Age effects on the climatic signal in Araucaria araucana from xeric sites in Patagonia, Argentina

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Background: At different cambial ages, trees experience changes in their structure and interactions with environmental conditions. Reciprocal mechanisms between tree age and physical resources, photosynthetic rates, and xylem production may influence hydraulic resistance and plant water stress. However, it is yet uncertain how these mechanisms are associated with changes in growth sensitivity to biophysical drivers, especially climate.
Aim: To establish age-associated climate – growth relationships in growth rings of *Araucaria araucana* trees from the temperate xeric zones of northern Patagonia, Argentina.
Methods: We analysed the growth in 211 *A. araucana* trees from four sampling sites, in three age classes: young (≤120 years), mature (121–275 years), and old (≥276 years). We explored the correlations between the signal strength of tree growth and climate, based on comparisons between each age-class chronology and monthly mean surface air temperature, total precipitation, and the Southern Annular Mode (SAM) index.
Results: The young trees showed higher correlations when their growth was compared with precipitation, air temperature, and the SAM index during austral spring and summer months of the same year. In contrast, growth in mature and old trees showed higher correlations with summer temperatures of the previous growing season.
Conclusions: The sensitivity of the radial-growth response of *A. araucana* to climate varies with age and is strongest in the rings of young trees.

Keywords: age class; dendroclimatology; SAM; pehuén; tree-ring

Introduction

During growth from seedling to adults, trees experience changes in their structure and in their interactions with the environment. It is understood that physiological processes of growth change with age (Hinckley et al. 2011), and these age-related changes are likely to be the result of complex tree-environment relationships (Day et al. 2002). For example, the interaction between tree age and environmental resources, photosynthetic rates, and xylem production influences hydraulic resistance and plant water stress. In observations on the relationship between water demand in trees under water stress, it has been found that hydraulic conductance decreased with age, with consequences for growth response to water availability (Ryan and Yoder 1997; Hubbard et al. 1999; McDowell et al. 2002).

Körner (2006) claimed that the rate of change in radial growth diminished with age in response to changing resource levels; many of these changes were likely related to acclimatising mechanisms in response to the environment. The fact that tree physiology undergoes changes in sensitivity to climate with age is also supported by tree-ring studies (e.g. Rozas et al. 2009; Vieira et al. 2009; Wang et al. 2009; Copenheaver et al. 2011; Linares et al. 2013; Mamet and Kershaw 2013; Wu et al. 2013). These contributions suggest that trees experience age-related changes in climate sensitivity, but not always in the same direction. In some species, radial growth in adult trees is more sensitive to climatic constraints than in younger trees (Szeicz and MacDonald 1994; Carrer and Urbinati 2004; Yu et al. 2008); in other species, climate sensitivity diminishes with age (Linderholm and Linderholm 2004; Rozas et al. 2009; Vieira et al. 2009). Hence, although recent research has recognised variable age-related responses to climate, knowledge gaps in this area persist (Hinckley et al. 2011).

Despite the above, dendroclimatology has largely been practised under the assumption that the relationship between climate and tree rings was independent of age (Fritts 1976). However, this can lead to bias. For example, in the development of long tree-ring chronologies, 'older' and assumedly more climate-sensitive trees are selected for sampling, and ring series from young trees in the record used for calibration against instrumental climatic data are often excluded. Therefore, if different tree species of different ages respond with variable intensity to climate conditions, climate-tree growth models based on solely old trees may underestimate or overestimate the strength of the climatic signal in a tree-ring chronology, depending on the species and ecological setting. There is a growing consensus that tree-ring chronologies constructed with trees from different age classes may help develop more robust series

and recover higher-quality climatic signals from tree rings in the high-frequency domain (Linderholm and Linderholm 2004; Esper et al. 2008; Vieira et al. 2009).

Despite the excellent data provided on long-term climate histories by South American forests (Roig and Villalba 2008; Boninsegna et al. 2009; Villalba et al. 2011), no studies on tree-age related climate–growth relationships have been undertaken. One species that provides valuable climate proxy data is the long-lived *Araucaria araucana* (Molina) K. Koch (pehuén), an endemic dioecious tree species (Roig and Villalba 2008) that occurs on the northern limits of the temperate Subantarctic forests of Argentina and Chile in northern Patagonia (Roig 1998). Previous research has indicated that radial growth in this species increased in years with cool and wet springs and summers (Villalba et al. 1989; Mundo et al. 2012; Muñoz et al. 2014). Besides the climate, other factors such as tree age or sex may be linked to variations in growth, as has

been reported by Cattaneo et al. (2013) for the subtropical forests of Araucaria angustifolia.

