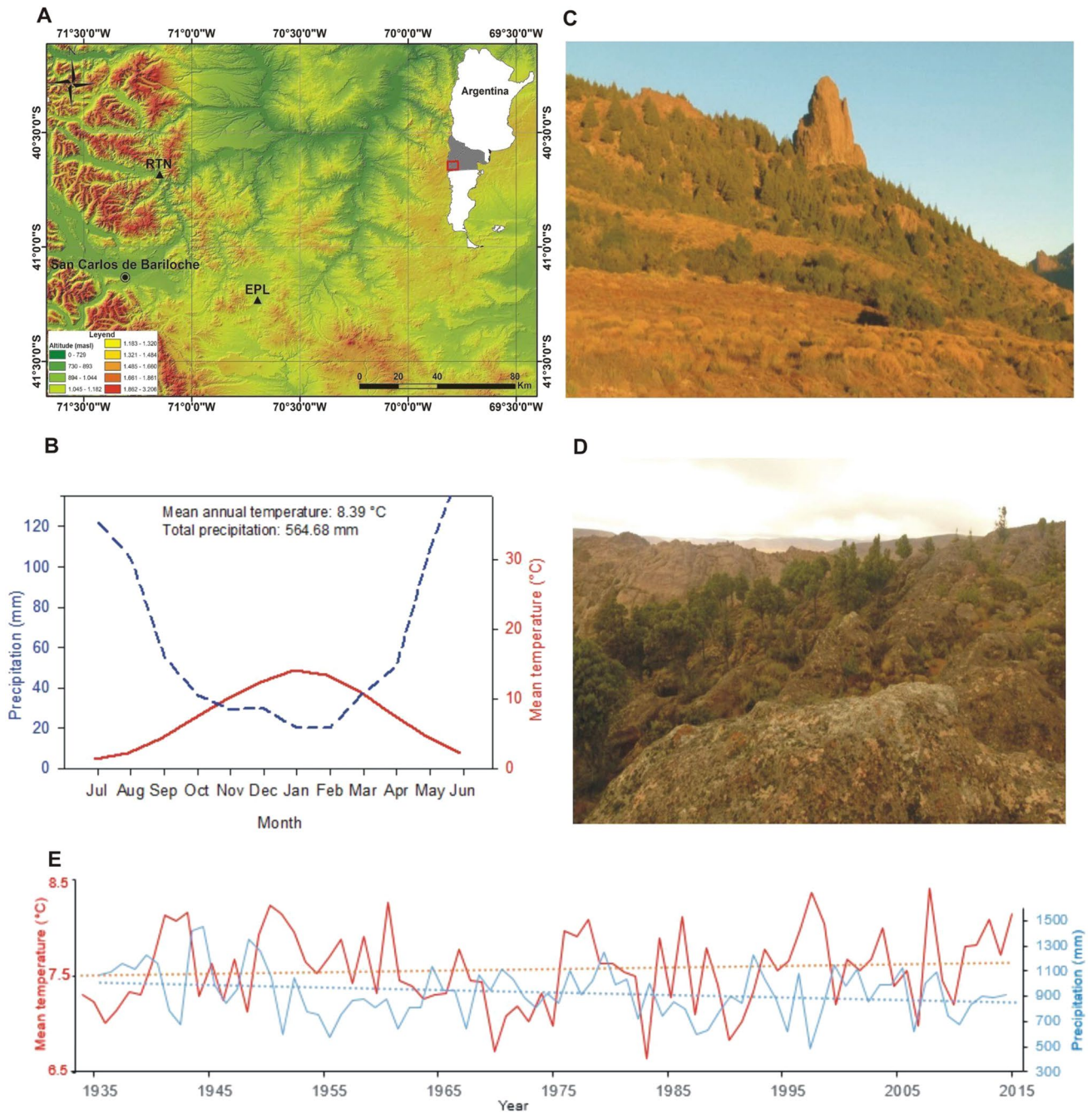
Fig. 1 A Location of the two study sites (triangles) in NW Patagonia, Argentina RTN, Río Traful (40° 41″ S, 71° 09″ W; 752 m a.s.l); EPL, Estancia Pilcaniyeu (41° 14″ S, 70° 41″ W; 1141 m a.s.l); **B** the Walter and Lieth climate diagram shows the behavior of temperature (solid red line) and precipitation (dashed blue line) in the study area for the period 1901–2015. **C, D** Show the *Austrocedrus chilensis* for-est landscapes at the RTN and EPL sites, respectively. **E** Long-term trends in annual mean temperature and annual total precipitation in the study region. Figures **B** and **E** were constructed with meteorological reanalysis data available at the database of the Royal Netherlands Meteorological Institute (KNMI) Climate Explorer (http://www.knmi.nl) with spatial resolution of 0.5° × 0.5° grid

