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Climatic signals in tree-rings of *Araucaria angustifolia* in the southern Brazilian highlands

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Abstract *Araucaria angustifolia* (Bertol.) O. Kuntze (Araucariaceae) is a Neotropical tree, widely distributed in subtropical mountain rain forests and nearby natural grasslands of Southern Brazil. This species produces annual growth rings, but its dendroclimatic potential is barely known. In the present paper, the long-term growth patterns of *A. angustifolia* were investigated using annual growth ring time series and association to climate over the last century. Wood cores of *A. angustifolia* trees growing in forest and grassland habitats were obtained with an increment borer. The cores were surfaced, measured and cross-dated. The dated ring-width time series were standardized and submitted to correlation and principal component analysis to verify growth trends among sites and trees. Growth-climate relationships were investigated using correlation and regression analyses, comparing the ordination axes scores to regional time series of precipitation and temperature. Due to anatomical irregularities, mainly partial rings, only 35 out of 60 trees were cross-dated. The correlation and ordination analyses showed common tree-growth trends within and between sites, indicative of a regional environmental force determining inter-annual cambial activity variation. Despite growing in distinct habitats and disturbance regimes, *A. angustifolia* trees share a common long-term growth pattern, which is significantly related to thermal conditions during the current and previous growing seasons. Moreover, site-specific characteristics may have influenced opposite growth responses and association to climate conditions between forest and grassland trees.

Key words: Araucaria forest, Campos grassland, dendrochronology, fire, partial rings.

INTRODUCTION

Growth rings of woody plants are a major source of high-resolution data for studies of long-term environmental changes, especially in regions under strong seasonal climatic variability (Fritts 1976; Schweingruber 1996; Vaganov *et al.* 2006). Dendrochronological studies are scarce in tropical and subtropical ecosystems, despite promising results that have been obtained since the early 20th century (see historical review in Mariaux 1981; Worbes 2002). The limited development of this science in the tropics can be attributed to the scarce frequency of tree species forming well-defined growth rings compared with temperate and arid floras (Stahle 1999). This situation has motivated an increasing number of studies dealing with the growth ring formation, particularly their wood anatomical features, the timing and dynamics of the tree ring formation and its links with phenological changes and climate seasonality (e.g. Boninsegna *et al.* 1989; Détienne 1989; Borchert 1999; Alves & Angyalossy-Alfonso 2000; Roig 2000; Callado *et al.* 2001; Roig *et al.* 2005; Lisi *et al.* 2008)

The tropics represent a key piece in the understanding of the planetary climatic system. Since few long-term instrumental or proxy climatic data exist for this zone, most of the dendrochronological studies in subtropical and tropical regions have focused on the identification of climate-sensitive species and further development of growth ring chronologies that could be used as proxy data for climatological investigation (e.g. Villalba *et al.* 1998; Bhattacharyya & Yadav 1999; Buckley *et al.* 2000; Fowler *et al.* 2000; Biondi 2001; Morales *et al.* 2004; Speer *et al.* 2004; Brienen & Zuidema 2005; Dünisch 2005). Few studies developed tree ring chronologies for other ecological applications (e.g. Stahle *et al.* 1999; Grau *et al.* 2003; Worbes *et al.* 2003; Brienen & Zuidema 2006; Martin & Fahey 2006).

Araucaria angustifolia (Bertol.) O. Kuntze (Araucariaceae) is a southeastern South America conifer that produces seasonal growth rings, but its dendrochronological potential is barely known. According to Oliveira

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et al. (2009) the growth rings in *A. angustifolia* are formed between the spring (October) and autumn (May) months, with the day length and temperature being the main environmental factors influencing the seasonal cambial activity. Seitz and Kanninen (1989), based on stumps of ten trees, developed a ring-width chronology with a high mean correlation among trees ($r = 0.6$ for a 54 year period), indicating annual growth synchronism among individuals for a subtropical forest in south Brazil. Lisi *et al.* (2001) found $\Delta^{14}C$ concentrations in dated growth rings of *A. angustifolia* in conformity with temporal changes of atmospheric $\Delta^{14}C$ concentrations from the effects of nuclear bombs during the 1960s. Such synchronization between atmosphere and wood isotopical series performed an independent evidence of annual growth ring formation in this species. Nevertheless, basic questions have not been addressed yet, such as: to what degree do tree-ring chronologies correlate among different sites? And how is tree-ring variability related to climate?

Araucaria angustifolia occurs naturally in the southern and southeastern Brazilian highlands (also in the northwest of Argentina and southeast of Paraguay) from 19°15′ to 31°30′ S and 41°30′ to 54°30′ W, and between 400 and 1800 m a.s.l. (Hueck 1972; Carvalho 2003). Its spatial distribution is associated with a subtropical climate (Backes 1999), characterized as mild-mesothermic with abundant and evenly distributed rainfall (Nimer 1989). The El Niño Southern Oscillation (ENSO) and the South Atlantic Convergence Zone (SACZ) are the main atmospheric circulation features determining temporal variations in those general climate characteristics. Above average rainfall and temperature tend to occur during the ENSO warm phase (El Niño), and lower rainfall and temperature during the cool phase (La Niña) (Aceituno 1988; Grimm *et al.* 2000; Montecinos *et al.* 2000; Fontana & Berlato 2003). During the spring (October–November) there is a clear spatial coherence in the southeast sector of South America facing the manifestation with either warm-humid or cold-dry signals (Montecinos *et al.* 2000). Also, the alternate conditions of drought and humidity during the summer are related to the migration and strengthening of the SACZ (Nogués-Paegle & Mo 1997). SACZ intensification is associated with a precipitation deficit over the South American subtropics. Instead, when the SACZ weakens, the precipitation in the region is abundant (Casarin & Kousky 1986; Diaz & Aceituno 2003).

In the region of natural occurrence of *Araucaria angustifolia*, the indigenous vegetation composes a forest-grassland mosaic. The forests, commonly known as Araucaria forests, are distinct associations among tropical and austral-antarctic floras (Rambo 1951, 1953, 1956a,b; Waechter 2002), in which *A. angustifolia* forms an emergent or canopy stratum, mostly on mountain slopes and upper river valleys (Jarenkow & Baptista 1987; Veloso *et al.* 1991). On the uplands, Araucaria forest patches intermingle with grassland (known as Campos), characterized by a dense stratum of tall tussock grasses (Klein 1960; Duarte *et al.* 2006b). Palaeopollen and charcoal evidence (Behling 2002; Behling *et al.* 2004; Behling & Pillar 2007), supporting earlier phytogeographical studies (Rambo 1951, 1953, 1956a,b; Klein 1975), show that Campos was the dominant vegetation type during the last glacial and post-glacial phases. Campos have been progressively colonized by Araucaria forest elements since 4000 years before present. This forest expansion process has been facilitated by changes in climate, with prevailing wetter and cooler conditions, but also restricted by fire and, later, grazing regimes (Pillar & Quadros 1997; Behling 2002; Behling *et al.* 2004; Behling & Pillar 2007). Under current climate conditions, Araucaria forest expansion over Campos can be detected, especially in mosaic areas undisturbed by fire and cattle grazing (Oliveira 2003; Pillar 2003; Oliveira & Pillar 2004). Moreover, *A. angustifolia* is frequently found as a pioneer tree colonizing Campos, and it is likely acting as an attractor to animals dispersing other forest diaspores (Duarte *et al.* 2006a).