In this study, we tested whether age was correlated with climate as shown by tree-ring evidence in *A. araucana* trees growing in the temperate xeric areas of northern Patagonia. We hypothesised that the different age groups would show different degrees of correlation with climate variables and hence indicate different climate sensitivities of different age groups.

Material and methods

Study sites

We selected four multi-aged open stands of *A. araucana* (Figure 1; Table 1) growing under similar environmental conditions and of comparable plant community composition, including ground flora species, such as *Adesmia*
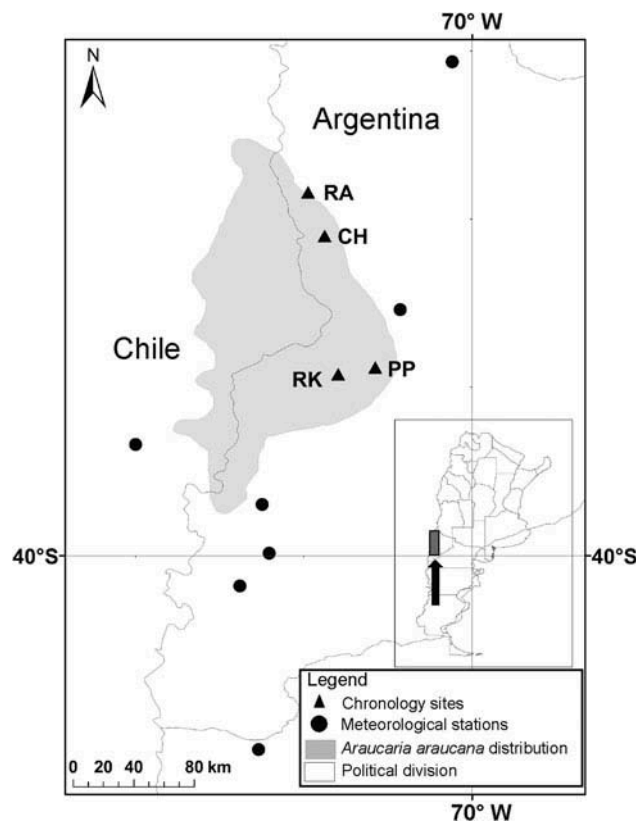
Figure 1.   Location of the study sites (triangles) and meteorological station (circles) in northern Patagonia, Argentina (see Table 1 for chronology codes and Table S2 for identification of meteorological stations). The grey-shaded area indicates the natural distribution of *A. araucana*.

Table 1.   Site and geographic characteristics of the four sampled *Araucaria araucana* xeric sites in the north of Patagonia, Argentina.

Sites	Number of tree/radii	Chronology time span	Latitude (S)	Longitude (W)	Elevation (m)	Aspect	Degree (°)
Río Agrio (RA)	75/44	1252–2007	37° 50′ 02,6′′	70° 58′ 38′′	1594	NE	7
Chenque-Pehuen (CH)	65/103	1391–2007	38° 05′ 59,9′′	70° 52′ 36′′	1653	NE	8
Primeros Pinos (PP)	43/82	1277–2008	38° 52′ 09,7′′	70° 34′ 26′′	1628	NE	7
Río Kilca (RK)	32/58	1190–2008	38° 53′ 53,1′′	70° 50′ 31′′	1442	NE	12

boronioides, Poa ligularis, Festuca pallescens, Mulinum spinosum, and *Eryngium paniculatum* (Roig and Roig 1994). All sampled stands developed on rock outcrops with a sandy matrix, providing a well-drained substratum. The regional climate was characterised by a mean annual air temperature of 12.4°C (the mean of the warmest and coldest months was 19.8°C and 5.1°C, respectively) and a total mean annual precipitation of 500 mm, concentrated in winter months (De Fina 1972) (Figure S1).