increase the species' dependence on water availability (Roig and Villalba 2008; Hadad et al. 2021). Climate in this region is strongly modulated by the dynamics established between the atmosphere-Pacific Ocean interactions at different latitudes in the Southern Hemisphere (Miller 1976; Garreaud et al. 2009). This interaction is the source of westerly moisture-rich winds whose flow intensity is closely linked to the north–south latitudinal displacement of the South Pacific subtropical anticyclone throughout the year (Taljaard 1967; Saavedra and Foppiano 1992; Roig and Villalba 2008). The
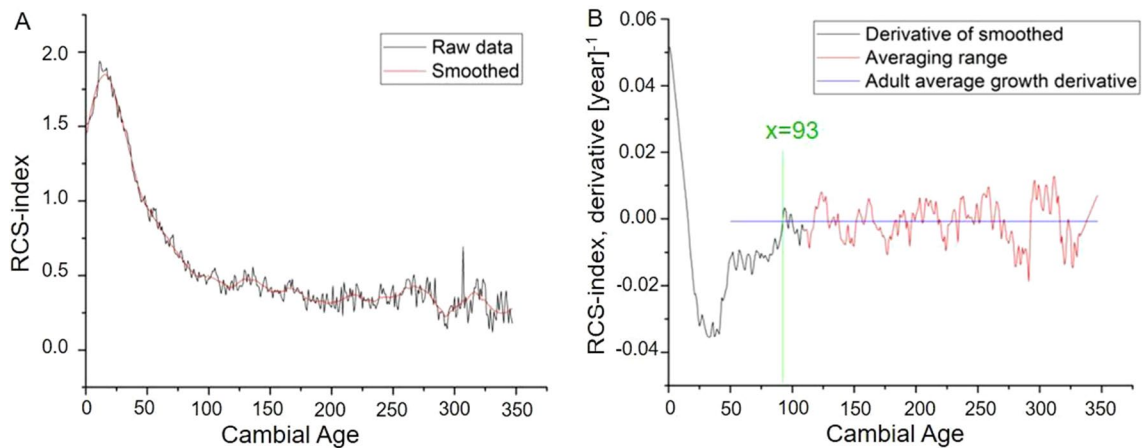
Fig. 2 **A** RCS-version chronology as a function of the aligned cambial age, referenced to actual or estimated pith dates for each tree core. The red line indicates the smoothed RCS curve. **B** Numerical derivative of the smoothed RCS curve. The transition point from young to mature wood (vertical green line) was defined as the point where drcs/dBA = 0, with upward slope

transit of these moisture-laden westerlies leads to most of the precipitation falling principally in winter, while a negative water balance occurs in summer, resulting in a Mediterranean-type climate (diCastri and Hajek 1976).

However, largely due to the massive Andes mountain range, precipitation experiences an extraordinary west-to-east gradient from > 2000 mm/year on the top of the Andes to ~ 600 mm/year towards the forest-steppe ecotone where our study sites are located (Hadad et al. 2020). Figure 1B summarizes the climate conditions for a grid sector between 40°–42′ S and 71.5°–70.5′ W, which includes the studied forest stands.

Sampling was carried out in April 2016 and included trees of different diameter classes (Fig. 1C, D). Two to three wood cores per tree were extracted at breast height (ca. 1.3 m above ground level) by means of a 5-mm-diameter increment borer.

Sample preparation, tree-ring measurement and age-class definition

In the laboratory, wood samples were mounted and polished following standard dendrochronological methods (Stokes and Smiley 1968). First, wood cores were visually crossdated with the help of a stereo microscope, and the dated ring widths were measured at a precision of 0.001 mm using a measuring table device (Velmex USA). After measurements, a statistical validation of both dating and measurement quality was performed using correlation analysis with the COFECHA software (version 6.06P; Holmes 1983). In total, 51 trees (108 series) from the RTN site and 39 trees (89 series) from the EPL site were measured and their dating validated by the mentioned crossdating function. All together, 31 of the 90 trees reached the pith. For cores that

did not reach the pith, the number of missing rings was estimated using the internal arcs to the pith i.e., following the geometrical method described by Duncan (1989). The estimated number of tree rings to the pith ranged between 5 and 10 years.

The radial growth of trees often follows a negative exponential curve where the width of the rings decreases as the tree ages (Fritts 1976), as exemplified in Fig. 2A. This inverse relationship between time and ring widths allowed us to identify a phase of higher growth, the young stage, from an older stage in which radial growth increments are comparatively smaller. We took advantage of this difference to define both young and mature age classes. To establish a mathematical criterion to identify these two growth phases, the derived Regional Curve Standardization index (RCS) (cubic spline function on a 60-year wavelength) (Helama et al. 2016) was obtained from the R package 'dplR' (Bunn et al. 2019) (see below in "Chronology development" section). The curve was first smoothed and then the first derivative was calculated with respect to cambial age (drcs/dBA). The point of transition was defined as the point where drcs/dBA = 0 (Fig. 2), which allowed the designation of the two age categories: young trees (< 93 years) and mature trees (≥ 93 years).

Chronology development

To evaluate the relationship between annual tree growth and climate, tree-ring data were detrended by curve-fitting procedures to remove portions of the variance associated with factors other than climate. The individual raw ring-width series were detrended using a smoothing cubic spline function with a 50% frequency cutoff on a 60-year wavelength using the R package 'dplR' (Bunn et al. 2019). The same spline function

was used to standardize both young and mature trees to avoid creating detrending-related biases. To reduce the influence of outliers in developing the chronologies, a biweight robust estimate of the mean was applied and the standard chronology was selected from the R package 'dplR' output. Several descriptive statistics were used to compare the two age-class standard chronologies. The quality of each chronology was evaluated in reference to the mean sensitivity (MS), standard deviation, mean correlation between tree-ring series (Rbar) and the expressed population signal (EPS) (Fritts 1976; Cook 1985). Rbar is an expression of the percentage variance in common. Rbar may vary in time as a consequence of changes of the signal strength, which in turn may be caused by differences in the sample size. The EPS statistic (Wigley et al. 1984) is estimated to assess how well a finite sample chronology compares with the theoretical population chronology based on an infinite number of trees. EPS strongly depends on the number of trees used in the construction of the mean chronology. We decided to analyze the common period 1936–2015 because this period comprises more than 19 series of each of the young and mature trees resulting in an EPS value > 0.85 for each chronology, the level of which indicates sufficient coherence of growth patterns within the site for robust climate inferences.