A better understanding of climate and vegetation dynamics in the southern Brazilian highlands can be substantially improved by the information derived from the application of dendrochronological techniques. In the present paper we investigate long-term growth patterns of *A. angustifolia* through high-resolution growth ring time series and its association with climate over the last century.

METHODS

Study location and climate

The study region is the highland plateau (around 1000 m a.s.l.), corresponding to the southeastern limit of the species distribution. The indigenous vegetation is a mosaic of Campos and Araucaria forest. Cattle grazing, logging, agriculture and silviculture have been the main land use. The study sites are an Araucaria forest stand, at Floresta Nacional de São Francisco de Paula (FSP; 29°25′44″S, 50°23′31″W; 866 m a.s.l.), a federal conservation unit (since 1945) in São Francisco de Paula municipality (Figs 1a,2a); and a group of *A. angustifolia* trees growing over Campos, at Fazenda Monte Negro (FMN; 28°35′37″S, 49°48′56″W; 1265 m a.s.l.), a private farm with extensive cattle grazing in the São José dos Ausentes municipality (Figs 1b,2a).

Both sites presented rock outcrops, indicating shallow soils. The terrain slope was approximately 5 and 20 degrees at FSP and FMN, respectively. According to FSP managers, selective logging of a few *A. angustifolia* trees occurred at the studied stand in the mid-1940s. At FMN, the grassland has been managed with fire by decades, as reported by local farmers and evidenced by carbonized bark and fire scars in several studied trees.

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Fig. 1. Study sites. Araucaria forest stand at Floresta Nacional de São Francisco de Paula, showing a large *Araucaria angustifolia* tree surrounded by smaller broadleaf trees (a) and a group of *A. angustifolia* trees established over Campos (grassland) at Fazenda Monte Negro (b).

The climate in the study region, as in the entire species distribution area, is mild-mesothermic with well-distributed rainfall throughout the year (Nimer 1989). According to regional meteorological data, the mean annual temperature is 16°C and the mean total annual precipitation is 1805 mm. Frosts on open areas and sporadic snowfall on higher altitudes may occur, especially in winter. Monthly normal temperature and precipitation for the study region are shown in Figure 2b.

Sampling and analysis of wood cores

Thirty living *A. angustifolia* trees were selected per site. The average trunk diameter at breast high of these trees was 70 cm (SD ± 14) at FSP and 46 cm (SD ± 14) at FMN; and the average total height was 18 m (SD ± 1) at FSP and 14 m (SD ± 3) at FMN. For each tree, between two and five transversal wood cores were obtained with the help of an increment borer (∅ = 5.1 mm), totaling 114 and 108 cores at FSP and FMN, respectively. The sampling was carried out in May 2004 and August 2005 at FSP, and in June 2004 and November 2004 at FMN.

The cores were mounted on wooden supports, air-dried and mechanically polished with sandpaper of gradually finer grades of grit (from 80 to 600 grains). The growth rings were inspected with a stereomicroscope and dated according to the methods described in Stokes and Smiley (1968). The calendar age of the growth rings was assigned according to the Schulman (1956) method, and widths measured with a Velmex Measuring System (precision of 0.01 mm). In order to check dating accuracy, the resulting ring-width time series were compared within and among trees at each collection site, by synchronizing patterns of wide and narrow growth ring (cross-dating), with the help of printed graphics and COFECHA software (Stokes & Smiley 1968; Holmes 1983). Cross-dating is only possible if tree-growth is influenced by climatic conditions. This gives a similar time-pattern of growth in a defined tree population, allowing the verification of annual tree ring formation and correction of primary dating errors caused by wood-anatomical irregularities, such as partial or false rings. After cross-dating, the width of partial growth rings was estimated according to the growth trends observed in complete cores of the same tree.

Standardized series and site chronologies

Ecological factors influencing tree-growth may be better identified after partitioning the time series of ring-width in different frequency-responses. In order to emphasize the year-to-year growth variation the cross-dated series were averaged for each tree and then standardized. For each tree series we fitted a cubic smoothed spline function, 50% frequency-response cut-off for 50 years segment length, and computed the ratios between observed and predicted values (Cook & Kairiukstis 1990). In ratio series the autocorrelation was filtered using autoregressive linear modelling (Cook 1985). The resulting series (standardized series) were dimensionless, with unit mean and linear autocorrelation close to zero.

Site chronologies were obtained by combining the standardized series on a bi-weighted robust mean series (Cook 1985; Cook & Kairiukstis 1990). The chronologies' quality was evaluated by the mean correlation between trees – $\bar{r}_b$, the mean correlation within trees (tree series *vs.* site chronology) – $\bar{r}_w$ and the mean sensitivity index – $\bar{s}$ (Fritts 1976; Holmes 1983; Cook & Kairiukstis 1990). The association between chronologies was verified using correlation analysis, computed for the common time-span and for moving windows of 30 years length lagged 1 year. To check the correlation significance 90% confidence limits were obtained through 1000 randomization iterations for each moving-window. Standardizations, growth-ring indices, $\bar{r}_b$ and $\bar{s}$ were computed on ARSTAN software (Cook 1985; Cook & Krusic 2005); $\bar{r}_w$ was computed on COFECHA software (Holmes 1983).

Tree-growth patterns and relationships with climate

To explore growth patterns among trees we carried out ordinations (principal component analysis), based on correlation matrices comparing trees by their standardized growth series. Ordinations were carried out for the 1911 to 2000 time period and for moving windows of 30 years in length lagged 15 years, within that period. In each ordination, only series longer than 75% of the window length were considered. These analyses were computed on MULTIV software (Pillar 2006). The use of PCA to explore growth patterns in tree-ring series has been