Sampling of tree cores

To collect samples representative of different ages, we sampled trees of all diameters in each stand. At least two increment cores per tree were taken at breast height (1.30 m), perpendicular at each other to capture potential variability in tree growth around the stem. From the four stands, 211 standing trees were sampled. In the laboratory, wood samples were air-dried, mounted on wooden supports, and sanded with progressively fine sandpaper to highlight tree-ring annual boundary structure. Ring widths were measured with a Velmex measuring system with a precision of 0.001 mm. The calendar age of the growth rings was determined with Schulman's method (Schulman 1956), that is, the date of the annual ring is where the year's growth begins. Quality control of the tree-ring series was made according to standard visual cross-comparison methods proposed by Stokes and Smiley (1968) and by statistical cross-dating procedures carried out with the COFECHA programme (Holmes 1983). Off-centre cores that did not reach the pith, but with full internal arcs close to the pith, were inspected to estimate the number of missing rings, using a geometrical method (Duncan 1989). This minimised potential offset errors of real cambial ages.

From the non-standardised tree-ring width series, we derived the mean value (M), mean sensitivity (MS), standard deviation (SD), and first-order autocorrelation (AC1) to analyse these variables by tree age (Fritts 1976). We also produced a regional tree-ring width chronology using the Regional Curve Standardisation (RCS) method, based on ring age alignment (years from pith) of trees in one area and their corresponding ring width mean for each age. The resulting curve was smoothed, by which each ring measurement was divided to create an RCS tree-ring index chronology (Briffa and Melvin 2011).

To discriminate age groups, we applied Fisher's algorithm (1958). All individual raw tree-ring width series were pooled into a single data set, and the corresponding cambial age was assigned to each ring width (i.e., the ring closest to pith is year 1, etc.). The algorithm was applied to the ring age sequence, and a cut-off point was decided when the variance between intervals reached a minimum value. We thus identified three tree age classes: young (≤120 years), mature (121–275 years), and old (≥276 years) (Table S1).

To relate tree growth with climate, tree-ring width index chronologies were developed for each age class. Since tree-ring variability is affected not only by climatic factors but also by stand dynamics and biological age (Fritts 1976), we filtered out the influence of both by using standardisation procedures (Cook 1985). Final chronologies were thus generated with conservative curve-fitting methods, such as a cubic smoothing spline function with a 50% frequency cut-off and a response period of 50 years. Individual indexed series were averaged, using a robust bi-weight estimate of the mean to enhance the common signal. After removing non-climatic trends with standardisation, residual tree-ring width chronologies were calculated for the three age classes based on a univariate autoregression model. This residual chronology emphasises the short-term (inter-annual) fluctuations in the final chronology (Cook 1985).

Statistical evaluations were used to indicate coherent variation among samples at each site (Cook and Kairiukstis 1990). One criterion is the expressed population signal (EPS), a statistic that assesses how well a chronology based on a finite sample compares to a theoretical chronology based on an infinite number of trees (Wigley et al. 1984). The EPS strongly depends on the number of trees used in the construction of a mean chronology and the strength of the correlation between series. While there is no significance level per se, a value of 0.85 is considered acceptable (Wigley et al. 1984). Another value that indicates agreement between cores at each site is the Rbar statistic (Wigley et al. 1984). Rbar shows the average correlation between all series, which is a percentage of variance for the common period. To examine the temporal variation of both Rbar and EPS, we constructed running series for each age class, based on a 25-year moving window with 10-year overlaps.

Climate data

Comparative climate reference data were monthly mean surface air temperature and monthly total precipitation, averaged into regional records with data from seven gauge stations near the tree-ring sampling sites. These data were available from 1912 to 2005 for temperature and from 1929 to 2001 for precipitation (Table S2). Therefore, for any age-class chronology, we calibrated the climate-growth system with records of 93 years for temperature and 72 years for precipitation, respectively. Additionally, we used high-resolution monthly data from the Southern Annular Mode (SAM) index, covering the period 1948–2002. This index is based on principal components of geodynamic height anomalies at 850 hPa (Thompson and Wallace 2000) and describes the dominant pattern of non-seasonal tropospheric circulation variations south of 20°S (Garreaud et al. 2009).