Climate data and statistical analysis

Mean monthly temperature (°C), total monthly precipitation (mm) and monthly SPEI-1 (Standardized Precipitation-Evapotranspiration Index) data for the period 1936–2015 were obtained from the Climatic Research Unit (CRU TS 4.01; Harris et al. 2020) using a gridded dataset (0.5° × 0.5° spatial resolution) provided by the Royal Netherlands Meteorological Institute (KNMI) Climate Explorer (http://www.knmi.nl; Trouet and van Oldenborgh 2013). The data come from six meteorological stations, ca. 200 km apart on average. The data corresponded to the grid point within 40°–42° and 71.5°–70.5° W, i.e. the closest coordinate to our study sites. The influence of climate on the tree-ring chronologies was assessed by Pearson's correlation analysis (Blasing et al. 1984). The possible influence of previous climate conditions on current growth was revealed by including the months previous to the growing season. This resulted in a correlation structure that spanned 21 months, from September of the previous growth period to May of the current growth period.

Based on the result of the correlation analyses, a Generalized Linear Mixed Model (GLMM; $p < 0.05$) was applied to analyze the effect of the age classes and climatic variables (total precipitation and mean temperature from November to March, and SPEI-1 from November to February of the previous and current growth period) on tree growth. The standard chronology was considered as the response variable, the two age classes as the fixed factor and the climatic variables as the numeric variables of fixed effect. The ring-width measurements and the sites were treated as random factors. Each GLMM was developed using the "lme4" package (Bates et al. 2019) in R software (R Development Core Team 2018). We first analyzed a full model taking into consideration all main effects and their double interactions; then we simplified it to obtain a minimal fitted model, evaluating the change in the value of deviance through a Chi-square test ($p < 0.05$) (Crawley 2013). The significance of fixed effects was evaluated using an F test type III deviance analysis, based on the "car" package (Fox et al. 2021). We analyzed the climatic variables in different models to comply with the absence of collinearity.

To study the temporal dynamics between the climatic variables and the age-class chronologies, moving correlations were performed based on 20-year windows lagged by 5 years. Additionally, the spatial correlation between the growth of *A. chilensis* and the mean temperature, total precipitation and SPEI-1 month were calculated with KNMI Climate Explorer tools (Trouet and van Oldenborgh 2013; http://climexp.knmi.nl/) for the period 1936–2015. The R Development Core Team (2018) software (packages: rcpp and treeclim) was used to calculate Pearson's linear correlations and moving correlations.

Results

Chronology characteristics

A total of 90 trees (44 young and 46 mature) were analyzed in this study. The series of young and mature individuals from the different sites were gathered into two groups with the objective of constructing regional chronologies by age range. This contributed to strengthening the replication of trees by age category and to increase the common signal in the chronologies ($r = 0.65$, $N = 92$ cores, $p < 0.05$ and $r = 0.72$, $N = 105$ cores, $p < 0.05$ for young and mature trees, respectively). The time span of the standard chronologies extended from 1924 to 2015 and from 1669 to 2015 for the young and mature trees, respectively (Table 1; Fig. 3). Over the common period 1936–2015, the mean ring width and the mean sensitivity were slightly higher in mature trees than in the young ones. The standard deviation was similar for mature and young trees and the mean Rbar was similar for both age classes (Table 1). Both chronologies showed EPS values above the threshold value of 0.85 over the common period 1936–2015 (Fig. 3).

Dendroclimatic modeling

The associations between radial growth and climate for the common period 1936–2015 indicated that trees from

Table 1 Descriptive statistics for standard *Austrocedrus chilensis* tree-ring chronologies according to age classes

Characteristics	Young (< 93 year old)	Mature (≥ 93 year old)
Chronology extension	1924–2015	1669–2015
Analyzed time span	1936–2015	1936–2015
Trees (cores)	44 (92)	46 (105)
Mean ring width (mm)[a]	0.952	0.983
Standard deviation[a]	0.191	0.193
Mean sensitivity[a]	0.155	0.161
Mean Rbar[b]	0.321	0.325
Mean EPS[b]	0.966	0.931

Data were extracted from the output of the COFECHA ([a]) and R package 'dplR' ([b]) software environment

both age classes exhibited essentially the same response to climate variability (Fig. 4). Overall, the influence of total precipitation on growth of the two age classes was positive and significant ($p < 0.05$) for November and December of the current growing season. During the previous year, the correlation with precipitation was positive and significant for the months of November and March for both age classes (Fig. 4A). Negative correlations with summer mean temperature were widespread, particularly for the spring-summer season (more months), covering the months from

November to February, regardless of whether it is the previous or the current year (Fig. 4B). This finding was observed for both age classes. For many of the aforementioned associations, however, differences were observed between age classes, as evidenced by the correlation level and the number of months showing significant correlations. Particularly, for previous (December and January) summer months, the correlations between mean temperature and the chronologies were, on average, slightly higher (mature: mean $= -0.255$, std $= 0.007$ and young: mean $= -0.178$, std $= 0.039$) and significant in a greater number of summer months in mature trees than in younger trees (Fig. 4B). Both age classes showed positive and significant ($p < 0.05$) correlations with the SPEI-1 for the current growing season for the months of November to January (Fig. 4C). However, the months from November to February of the previous growing season were found to be more sensitive in mature trees than in younger trees, as indicated by the higher correlation strength. Only the SPEI-1 value in February was significant ($p < 0.05$) with young trees (Fig. 4C).