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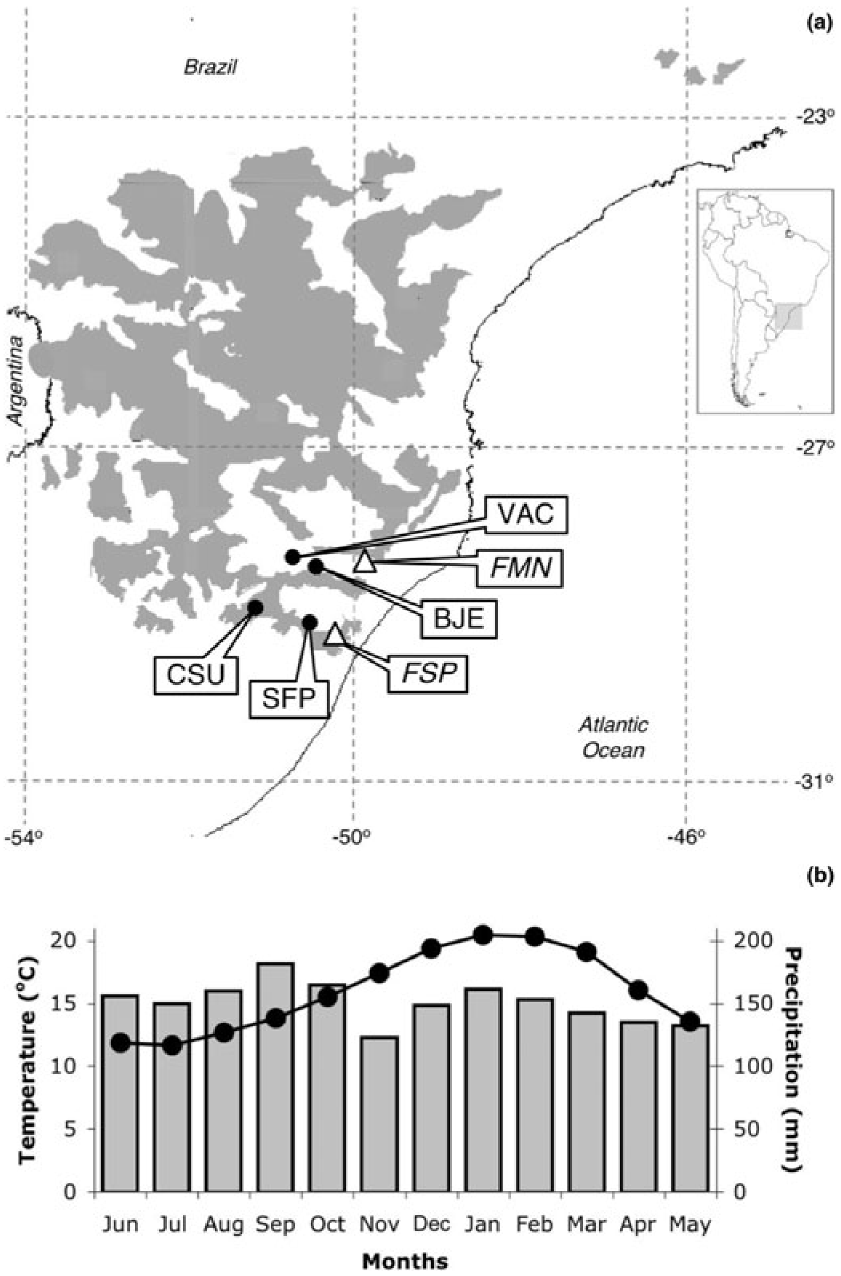

Fig. 2. (a) Location of the study sites (triangles), meteorological stations (dots) and the geographical distribution of *Araucaria angustifolia* (grey patches); (b) long-term monthly averages of mean temperature (line) and total precipitation (bars) for the study region. See Table 2 for meteorological data specifications. BJE, Bom Jesus; CSU, Caxias do Sul; FMN, Fazenda Monte Negro; FSP, Floresta Nacional de São Francisco de Paula; SFP, São Francisco de Paula; and VAC, Vacaria.

applied elsewhere, but based on correlation between site chronologies (e.g. Villalba *et al.* 1998; Szeicz *et al.* 2000; Díaz *et al.* 2002; Filippo *et al.* 2007).

Tree-growth and climate associations were investigated applying correlation and regression analyses. As regional descriptors of tree-growth we considered the first two principal components generated for the 1911 to 2000 time period. The climate variables were annual series of total precipitation and mean temperature, recorded monthly in four meteorological stations near the sampled sites, but spanning different periods (Fig. 2a; Table 1). After centring, the climate series were averaged among sites to generate a single regional annual series for each monthly variable, covering the 1913 to 1998 period. The tree-growth series (principal components) were then correlated to each of these series of monthly variables, matching the series by the same year (lag = 0) or by the previous year (lag = 1, e.g. tree-growth of 1990 matching the climate data of 1989). By ordering the resulting correlation coefficients chronologically, we generated a correlation profile, highlighting monthly periods of stronger climatic influence on tree-growth. The climate variables in those periods were used as factors in regression

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Table 1. Meteorological stations location and record period

Abbreviation	SFP	CSU	BJE	VAC
Municipality	São Francisco de Paula	Caxias do Sul	Bom Jesus	Vacaria
Latitude	29°20′S	29°10′S	28°40′S	28°33′S
Longitude	50°31′W	51°12′W	50°26′W	50°42′W
Elevation a.s.l.	912 m	759 m	1047 m	954 m
Record period	1913–1961	1931–1998	1948–1998	1931–1997

models predicting the annual tree-growth described by the principal components. Only uncorrelated climatic variables were included in the models to avoid multi-collinearity. Randomization tests were applied to evaluate the statistical significance of the regression models (Manly 1991).

RESULTS

Site chronologies

The synchronization of the tree ring width series indicated a common growth trend among *A. angustifolia* trees within both study sites: 17 trees at FSP and 18 at FMN were successfully cross-dated. Anatomical irregularities, mainly partial rings and periods of fuzzy growth ring boundaries caused difficulties for cross-dating, leading to a smaller sample size in the chronology. The occurrence of those tricky anatomical features increased with tree age, especially at FMN. Hence, at that site some older trees were not completely cross-dated, with the earlier portions excluded from further analyses. Intra-annual density fluctuations (false rings) and resin deposition were also observed but did not present major difficulties for accurate dating (Fig. 3).

The period represented by five or more trees spanned from 1882 to 2003 at FSP, and from 1861 to 2003 at FMN. Descriptive statistics and graphical representation of FSP and FMN chronologies are shown in Table 2 and Figure 4, respectively.

According to visual inspection of individual ring-width series, the logging at FSP in the mid-1940s, as reported by local managers, was not associated with release or suppression trends in the sampled trees. That disturbance event thus was not likely to produce a bias in the site chronology.

The correlation between FSP and FMN chronologies considering the total common period (122 years) was $r = 0.31$ ($P = 0.002$). However, according to the moving window analysis, the strength of this association increased from earlier to latter periods, being significant after 1925 (Fig. 5).

Tree-growth patterns and relationships with climate

The ordination analysis for the overall period (1911 to 2000) revealed convergent and divergent growth trends between FSP and FMN trees. The first principal component (PC1) defined a direct association between FSP and FMN trees – a convergent trend, while the second principal component (PC2) showed opposite relation between the sampled sites – a divergent trend. The growth-variance explained by PC1 (25%) was approximately twofold higher than PC2 (13%), indicating that the convergent trend was more relevant than the divergent one. Ordination analyses in shorter time periods (30 year windows) indicated that these patterns were consistent through time (Fig. 6).

The profiles describing the correlation between the principal components and climate variables showed monthly periods with relevant climatic influence on annual tree-growth. Therefore, distinct climatic signals were linked to PC1 and PC2 (Fig. 7). Convergent growth trends (PC1) were mostly related to thermal conditions during the autumn and summer months. The correlation between PC1 and mean temperature was negative for the previous May, negative for the current December and January, and positive for the current May and June. These climate variables combined in a linear model explained 32% ($P = 0.0001$) of PC1 variation (Fig. 8). Divergent growth trends (PC2) were weakly associated with climate; the most relevant trend was a negative correlation to total precipitation in August preceding the current growing season. Thus, August rainfall was directly associated with growth on FMN and inversely on FSP. Nevertheless, this variable explained only 8% ($P = 0.0088$) of PC2 variation (Fig. 8).