Statistical analyses

Tree rings. In order to test the effect of a random factor on tree-ring width, we used a generalised linear model (GLM). Tree-ring widths were the dependent variable, and age-groups and sampling sites were the independent

variables. After a number of trials, we used a GLM that included the effects of age groups, sites, and the interaction term between age groups and sites. Tree-ring widths were linearised using the $\log(x + 1)$ transformation (Legendre and Legendre 2012). Analysis if variance (ANOVA) regression test and the determination coefficient (R^2) were also calculated (Kuehl 2001). The independent percentage of each factor's variance was determined with hierarchical partitioning (HP), as the GLM only provides information on the significance of each factor (Chevan and Sutherland 1991). This analysis calculates goodness of fit measures for the entire hierarchy of models using all combinations of independent variables and is usually employed as a complement to GLM (Olea et al. 2010). All these analyses were carried out in the R version 3.1.0 environment (Mass library, http://www.r-project.org/).

Climate–tree ring-width correlations. The influence of climatic factors on the annual growth of *A. araucana* forests was investigated by comparing Pearson correlations between residual chronologies and monthly temperature, precipitation, and SAM records. We took into account the regional chronologies of all age classes. The correlation analysis made it possible to identify the main climatic factors that influenced tree growth as well as the seasonality and strength of the climate response (Fritts 1976). Because climatic conditions from the prior year can influence growth, correlations were carried out for each month of a 21-month span encompassing two growing periods.

Results

Fisher's algorithm identified three classes of cambial age, each one corresponding to young (mean 81.1 years), mature (mean 176 years), and old (mean 358 years) classes, respectively (Table 2). Within the young and mature classes, there was a greater range of mean widths, while in old trees the mean width diminished significantly ($R^2 = 0.06$, $P < 0.05$). The regression curves fitted to the first-order autocorrelation values were significant in all classes, but young trees showed the strongest signal and trend (young: $R^2 = 0.29$, $P < 0.001$; mature: $R^2 = 0.03$,

Table 2. Descriptive statistics for the individual raw tree-ring width series for each of three age-class category of *Araucaria araucana* in the xeric forests of northern Patagonia, Argentina.

Attributes	Age class		
	Young	Mature	Old
Chronology length	1888–2008	1773–2008	1190–2008
Number of trees (radii)	50 (68)	85 (152)	76 (148)
Mean value	1.037	0.927	0.432
Standard deviation	0.395	0.333	0.170
Mean sensitivity	0.189	0.201	0.206
First-order autocorrelation	0.783	0.706	0.710

Note: Young (<120 years), mature (121–275 years), and old (>276 years).

$P < 0.05$; old: $R^2 = 0.05$, $P < 0.05$). The RCS curve showed the expected decrease in growth with age (Figure 2).

The average correlations between all series defined by Rbar were 0.202 (1888–2008), 0.211 (1773–2008), and 0.194 (1190–2008) for young, mature, and old tree-ring chronologies, respectively. The young and mature chronologies showed EPS values above the 0.85 level for all periods. Old trees showed a similar pattern, but just before the year 1450, the EPS fell below 0.85, probably due to the reduced sample size for this period (Figure 3).

GLM showed significant effect of sites only for young and mature trees ($P < 0.001$), but this effect was low, according to HP test (Table 3). Consequently, a regional model could be used. The overall R^2 was 0.87, and the ANOVA test was significant for the factors of site ($F = 12.596$, $P < 0.001$), age ($F = 1.620$, $P < 0.001$), and the interaction between the two ($F = 13$, $P < 0.001$) (Table 3); age explained 89.3% of growth variance and site explained 10.7%. These results showed that the factors age groups and sites had an effect on radial growth. However, it was possible to use a regional model for different age groups due to the low percentage of variability in growth that was affected by site factors (10.7%).

Correlation between regional climate and residual chronologies

Comparisons between regional climate data and regional residual chronologies of all age classes combined showed that mean surface air temperature was significantly and negatively correlated with the regional chronology during the summer months of January, February, and March of the year prior to the growth period and November and December during the current year of the growth period (Figure 4A). Precipitation was significantly and positively correlated with the regional chronology during January of the prior growth period and September of the current growth period (Figure 4B). Moreover, the SAM index showed negative correlations with the regional chronology for all months between October and February during the current growth period, with significant values during January and February (Figure 4C).