The different sensitivity of age classes to climate was corroborated with the GLMMs analysis (Table 2). In general, radial growth was similar between the young and mature classes ($X^2 = 0.9253$; $p = 0.34$). We observed that total precipitation in the prior and current growing seasons (from November to March) had a positive influence on radial growth. The mean temperature in the prior growing season had a negative influence. Likewise, these variables had a

Fig. 3 The developed *Austrocedrus chilensis* tree-ring standard chronologies (black line curve) and the number of samples analyzed (gray area) of young (< 93 years) (**A**) and mature (≥ 93 years) (**B**) trees, respectively. A 10-year cubic smoothing spline (red line curve) is shown to highlight the multidecadal variability in each chronology. The periods with EPS values greater than 0.85 are indicated by the green line and the RBAR values by the blue line
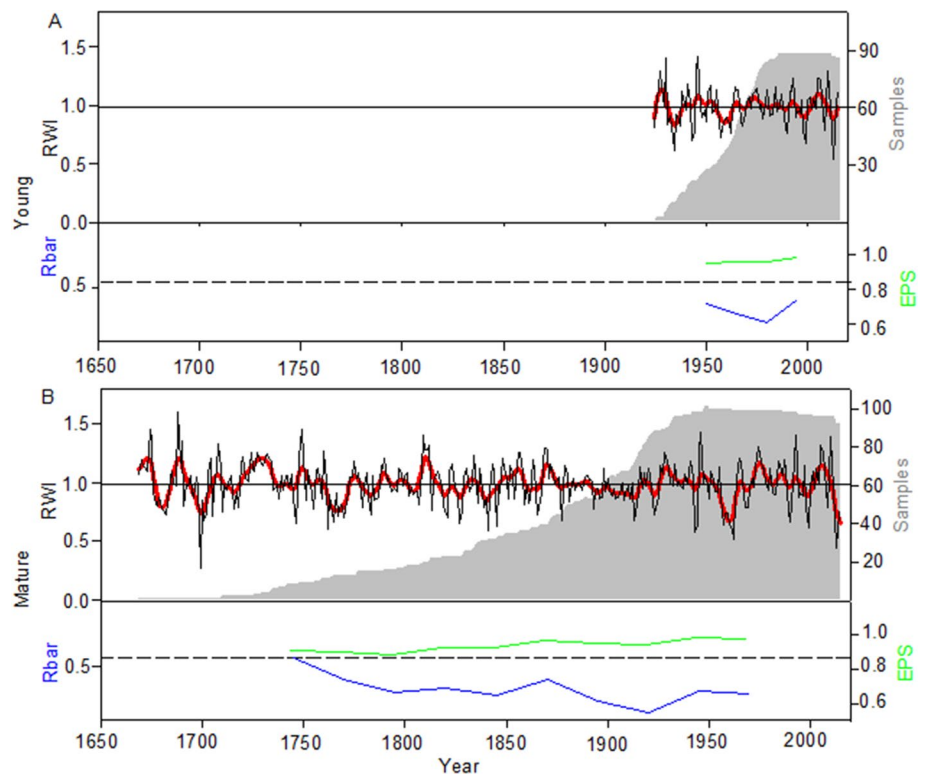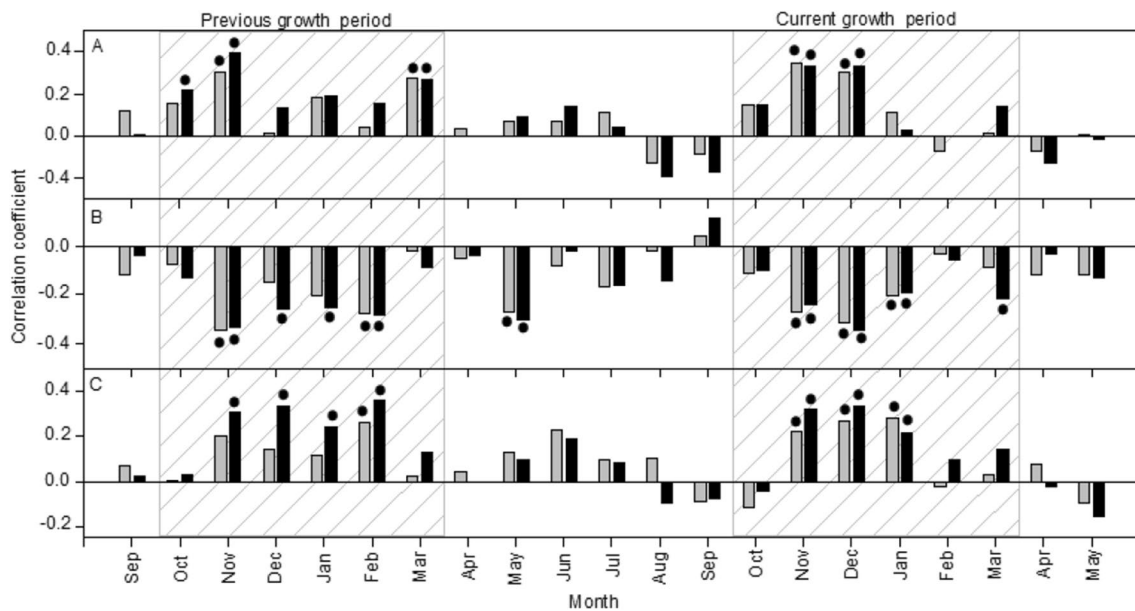
Fig. 4 Pearson's correlation coefficients resulting from comparing tree-ring standard chronologies of *Austrocedrus chilensis* with total precipitation (**A**), mean temperature (**B**) and SPEI-1 (**C**) for the period 1936–2015 and for both age classes. Black bars represent the mature trees (≥ 93 years) while gray ones correspond to young trees (< 93 years). Black circles indicate significant correlations ($p < 0.05$). The cross-hatched area represents the set of a priori defined months when the start and end of the active vegetative development occurs (including current and previous growing seasons, respectively)