DISCUSSION

Tree-ring time series and growth patterns

Tree-ring series of *Araucaria angustifolia* were successfully cross-dated and combined in site chronologies. However, partial rings made cross-dating a very difficult task at both analyzed sites. These abnormal growth rings, resulting from discontinuous cambium activity over the meristematic sheath (Kozlowski 1971; Larson 1994), represent an important limitation for dendrochronological development in many tropical and subtropical species (Dunwiddie 1979; Ogden 1981; Ash 1983; Norton *et al.* 1987; February & Stock 1998; Bergin 2000; Worbes 2002; Brienen & Zuidema

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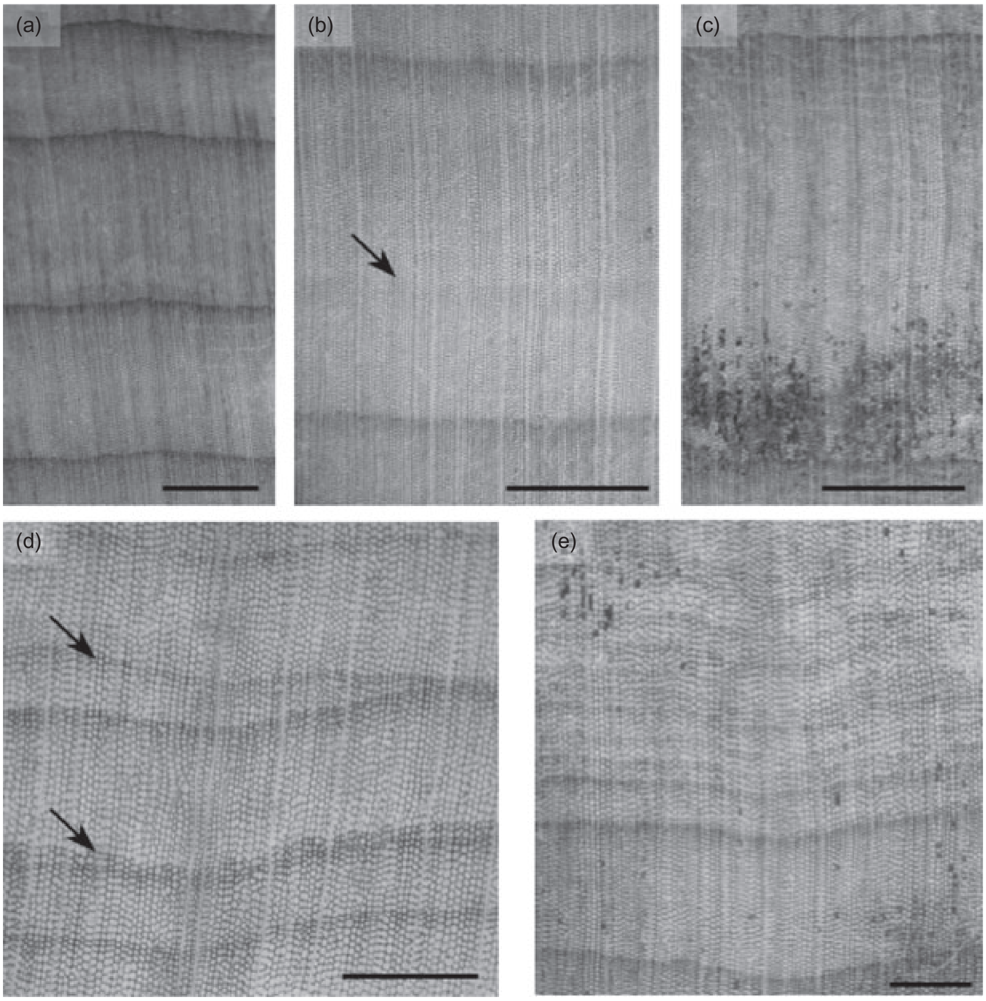

Fig. 3. Growth ring features of *Araucaria angustifolia*. In (a) typical growth rings, with conspicuous earlywood and latewood cells; (b) intra-annual density fluctuation (arrow); (c) resin deposition; (d) partial rings (arrows); and (e) conspicuous growth rings preceding a period with growth rings of fuzzy boundaries. Scale bars, 2 mm.

Table 2. Descriptive statistics of *Araucaria angutifolia* ring-width chronologies

	FSP	FMN
Time span	1882–2003 (122 years)	1861–2003 (143 years)
Number of trees	17 (out of 30)	18 (out of 30)
Number of cores	54 (out of 114)	62 (out of 108)
Number of growth rings	1621	1911
Mean series length	122 years (SD ± 16)	90 years (SD ± 25)
$\bar{r}_b$	0.25 (SD ± 0.04)	0.34 (SD ± 0.06)
$\bar{r}_w$	0.49	0.57
$\bar{s}$	0.24	0.16

FMN, Fazenda Monte Negro; FSP, Floresta Nacional de São Francisco de Paula; $\bar{r}_b$, mean correlation between trees; $\bar{r}_w$, mean correlation within trees; and $\bar{s}$, mean sensitivity index.

2005). Partial rings had been reported in *A. angustifolia* (Seitz & Kanninen 1989; Oliveira *et al.* 2009) and other Araucariaceae, such as *Araucaria cunninghamii* (Ogden 1981; Ash 1983), *Agathis robusta* (Ash 1983), *Agathis moorei* (Détienne 1989), *Agathis australis* (Dunwiddie 1979; Norton *et al.* 1987) and *Wollemia nobilis* (Heady *et al.* 2002). As in *A. angustifolia*, partial rings are frequent in *Agathis australis* and *Pinus ociden-*