Comparison of age-class chronologies with climatic variables

The comparison of age-class chronologies with climatic variables – in order to analyse the relative contribution of each age class in the regional chronology – showed some differences. The young tree-ring chronology showed a significant and negative relationship with temperature from October to December of the current growth period; mature and old trees showed a similar trend, but correlations were not significant. Mature and old trees had substantially larger correlation values with temperature from January to April of the previous year (Figure 4A). Precipitation had a direct effect on radial xylem
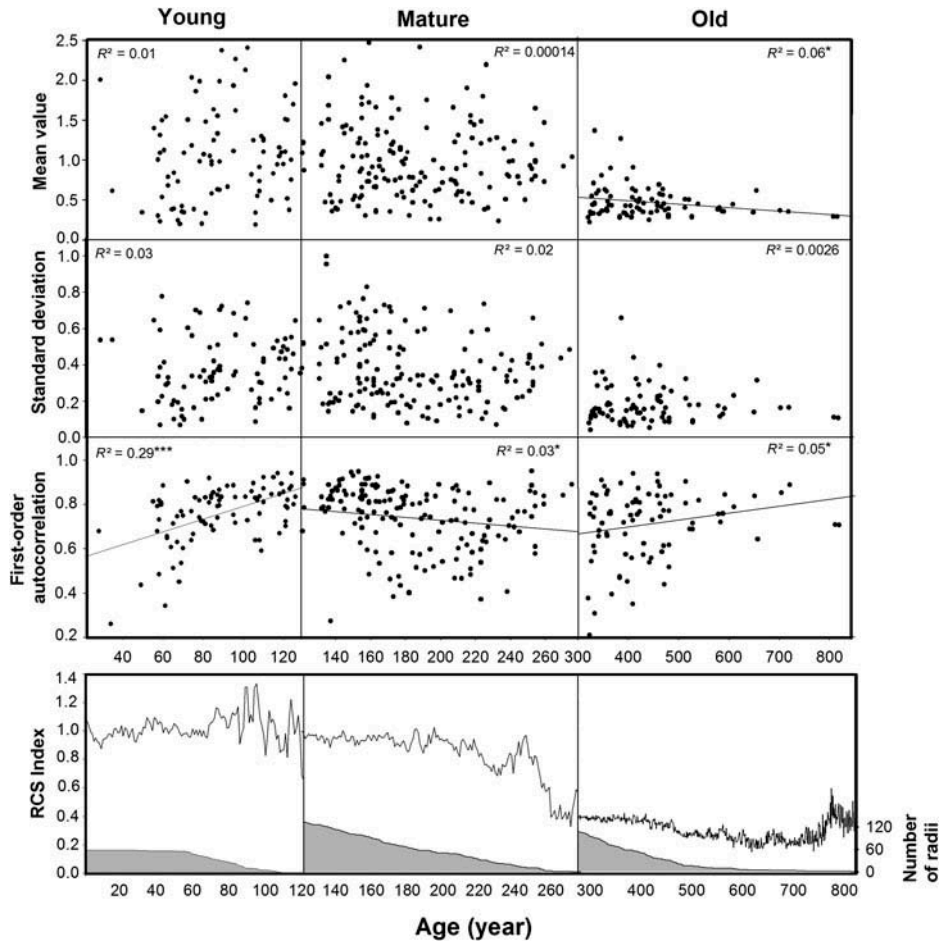
Figure 2.   Selected statistics of the individual measurement series for young (<120 years), mature (121–275 years), and old (>276 years) *Araucaria araucana* trees, calculated by ARSTAN. The regression line and coefficient are shown for each case (*P < 0.05; ***, P < 0.001). At the bottom, the regional curve (RCS) chronology for each age class is shown.
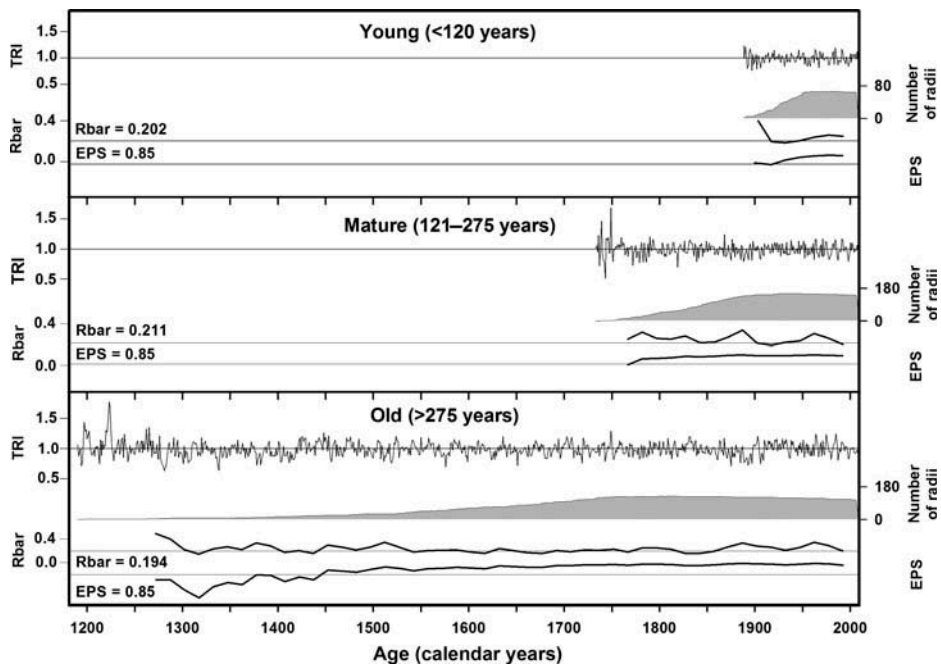