Table 2 Analysis of deviance (*F* test type III; $p < 0.05$) of the models fitted (GLMMs; $p < 0.05$) to evaluate the effect of age classes and climatic variables (total precipitation and mean temperature from November to March and SPEI-1 from November to February of the previous and current growth period) on radial growth (mm) of *Austrocedrus chilensis*

Fixed effects	df	X^2	p value
(Intercept)	1	13.52	0.0002
Precipitation_previous period	1	30.18	3.95e−08
Precipitation_current period	1	27.95	1.25e−07
Temperature_previous period	1	7.6	0.006
Age classes*precipitation_previous period	1	15.83	6.92e−05
Age classes*precipitation_current period	1	8.82	0.003
Age classes*temperature_previous period	1	23.67	1.14e−06
(Intercept)	1	3141.87	<2.2e−16
SPEI_previous period	1	23.82	1.058e−06
SPEI_current period	1	8.81	0.003
Age classes*SPEI_previous period	1	15.61	7.768e−05

*Interactions between factors

differential influence on age classes (significant interactions between age classes and said climatic variables), where we observed that mature trees reacted with greater sensitivity. On the other hand, we observed that the SPEI-1 from the previous period and current growth period (from November to February) had a positive influence on the ring widths of *A. chilensis* and that the mature trees reacted with greater sensitivity to the SPEI-1 during the previous growth period (significant interaction between age classes and SPEI-1 from previous growth period).