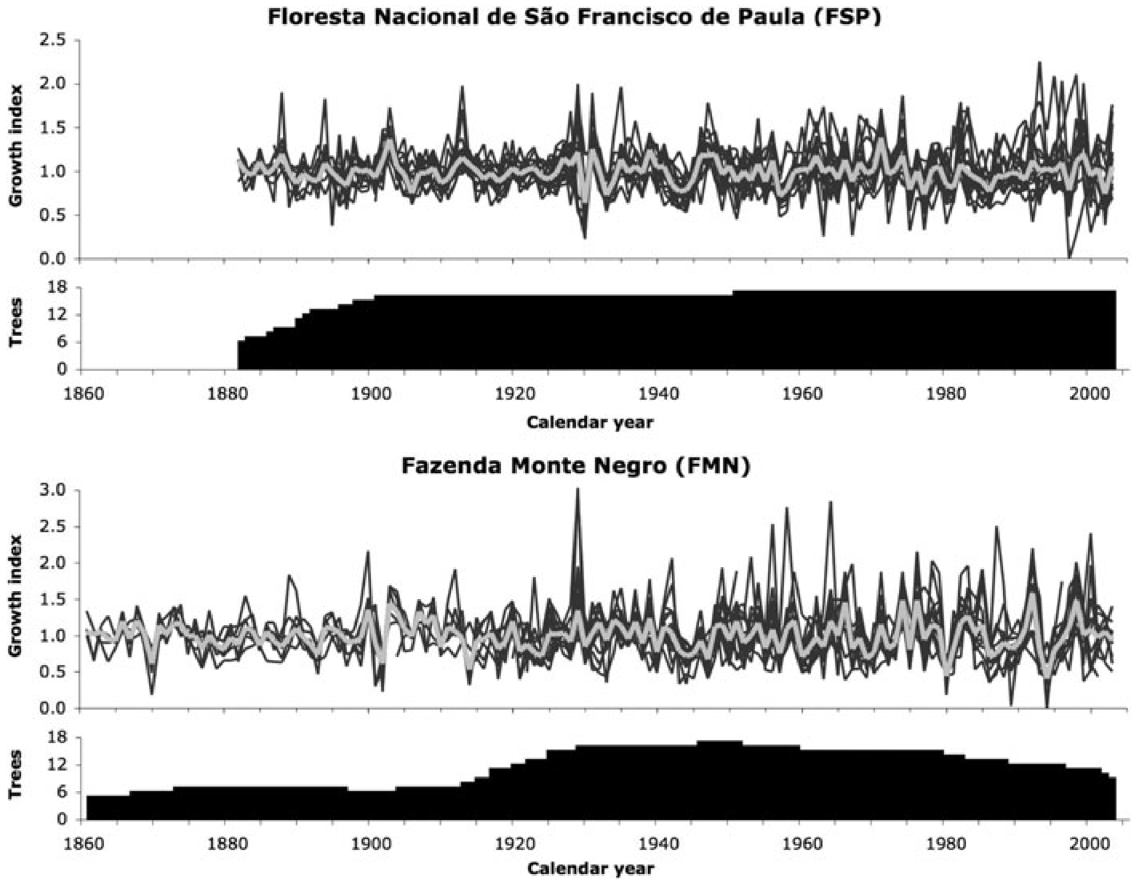

Fig. 4. Ring-width chronologies of *Araucaria angustifolia* from Floresta Nacional de São Francisco de Paula (FSP) and FMN (Fazenda Monte Negro). For each chronology the standardized series per tree (black lines), the bi-weighted robust mean (grey line) and the sample size (number of trees) are shown.

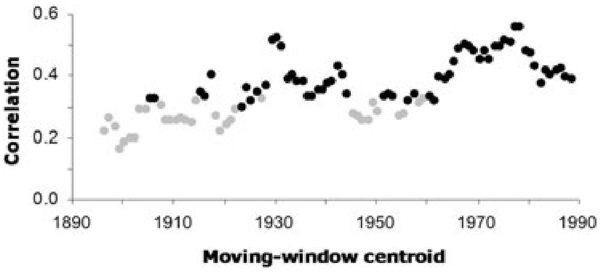

Fig. 5. Correlation between ring-width chronologies of *Araucaria angustifolia* from Floresta Nacional de São Francisco de Paula (FSP) and Fazenda Monte Negro (FMN) on 30-year moving-windows. The black dots identify significant correlations (non-significant in grey), considering a 90% confidence limit obtained through 1000 randomization iterations for each moving-window.

talis but careful cross-dating allowed long-term ring-width chronologies to be developed with these species (Buckley *et al.* 2000; Fowler *et al.* 2000; Speer *et al.* 2004; Boswijk *et al.* 2006). Further studies concerning the occurrence and morphology of partial rings in *A. angustifolia*, as did Lorimer *et al.* (1999) with *Acer saccharum*, would help the cross-dating of wood samples, particularly those obtained with increment borers.

The intra-annual density fluctuations (false rings) in *A. angustifolia* were generally a band of latewoodlike cells within the earlywood. Because the temporal variation of false-ring formation in a given tree population is commonly related to climate conditions (e.g. Wimmer *et al.* 2000; Rigling *et al.* 2002; Cherubini *et al.* 2003; Vieira *et al.* 2009) we surmise that those false rings in *A. angustifolia* would be related to a short dry period during the growing season causing a temporary reduction of cell elongation. Further studies about such tree-ring anomalies may provide valuable dendroclimatic information.

Growth synchronization within trees at FSP and FMN corroborates preliminary dendrochronological investigation showing a common growth trend for *A. angustifolia* trees growing in a subtropical forest at São João do Triunfo (SJT), in the Paraná state, Brazil (Seitz & Kanninen 1989). The growth correlation within sites was similar at FSP and FMN ($\bar{r}_b \approx 0.3$), but lower than that found in SJT ($\bar{r}_b = 0.6$). Such a difference may really indicate a stronger common growth signal