Figure 3.   *Araucaria araucana* residual regional tree-ring width index (TRI) chronologies by age class. The shaded area corresponds to the sample depth of each chronology. The Rbar and EPS curves for class-age chronologies are indicated at the bottom of each sample depth histogram.

Table 3. Results of a generalised linear model (GLM), showing the effect of age groups of *Araucaria araucana*, sites, and the interaction between the two factors (age groups × sites).

Factor	Estimate	Standard error	*t*-Value
Site: CP	0.324	0.013	25.302***
Site: PP	0.492	0.010	47.263***
Site: RA	0.395	0.006	64.451***
Site: RK	0.458	0.013	35.925***
Age: Mature trees (M)	0.249	0.016	16.012***
Age: Young trees (Y)	0.467	0.024	19.846***
PP × Y	−0.152	0.030	4.37E-07***
RA × Y	−0.051	0.025	0.043***
RK × Y	−0.217	0.035	4.20E-10***

Note: ***$P < 0.001$.

development, with significant correlations during September and October of the current growing period and January of the previous one. Again, rings of younger trees showed a strong positive response to precipitation in the current year's spring, a season with high soil humidity and relatively low air temperatures (Figure 4B). Comparing the growth of *A. araucana* and the SAM index, there was a strong negative relationship between all age-class chronologies and November and February of the current growth period, and correlations were notably weaker during the prior growth year (Figure 4C).