The moving correlation analysis indicated that the growth-climate associations of *A. chilensis* were not stable during the period between 1936 and 2015 (Fig. 5). In recent decades (after 1970), the correlations calculated between standard chronologies and October to December precipitation were higher, particularly for the prior growing season for both age classes (Fig. 5A, B). In the case of the previous period, the correlation coefficients with the total precipitation in November were higher in mature trees from the 1970s onwards, a fact that was not evidenced in young trees (Fig. 5A, B). In the case of mean temperature, the October and February months during the previous period evidenced negative and significant ($p < 0.05$) correlations, although with dissimilar continuity during the analyzed period (Fig. 5C, D). During the current growth period, the correlation values tended to be negative, although they reached levels of significance ($p < 0.05$) after the 1950s (Fig. 5CD). Although the trends were similar for young and mature trees, a decrease in the number of significant correlations was observed for young trees during the second half of the 20th century. The relation between tree growth and SPEI-1 was similar for both age classes (Fig. 5E, F). However, during the previous growth season, the correlation after the 1970s was more positive and significant ($p < 0.05$) in mature trees than in young trees.
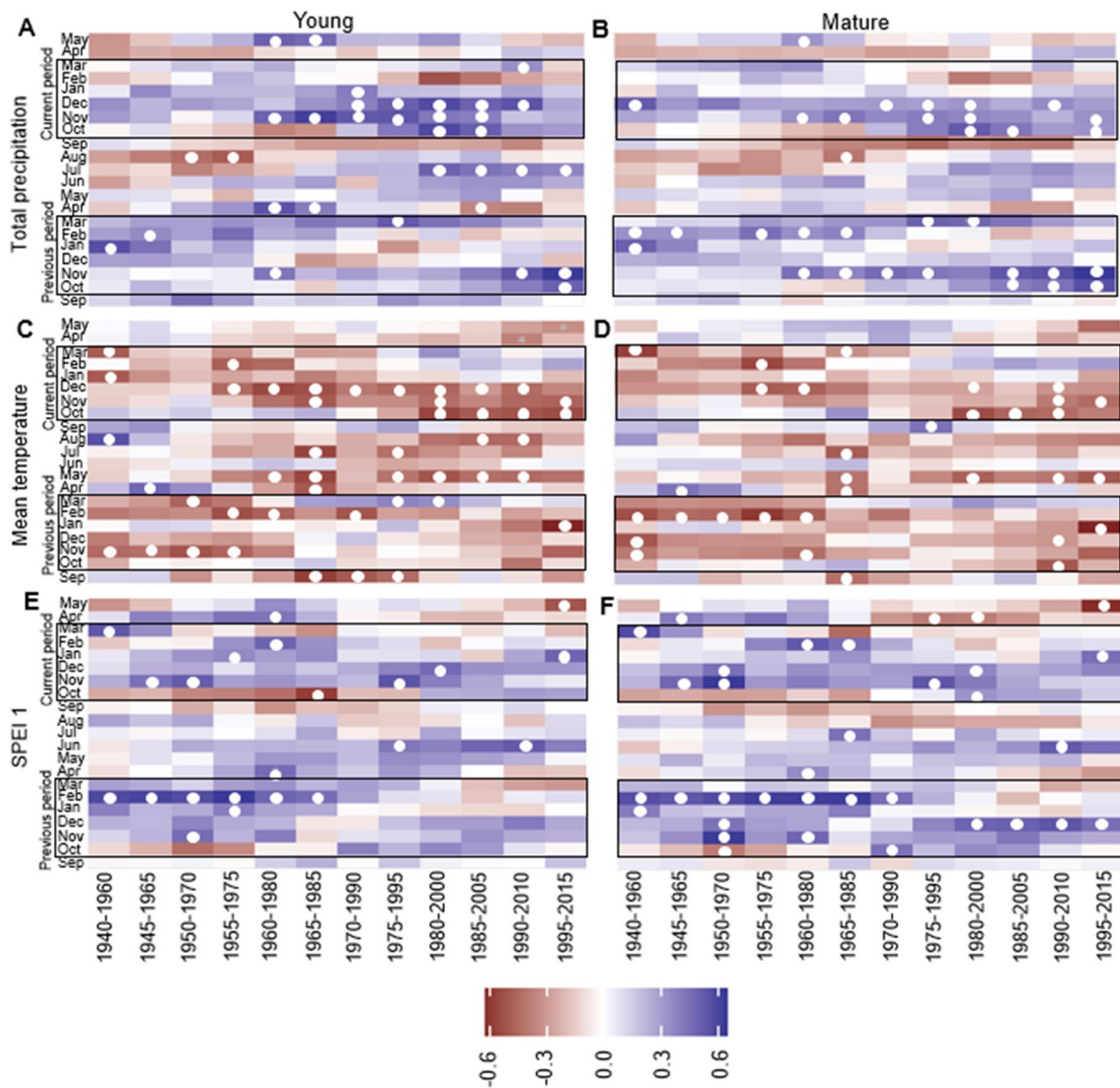
Fig. 5 Moving correlations (20-year windows lagged by 5 years) established between *Austrocedrus chilensis* standard chronologies and (i) total precipitation (**A**, **B**), (ii) mean temperature (**C**, **D**) and SPEI-1 (**E**, **F**) for young (<93 years; left panel) and mature (≥93 years; right panel) trees for the period 1940–2015. The area inside the black rectangles represents the current (top) and previous (bottom) growth period. White circles indicate significant correlations (*p* < 0.05)

To spatially extend our initial comparisons, we explored linkages to precipitation, air surface temperatures and SPEI-1 on a regional scale in Patagonia. The spatial correlations showed that there is a high positive correlation between the growth of *A. chilensis* and precipitation from November to March and with both previous and current growing season. These correlations are significant over most of the western Patagonia region (Fig. 6A). The spatial correlations also showed a high negative correlation between the growth of *A. chilensis* and the mean temperature in the same period (Fig. 6B). We observed a positive and significant (*p* < 0.05) spatial correlation between both age classes and SPEI-1. In all these analyses (Fig. 6C) the correlation coefficients were higher in mature than in young trees, especially for the

previous growing season. This broadly corroborates what was observed in Fig. 4C, where mature trees showed more significant correlations than young trees, both for the previous and current growing season.

Discussion

Our dendroclimatological analysis confirmed that radial growth of *A. chilensis* trees was positively linked to spring-early summer total precipitation and inversely to spring-summer mean temperature, indicating a clear drought signal corroborated by comparisons with the SPEI-1. Hadad et al. (2021) reported similar correlations between the