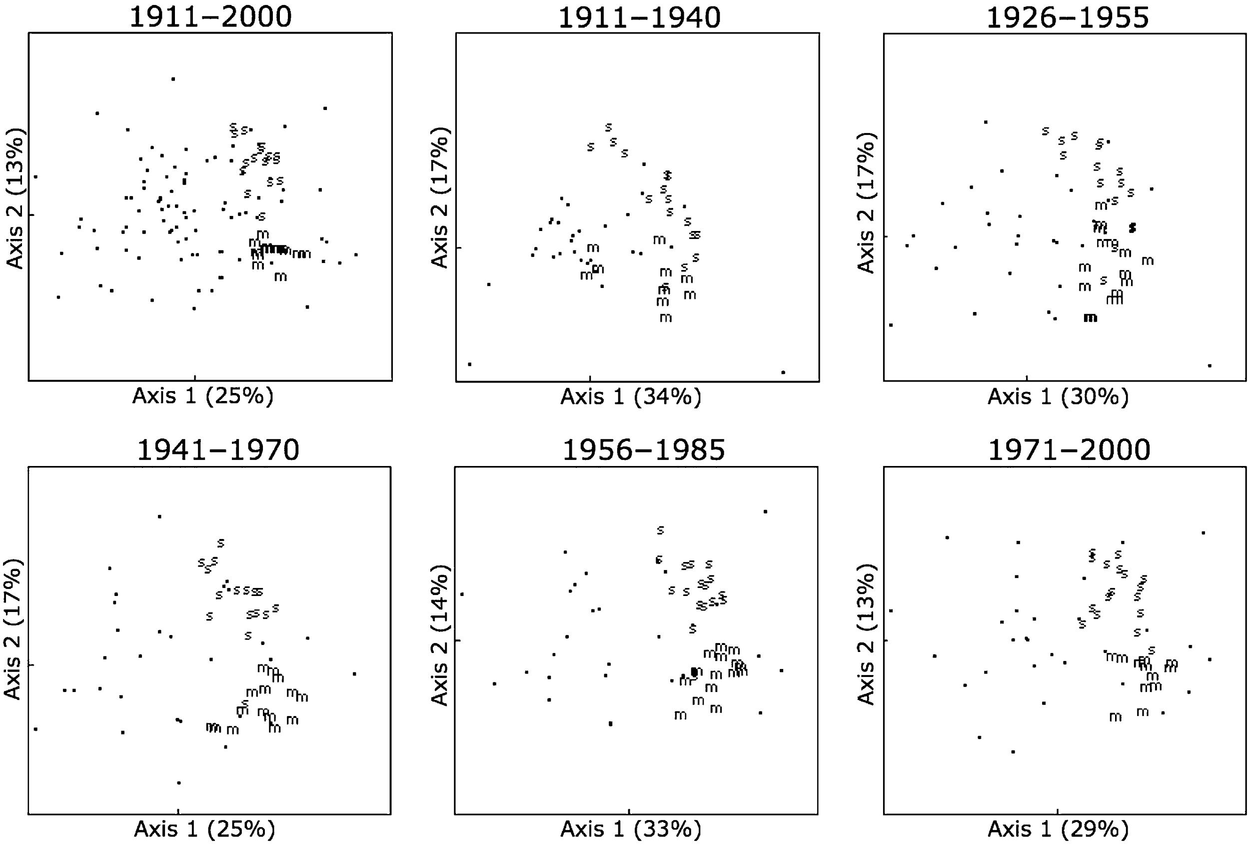

Fig. 6. Ordination analyses of years (dots) described by standardized growth series of trees from Floresta Nacional de São Francisco de Paula (s) and Fazenda Monte Negro (m), in different time intervals.

at SJT, but also may be related to particular sampling, standardization and correlation computation (series length) methods. Rather than differences, those results indicate that growth ring chronologies of *A. angustifolia* may be developed over a larger geographical extent, since SJT is about 380 km north from FSP and FMN.

The mean sensivity of *A. angustifolia* was medium when compared with tree species from temperate, subtropical and tropical zones; the inter-series correlation was also moderate compared with temperate and subtropical species, but high compared with tropical species (Table 3). Nevertheless, such comparisons must be taken carefully because mean sensitivity and inter-series correlation are influenced by many environmental and biological factors not considered here (Fritts 1976). Especially, the levels of inter-series correlation are highly influenced by the number of observations (series length).

Correlation and ordination analyses comparing growth time-series demonstrate that trees at FSP and FMN, which are approximately 100 km distant and growing under distinct habitat and disturbance regimes, share a relevant year-to-year growth signal. Such a regional growth trend is strong evidence of seasonal cambial activity (Fritts 1976; Stahle 1999), confirming annual growth ring production in *A. angustifolia* (Seitz & Kanninen 1989; Lisi *et al.* 2001; Oliveira *et al.* 2009) and suggesting the existence of regional environmental factors forcing inter-annual growth trends.

Considering the moving-correlations between FSP and FMN chronologies, non-significant correlations prior to 1925 would be related to low sample size in the earlier period, especially in FMN (see Fig. 4). Also, growth sensitivity to climate variation may differ between young and old trees, like that observed in *Pinus pinaster* (Vieira *et al.* 2009). If it is true, we supose that young *A. angustifolia* trees would be more influenced by local (e.g. disturbances, soil nutrition) than regional (climate) factors, resulting in non-significant correlation between site chronologies in the earlier period.

Ordination analysis evidenced spatial patterns related to long-term growth of *A. angustifolia*. The first principal component (PC1) highlighted convergent tree-growth between FSP and FMN, while the second principal component (PC2) showed divergent growth between those sites. We infer that these patterns were linked to environmental forces operating at different

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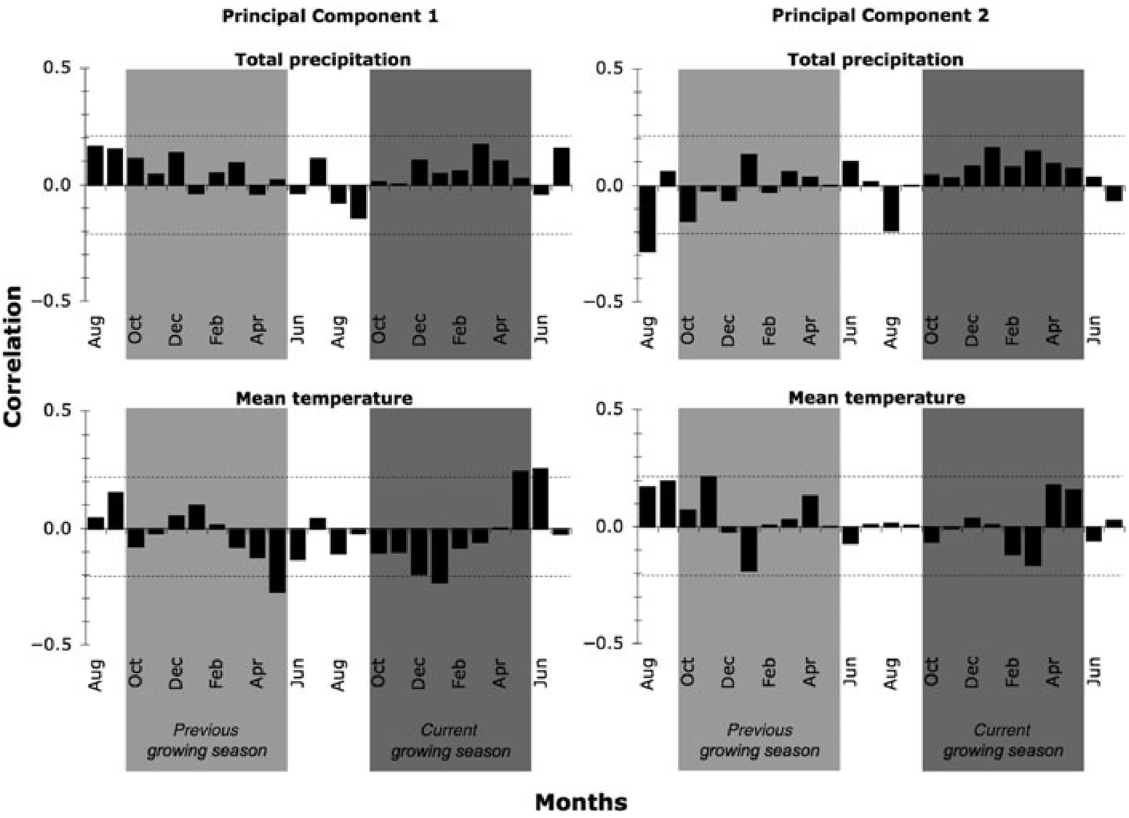

Fig. 7. Correlation between annual tree growth (principal components) and monthly climate variables (departures of total precipitation and mean temperature). Shaded periods identify the previous and current growing seasons and dashed lines the 95% confidence limits.

spatial scales: convergent trends should be related to regional environmental factors and divergent trends to local environmental factors influencing the tree-growth response to macro-environmental conditions. According to these hypotheses, year-to-year growth variation of *A. angustifolia* would be more influenced by regional than local scale factors, since PC1 represents a larger growth variation in the system than PC2.