Discussion

We found that sensitivity of the radial-growth response to climate of *A. araucana* trees varied with age, and it was strongest in the rings of young trees. Previous dendrochronological research showed that the annual growth variability of trees in Patagonia could primarily be related to water or temperature limitation, in function of species and site characteristics (Roig and Villalba 2008). In *A. araucana* trees from xeric and mesic environments, ring-width variability has been found to be mainly related to surface air temperatures during summer and autumn of the preceding growing season and with spring temperatures of the
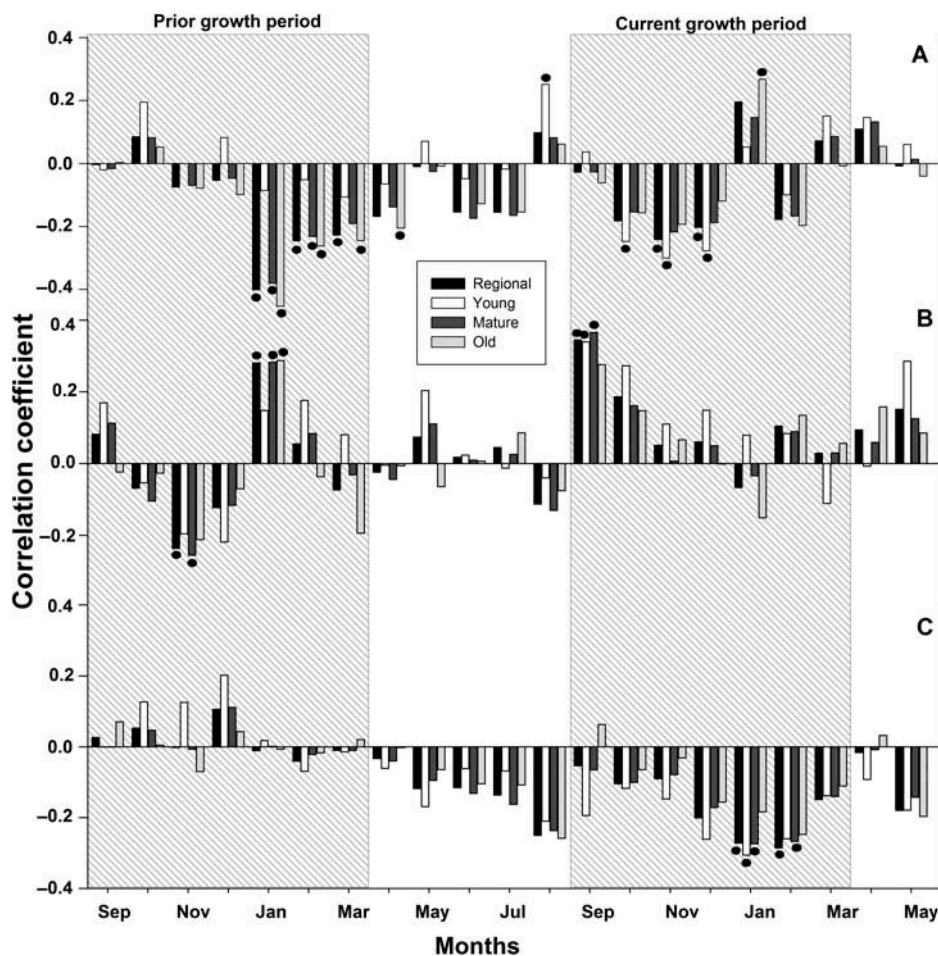
Figure 4. Correlation coefficients for comparisons between regional and residual ring-width chronologies for each age class of the sampled *Araucaria araucana* trees with: (A) regional monthly mean temperature (1912–2005), (B) total monthly precipitation (1929–2001), (C) Southern Annular Mode index (1948–2002). Black dots indicate significance at the 95% confidence level for the correlation coefficient. Shaded areas indicate current (right) and previous (left) growth seasons. Young (<120 years), mature (121–275 years), and old (>276 years).

current growth period (Villalba et al. 1989; Mundo et al. 2012; Muñoz et al. 2014).

Our results broadly replicate these empirical trends, but also detect that spring–summer precipitation was a strong and positive factor for radial growth in *A. araucana* trees. The correlations between climate and variability of growth were similar in the different age classes. However, temperature variations during the current spring–summer months had larger effects on younger trees, while mature and old trees indicated the largest and most significant correlations with summer and autumn temperatures in the prior growth period. A physiologically plausible explanation for this lag in response by mature and old trees is that photoassimilates stored during the autumn are remobilised for the following year's earlywood formation, thereby extending the response time by several months. Similarly, Hill et al. (1995) and Robertson et al. (1997) reported a high correlation between $\delta^{13}C$ in *Quercus robur* earlywood and the prior year's latewood. Moreover, branch-level ^{14}C labelling of *Pinus sylvestris* has shown that photoassimilates from the previous year were used for earlywood formation (Hansen and Beck 1990); Kagawa et al. (2006) showed that 43% of carbon in the starch pool of *Larix gmelinii* was carried over to the following year.

We also explored links between the SAM index and the radial growth of *A. araucana*. SAM is an expression of large-scale atmospheric variability and significant forcing of intra-seasonal to decadal climate variability in middle to high Southern Hemisphere latitudes. It is characterised by persistent water deficit in northern Patagonia during the positive phases, which are associated with a decrease in surface pressure over Antarctica that results in the strengthening and poleward shift of mid-latitude westerlies (Garreaud et al. 2009). This water deficit negatively affects *A. araucana* growth, as demonstrated by Mundo et al. (2012). Trees younger than 120 cambial years in our study appeared sensitive to the monthly SAM index, indicating an apparent larger sensitivity to soil water deficit and warmer air temperature during this stage of tree ontogeny.