Fig. 6 Spatial correlations between young and mature *Austrocedrus chilensis* trees and total precipitation (**A**), mean temperature (**B**), SPEI-1 (**C**) of the previous (left column; November to March) and current growing season (right column; November to March), respectively. The period analyzed was 1936–2015 for both age classes. The significance of correlations presented in the maps is at $p < 0.05$. The rectangular outline in each map indicates the study site area. Maps were developed using the KNMI Climate Explorer webpage (http://climexp.knmi.nl/)
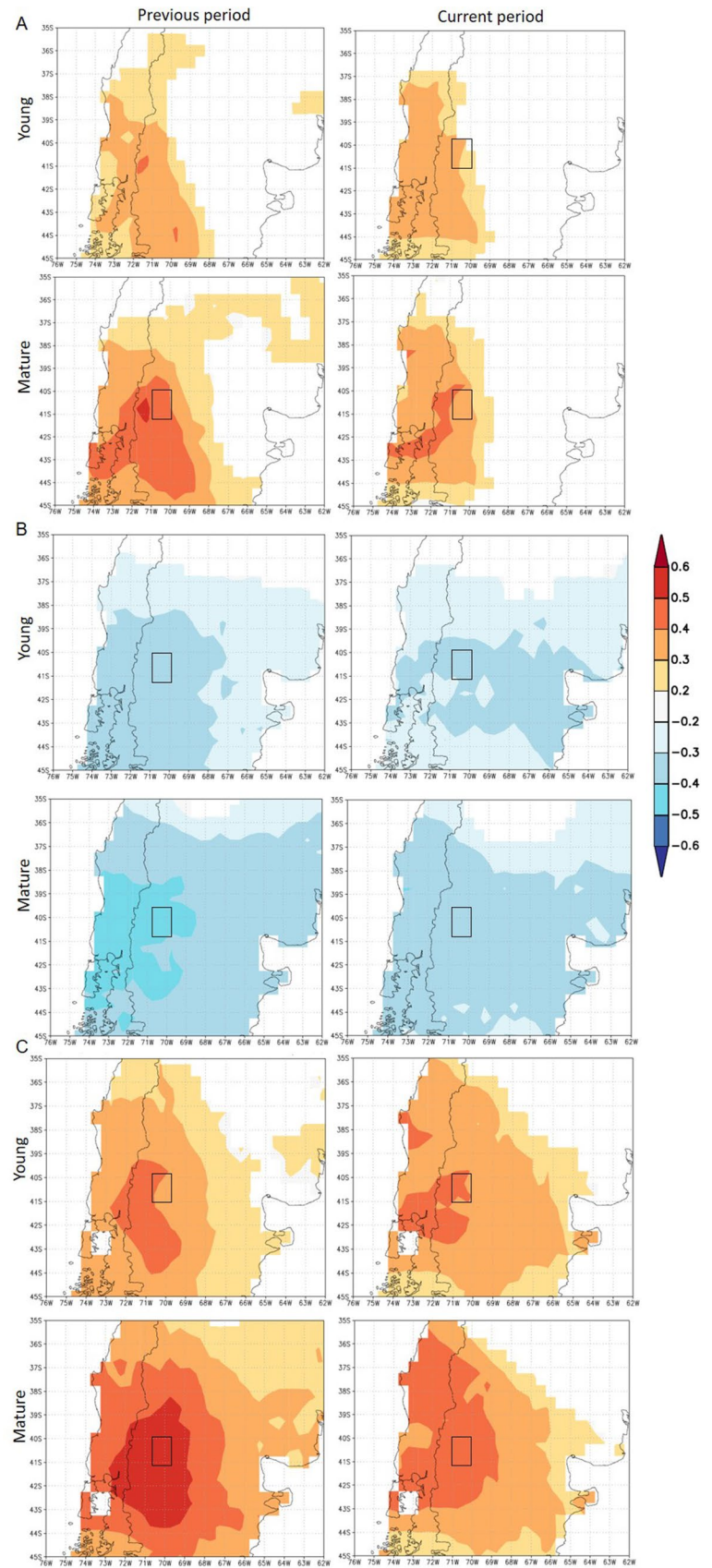
radial growth of *A. chilensis* populations located further north of our study sites and the SPEI-1 between November and December for the period 1930–2013. These results confirmed that insufficient soil moisture negatively impacts the growth in *A. chilensis* trees (Villalba and Veblen 1996; Villalba et al. 1998; Mundo et al. 2010; Hadad et al. 2021). The incidence of high air temperatures, for instance, may enhance the impact on the physical and biological environment by increasing the evapotranspiration rate and vapor pressure deficit, so a significant worsening of the severity of the water availability in the soil is expected (Williams et al. 2013). This situation may be occurring in the studied *A. chilensis* forests, which are subject to an extended period of water stress between the months of October and March.

The strong association between radial growth and water availability in spring is linked to the Mediterranean-type climate regime prevalent in the region, where precipitation is concentrated during the winter period. As the mean temperature increases during the spring-summer season, the snow accumulated during winter melts and infiltrates the soil, providing the necessary moisture conditions for the beginning of growth during spring. However, the results did not show a consistent link between the amount of water precipitated in winter and radial growth variability, nor did it link to a long residence of percolated water in the soils late in the summer. It is possible that due to the high permeability of the substrate (rocky and sandy) there is a relatively low water retention in the soil matrix and the root zone, so winter water resources may not be sufficient to maintain growth late in the summer. This could justify the importance (and only recognized link) of rain during November and December, evidenced by positive and statistically significant associations, particularly during the current year of growth. These results are consistent with those reported in other studies (e.g., Schulman 1956; Boninsegna 1988; Villalba et al. 1998; Roig et al. 2006; Le Quesne et al. 2006).

Despite this general characterization of the radial growth-climate association of *A. chilensis*, the striking result of this study concerned the significant sensitivity to drought observed in both young and mature trees. Our analysis showed a higher level of sensitivity to drought conditions in mature trees. *Araucaria araucana* (Molina) K. Koch), a conifer from western Patagonia that usually shares sites with *A. chilensis*, shows similar growth responses to climate. Hadad et al. (2015) indicated that radial growth in young *A. araucana* trees was more strongly correlated with temperatures during the current growing season, while mature trees showed a more marked sensitivity to the summer mean temperatures of the previous growing season.