Tree-growth links to climate

Based on those hypotheses, when compared with regional climate variables, PC1 will present stronger association to climate than PC2. Our correlation and regression analyses describing the linear association between ordination axes and climate variables confirm that expectation and support the hypotheses. Moreover, our results reinforce the relevance of climatic conditions for inter-annual variation of secondary growth in *A. angustifolia*.

Convergent growth trends were related to temperature conditions during the summer and autumn months. The negative growth response to temperature for the current December and January may indicate water stress due to increased evapotranspiration in hot months. Similar growth response was found in *Araucaria araucana* (Molina) K. Koch growing in xeric Patagonian sites (Villalba *et al.* 1989). In high-elevation subtropical Andean sites, under a seasonal precipitation regime, some tree species presented a negative growth response to summer temperature, synchronous to a positive response to precipitation (Morales *et al.* 2004). In *A. angustifolia*, however, correlations between PC1 and precipitation during the current growing season months were not statistically significant (despite being positive). We conjecture that growth relationships to autumn temperature, negative for the previous May and positive for the current May and June, suggest that temperature would determine whether *A. angustifolia* will mobilize carbohydrate for wood formation (Kozlowski & Pallardy 1997) in the late growing season or store it for the next growth period. It would mean that high autumn temperature influences the current growth ring, under development since the previous spring (Oliveira *et al.* 2009), to be wide. Although May and June correspond to the late growing season (Oliveira *et al.* 2009), stored carbohydrates would be the main energy source for wood formation related to the temperature stimulus. Thus,

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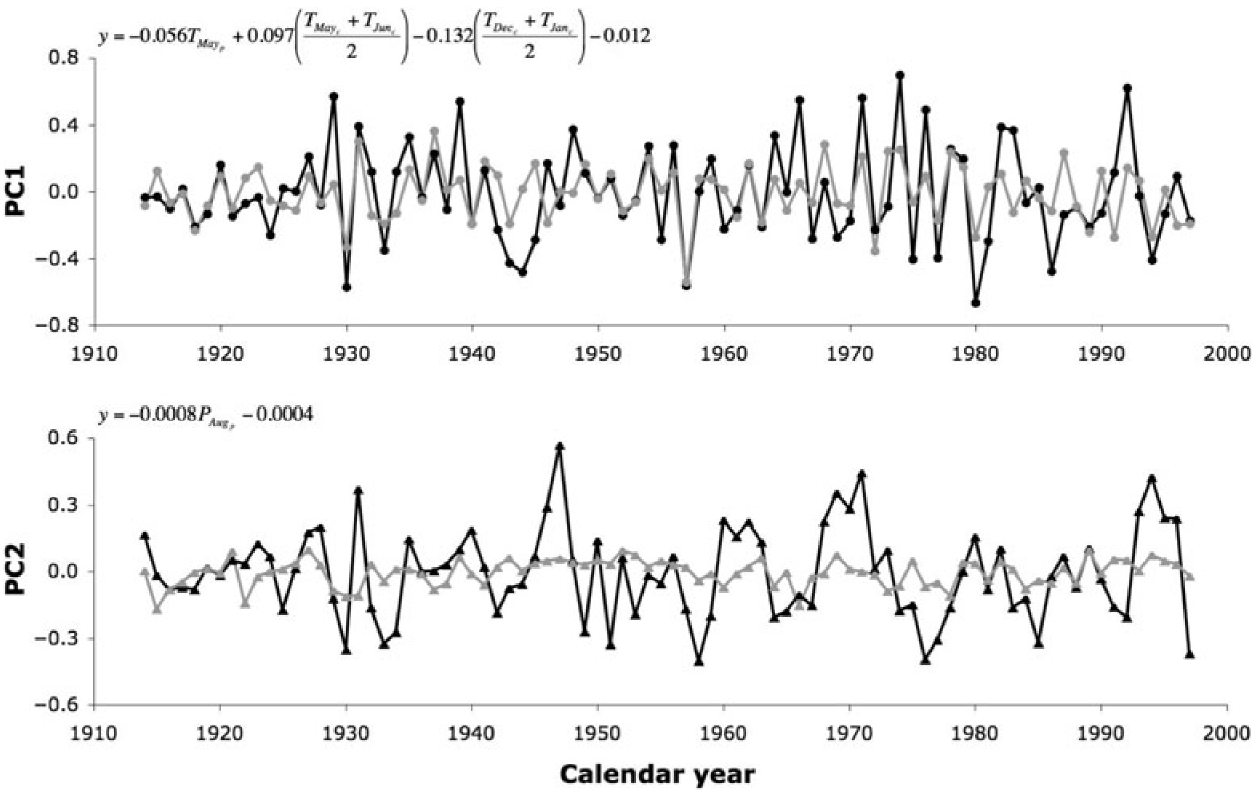

Fig. 8. Observed (black lines) and predicted (grey lines) annual tree-growth, described by the first (PC1) and second (PC2) principal components. Predictive models based on climate variables are shown above each graphic, where *T* and *P* are, respectively, departures of mean temperature and total precipitation in a given month of the current (*c*) or previous (*p*) year.

high autumn temperature also implies that a lower level of stored carbohydrate would be available for the next growing season, determining the new growth ring to be narrower. Opposite relations would be expected under low autumn temperatures.

Dendroclimatic research in *Agathis australis* (Buckley *et al.* 2000) revealed that its annual radial growth is mostly dependent on rainfall during the previous growing period, but growth-temperature relationships were similar to those that we observed in *A. angustifolia*: negative correlations with temperature on the current growing season (mainly, December and January) and the previous autumn (May). According to those authors, clear sunny days in early summer (October to December) may be associated with cold nights, which bring down mean temperatures. Thus, negative correlation to current summer temperature must reflect a direct influence of sunshine hours on radial growth. The authors did not discuss the growth association with previous autumn temperature.

Convergent growth variation of *A. angustifolia* was associated with temperature but not to precipitation. A dendrochronological study of *Cedrela fissilis* Vell., a deciduous Meliaceae tree, growing in the Araucaria forest in Paraná (Brazil), revealed a significant long-term correlation to temperature and no correlation to precipitation (Dünisch 2005). Moreover, intra-annual cambial activity of *A. angustifolia* and, apparently, *C. fissilis* is mainly influenced by seasonal temperature and photoperiod variation (Dünisch 2005; Oliveira *et al.* 2009). This evidence points to temperature as a major regional factor determining seasonal and inter-annual cambium activity of trees in subtropical mountain rainforests of southern Brazil.