Our results showed that there were higher correlations between tree rings with temperature and precipitation in younger *A. araucana* during the initial stages of the current growing period, which documents differences in climate sensitivity on growth by age category. The hydraulic limitations can only partially explain how age may control the climate sensitivity of trees (Carrer and Urbinati 2004; Yu et al. 2008). Hubbard et al. (1999) found that hydraulic conductance was 44% lower in old *Pinus ponderosa* trees compared to young trees, as calculated from leaf water potential and leaf gas exchange measurements on 1-year-old needles. This hydraulic limitation could contribute to the slowing of growth of trees as size increases (Ryan et al. 1997). Therefore, the difference in climate sensitivity by age found in *A. araucana* may find justification in the previously mentioned concepts of hydraulic limitation.

There is evidence that as trees increase their age, both growth and metabolism may potentially vary (Day et al.

2001; Mencuccini et al. 2005; Bond et al. 2007), including the response of growth meristems to the abiotic factors. Trade-offs between structural and functional growth opportunities may be a plausible explanation for age-related climate sensitivity in *A. araucana*. Decrease in soil water availability is eventually followed by stomatal closure, which leads to a reduction in the production of photosynthates, growth hormones, and their subsequent transport to meristematic sites, including roots, which further decreases water absorption (Kozlowski and Pallardy 1997; Ryan et al. 1997; Martínez-Vilalta et al. 2007; Pallardy 2008). Rozas et al. (2009) claimed that lateral root growth and root grafting during tree development in *Juniperus thurifera* might partly explain the age-related growth sensitivity to summer water deficit. A more extensive root system allows older trees to explore diverse microtopographic soil nutrient and hydrological conditions, unlike younger trees with more limited root networks (Kozlowski and Pallardy 1997; Voelker 2011). This may explain why older trees may be more buffered from large climate variations, as claimed by Voelker (2011). In relation to these considerations, we observed roots of 10 cm in diameter at a distance of 30–40 m from trunks of old *A. araucana* trees.

The effect of age on the climate signal in the growth rings can yield surprising results. Our research suggests that the inclusion of young trees in the construction of long-term tree-ring chronologies may increase the resolution (in the high-frequency component) of the climatic signal of tree rings. According to Vieira et al. (2009), age-dependent responses to climate provide important clues for predicting how young and old trees reacted to climate change in the past and how today's young trees may respond in the future. Traditionally, the effects of young trees in dendroclimatic model comparisons with contemporary climate data have been underestimated by the preferential use of older trees to produce the longest possible tree-ring records (Briffa and Osborn 1999). As has been demonstrated in this article, the young trees showed greater tree-growth sensitivity to climate variation. Consequently, the inclusion of young *A. araucana* trees in building a tree-ring chronology will increase the signal strength by integrating a full range of tree-ring age classes during the instrumental calibration period.

Conclusions

This study has demonstrated that, in the xeric fragmented forests of *A. araucana*, the signal strength of the climate-growth correlation has a non-stationary nature, varying significantly with tree age. While the young trees are more sensitive to precipitation during the current growing season, trees older than 120 years are more sensitive to temperature during the previous year's growing season. In the context of climate change, Patagonia has experienced an increase in temperature and decrease in precipitation during the last century. If this trend continues and intensifies, it will not only affect the growth of both young and

old trees but will affect the future dynamics and conservation of the *Araucaria* forests. Since *A. araucana* woodlands extend across a west-to-east diminishing precipitation gradient, our current conclusions are biased towards growth behaviours in the driest portion of the gradient. Trees from more humid environments should be tested, as well as other species, to explore geographic variability in the climate–growth relationship to allow developing better interpretations of forest ecology–climate interactions and the development of conservation policy in relation to climate variability and climate change.

Acknowledgements

Supplemental data

Supplemental data for this article can be accessed here.

Notes on contributors

Martín A. Hadad is a postdoctoral researcher. His research addresses the dynamic and structure of natural populations of temperate woody species.

Fidel A. Roig Juñent is a senior researcher in CONICET. His research addresses the impacts of climate variability and change on forest communities and wood ecology of semidesert temperate woody species.

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