The differential growth-climate response between age classes may be related to the many structural and physiological changes that trees undergo during their ontogeny, including, characteristics of the foliar area and root biomass

(Ryan et al. 1997), photosynthetic rate and hydraulic conductance of the stem (Ryan and Yoder 1997; Bond 2000), differential allocation of resources to different functions (Sinclair et al. 2012), among others. The changes observed as a tree ages are a reflection of different internal mechanisms and processes that are expressed in response to the same environmental factors (Hadad et al. 2015). In this sense, the productivity of trees decreases as individuals grow and age, a process being generally explained by the mechanism of hydraulic resistance (Carrer and Urbinati 2004; Yu et al. 2008). Ryan and Yoder (1997) claimed that hydraulic limitation is more associated with the age condition (in this case, mature trees), since it is observed that there is a greater demand for water in old trees during water stress conditions. When this type of stress occurs, dehydration of the plant is triggered by evapotranspiration excess that reduces meristematic activity and inhibits root development (Kozlowski and Pallardy 1997; Ryan et al. 1997; Martínez-Vilalta et al. 2007; Pallardy 2008). In this regard, there is evidence that hydraulic conductivity decreases with age, as observed in *Pinus ponderosa* Douglas ex Lawson and *Pseudotsuga menziesii* var *menziesii* (Mirb.) Franco (Hubbard et al. 1999; McDowell et al. 2002).

The analysis of the temporal stability of the growth-climate associations between young and mature *A. chilensis* trees showed notable dynamics throughout the last century. Periods in which the climate response was strengthened or reduced were evidenced. Temporal variations in the significance of the correlations between growth and climate could be due to the interaction of a set of factors, including internal growth dynamics, competition between trees, the quality and/or geographic proximity of the climate information, or the greater impact of climate due to the accentuation of processes in the atmospheric circulation, among others (Lindner et al. 2010; Aussenac et al. 2017). Concerning mean temperatures, November–February was indicated as the period of months when mean temperatures were inversely associated with growth, but this connection fluctuates over time. However, the strength of the growth–temperature relationship with October and February has increased in recent decades. The expansion of this climate signal recorded in *A. chilensis* trees during the last 30–40 years could constitute an indication of a vigorous green-up caused by rising temperatures in late winter and early spring, whose trigger could be linked to the effects of global warming. This is consistent with observations of changes in historical growth phenology linked to recent increases in mean temperature (Badeck et al. 2004; Cleland et al. 2007), arguing that the expansion of the active growth period exposes many plant developmental processes to a greater vulnerability to early spring frosts and droughts (Ma et al. 2018; Richardson et al. 2018; Hansen et al. 2012) found that the probability of unusually warm seasons is changing. Mainly after the 1970s,

the temperature distribution shifted towards more positive seasonal anomalies, which is considered a consequence of global climate change (IPCC 2018). There is support that anomalies will continue to increase over the coming decades, producing even more extreme climate anomalies (Hansen et al. 2012). This could explain the more significant correlations observed after the 1970s, especially for October mean temperature. Other studies found similar results in trees from South America (Villalba et al. 2012; Alvarez et al. 2015; Suarez et al. 2015; Holz et al. 2018).

In dendroclimatology, *A. chilensis* has proven to be a valuable proxy species to study climate variability (e.g. Morales et al. 2020; Hadad et al. 2021; Matskovsky et al. 2021). Currently, the dendroclimatic value of *A. chilensis* has been recognized based on chronologies made up of trees with mixed ages. However, it is important to consider that trees, as long-living organisms, may express multiple physiological adaptation strategies through their life cycle (Fromm 2013). Therefore, identifying the sensitivity to climate in trees of different ages becomes relevant to elucidate not only aspects of the species' ecophysiology but also to provide valuable information for its application in climatic reconstructions and in the implementation of management and conservation policies in the face of climate change risk scenarios. Finally, and taking into account that future climate models project warmer and drier conditions for the northern Patagonia sector, it is relevant to know how *A. chilensis* trees respond to climate in relation to their age. It could be assumed that a lower climate sensitivity of young trees could result in less severe effects in the face of future climate change. There is evidence that tree-ring time series derived from old trees could overestimate the impact of climate change (Klesse et al. 2018). Our results can provide insights about potential consequences of changing environmental conditions on forest dynamics.

Conclusions

When performing climate reconstructions from tree rings, it is normally assumed that trees respond similarly to climate conditions regardless of their age. However, if the intensity of the climatic signal had any relationship with age, it is possible that chronologies developed only from mature trees or by mixing age classes could be influencing the signal quality of the proxy climatic data provided by tree rings. The results obtained in this study demonstrate the complexity of the linkages between radial growth, tree age and climate variability. In this sense, the growth responses of *A. chilensis* evidenced differences in climate sensitivity between the established age classes. Results indicated that the contribution of mature trees in the chronology should increase the climatic signal, especially if the climate history is desirable to reconstruct.

Furthermore, the identification of these growth response intensities with respect to climate and age is of particular interest to achieve a more detailed understanding of the ecology of these forests, for which aspects of natural dynamics could be more finely interpreted and applied in the formulation of forest restoration programs. Based on the results we obtained, it will be helpful to extend the approach used here to a range of habitat types throughout the natural distribution of *A. chilensis*. Other variables, such as soil type, sex and genetic diversity, should be considered as possible factors influencing the response of trees to climate due to their age.

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Code availability Not applicable.

Declarations

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