Divergent growth trends were inversely related to total precipitation in August of the previous growing season, that is, the correlation was negative in FSP (forest) and positive in FMN (grassland). This pattern suggests an interaction between regional climate (rainfall) and local disturbance (fire regimes in grassland) affecting tree-growth. In traditional cattle raising farms, Campos are burned systematically (every 2 or 3 years) in order to remove dead herbaceous biomass and stimulate grass resprounting in spring. Anthropogenic fires on Campos are usually ignited between August and September (Heringer & Jacques 2001). August rainfall must influence fire characteristics, being inversely related to fire intensity (Pillar 2003). Fire management may influence *A. angustifolia* trees established over Campos by reducing tree-growth due to injuries on plant tissues; or improving tree-growth by making available mineral nutrients resulting from

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Table 3. Descriptive statistics of *Araucaria angutifolia* ring-width chronologies compared with some tree species from temperate, subtropical and tropical zones. When more than one chronology was considered the values were averaged. The number of chronologies in which the values were based is shown in parentheses

Zone	Species	$\bar{s}$	$\bar{r}_b$	$\bar{r}_w$	Data source
Subtropical	*Araucaria angustifolia*	0.20$^{(2)}$	0.40$^{(3)}$	0.53$^{(2)}$	Seitz and Kanninen (1989); the present study
Temperate	*Araucaria araucana*	0.08$^{(1)}$			Innes *et al.* (2000)
Temperate	*Podocarpus nubigena*	0.10$^{(2)}$			Innes *et al.* (2000)
Temperate	*Pilgerodendron uviferum*	0.11$^{(4)}$			Innes *et al.* (2000)
Temperate	*Fitzroya cupressoides*	0.17$^{(24)}$	0.24$^{(24)}$		Innes *et al.* (2000); Lara *et al.* (2000)
Temperate	*Austrocedrus chilensis*	0.20$^{(26)}$			Villalba and Veblen (1997); Innes *et al.* (2000)
Temperate	*Larix decidua*	0.26$^{(17)}$	0.48$^{(24)}$		Frank and Esper (2005); Carrer & Urbinati 2006
Temperate	*Nothophagus pumilio*	0.28$^{(16)}$			Villalba *et al.* (1997); Innes *et al.* (2000)
Temperate	*Pinus ponderosa*	0.35$^{(21)}$	0.45$^{(21)}$		Fritts and Shatz (1975)
Temperate	*Pseudotsuga menziesii*	0.38$^{(44)}$	0.40$^{(44)}$		Fritts and Shatz (1975)
Temperate	*Pinus edulis*	0.42$^{(11)}$	0.36$^{(11)}$		Fritts and Shatz (1975)
Temperate	*Abies alba*		0.29$^{(11)}$		Frank and Esper (2005)
Temperate	*Picea abies*		0.29$^{(5)}$		Frank and Esper (2005)
Temperate	*Pinus cembra*		0.25$^{(30)}$		Frank and Esper (2005)
Subtropical	*Polylepis tarapacana*	0.19$^{(1)}$	0.33$^{(1)}$		Morales *et al.* (2004)
Subtropical	*Prosopis ferox*	0.28$^{(1)}$	0.27$^{(1)}$		Morales *et al.* (2004)
Subtropical	*Junglans australis*	0.30$^{(3)}$	0.37$^{(3)}$		Morales *et al.* (2004); Villalba *et al.* 1985
Subtropical	*Alnus acuminata*	0.30$^{(1)}$	0.29$^{(1)}$		Morales *et al.* (2004)
Subtropical	*Cedrela angustifolia*	0.33$^{(2)}$	0.42$^{(2)}$		Villalba *et al.* 1985
Subtropical	*Agathis australis*		0.58$^{(9)}$		Buckley *et al.* (2000)
Subtropical	*Cedrela fissilis*			0.56$^{(1)}$	Dünisch (2005)
Tropical	*Tectona grandis*	0.34$^{(4)}$	0.21$^{(1)}$		Shah *et al.* (2007); Ram *et al.* (2008)
Tropical	*Pterocarpus angolensis*		0.53$^{(2)}$		Stahle *et al.* (1999)
Tropical	*Cedrela odorata*		0.24$^{(1)}$		Dünisch *et al.* (2003)
Tropical	*Swietenia macrophylla*		0.19$^{(1)}$		Dünisch *et al.* (2003)
Tropical	*Tachigali vasquezii*			0.18$^{(1)}$	Brienen and Zuidema (2005)
Tropical	*Peltogyne* cf. heterophylla			0.26$^{(1)}$	Brienen and Zuidema (2005)
Tropical	*Cedrelinga catenaeformis*			0.29$^{(1)}$	Brienen and Zuidema (2005)
Tropical	*Amburana cearensis*			0.35$^{(1)}$	Brienen and Zuidema (2005)
Tropical	*Pinus occidentalis*	0.44$^{(1)}$		0.44$^{(1)}$	Speer *et al.* (2004)
Tropical	*Bertholletia excelsa*			0.48$^{(2)}$	Brienen and Zuidema (2005)
Tropical	*Cedrela odorata*			0.57$^{(1)}$	Brienen and Zuidema (2005)
Tropical	*Cedrela fissilis*			0.65$^{(1)}$	Dünisch (2005)

$\bar{r}_b$, mean correlation between trees; $\bar{r}_w$, mean correlation within trees; and $\bar{s}$, mean sensitivity index.

burned Campos biomass. Our evidence indicates that the former situation is a more likely explanation for the positive relation between tree growth and precipitation in August for the grassland site (FMN). More intense grassland fires, due to lower rainfall during the ignition period (August), would cause damages to *A. angustifolia* trees established on grasslands (FMN), reducing tree-growth 2 years later.

Outlook to further dendroecological investigations

The formation of annual and climate-sensitive growth rings in *A. angustifolia* allow new opportunities to derive useful information for ecological studies in pluvial mountain ecosystems of subtropical South America. The counting of growth rings provides an estimation of tree age. Therefore, additional cross-dating of ring-width patterns may enhance age determinations to calendar year resolution. Studies on population structure of *A. angustifolia*, focused mostly on tree-size parameters (e.g. Souza 2007), would be improved in temporal scale by the simple application of dendrochronological techniques.

Hypotheses concerning the growth response of *A. angustifolia* to environmental variation, based on short-term experiments (e.g. Mósena & Dillenburg 2004), could be verified using analyses of longer ring-width time series. On the other hand, further ecophysiological investigations could clarify our hypotheses concerning mechanisms of regional climate and site-specific influence on tree growth.

Historical records of fire in Campos could be obtained through the analysis of fire scars in *A. angustifolia*. Such fire chronologies, therefore, could be used to test our hypothesis concerning the precipitation-fire-growth relationships.

Past and current anthropogenic disturbances, mostly logging, fire and grazing, seem to influence the tree-ring variation in *A. angustifolia*, and are highly frequent over the species geographical range. Further dendroclimatological studies would thus focus on low-disturbed remnants to diminish non-climatic signals. Small forest patches (approximately 5 ha) with old-growth trees (approximately 400 years old) were found in the studied region (J. M. Oliveira personal observation). In Campos, however, the existence of old growth *A. angustifolia* populations is dependent on fire-grazing management because in the absence of those disturbances, forests tend to expand over grasslands (see Behling & Pillar 2007). In areas where Campos have not been managed for decades, like in some Conservation Units, it is possible to study the disturbance effect on tree growth by comparing managed versus non-managed periods in tree-ring series.

The development of new tree-ring chronologies would help to better understand the influence of regional climate conditions on *A. angustifolia* growth in the Brazilian highlands. Moreover, the existence of multi-centennial *A. angustifolia* trees would bring a unique opportunity for climate reconstructions in eastern subtropical South America.

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