

Tree-growth responses across environmental gradients in subtropical Argentinean forests

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Abstract Subtropical forests in montane ecosystems grow under a wide range of environmental conditions. However, little is known about the growth responses of subtropical trees to climate along ecological gradients. To assess how, and to what extent climate controls tree growth, we analyzed tree responses to climate for 15 chronologies from 4 different species (*Schinopsis lorentzii*, *Juglans australis*, *Cedrela lilloi*, *Alnus acuminata*) across a variety of environments in subtropical forests from northwestern Argentina (22–28°S, 64–66°W). Using correlation and principal component analysis, site and species differences in tree-growth responses to precipitation and temperature were determined along the elevation gradient from the dry-warm Chaco lowlands to the wet-cool montane Yungas. Our results show that species responses differ

according to the severity in climate conditions along the elevation gradient. At sites with unfavorable conditions, mainly located at the extremes of the environmental gradient, responses of different species to climate variations are similar; in contrast, at sites with relatively mild conditions, tree growth displays a large variety of responses reflecting differences in both local environmental conditions and species physiology. Our research suggests that individualistic responses to environmental variability would determine differences in the type and timing of the responses of dominant trees to climate, which ultimately may shift species' assemblages in montane subtropical regions of South America under future climate changes.

Keywords Dendroecology · Climate responses · Environmental gradients · Yungas and Chaco forests

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Introduction

Individual tree responses to environmental changes have long-term implications for the structure and composition of forests. Several approaches have been used to determine the environmental factors that control tree growth (Oliver and Larson 1990). All local scale, soil conditions and disturbances regimes determine forest composition and rates of growth between trees separated by a few meters (Glock 1955;

Fritts 1976). However, at larger spatial scales the influence of microsite is less relevant and common patterns of tree growth can be identified (Delcourt et al. 1983). In mountainous regions, topography substantially modifies local environmental conditions by altering the regional climate and its interactions with soil properties (Oberhuber and Kofler 2000). In line with these observations, climatic factors affecting the growth of a particular species vary between sites and regions. In addition, the yearly seasonal period in which tree growth is influenced by climate varies between species (Glock 1955; Fritts 1974).

Exogenous and endogenous factors at stand level modulate tree growth, and variations in ring width have widely been used to ascertain these controls (Fritts 1974). Several dendroecological studies have dealt with climate-tree growth relationships along environmental gradients, encompassing different species and plant communities. For instance, major differences in growth responses to climate of several conifers from arid sites in western United States, are associated with site characteristics such as slope, elevation and aspect (Fritts 1974). In the Colorado Front Range, Villalba et al. (1994) found that abrupt environmental gradients determine different growth responses of a particular species to climate variations. Oberhuber and Kofler (2000) also indicated that forest stands growing under similar topographic conditions showed a large agreement in year-to-year variability in radial tree growth. In contrast, other authors reported that most variability in radial growth patterns and response to climate is largely accounted for by species differences (e.g. Graumlich 1993, Peterson and Peterson 1994). Analyzing the response of tree growth to climate in a mixed conifer-deciduous forest in the Great Lakes region, Graumlich (1993) identified three different groups (mesic hardwoods, drought-tolerant hardwoods, and pines) related to the structural and functional characteristics of the species, and noted that growth differences between species were more important than between sites. Similarly, tree-ring width chronologies from a particular species in northwestern United States are more closely related to each other than to chronologies from other species growing on the same site (Peterson and Peterson 1994).

Subtropical forests in northwestern (NW) Argentina extend across a wide range of climatic and topographic environments, ranging from extremely warm and xeric conditions in the Chaco lowlands (400 m) to cool and moist sites at higher elevations in the montane Yungas

(1,900 m). Previous studies on tree growth in the subtropical mountain forests from NW Argentina have provided a preliminary account of the large-scale patterns of climate variability influencing radial growth (Villalba et al. 1992; Ferrero 2011), but these studies were largely based on tree-ring chronologies from *Juglans australis*. The original network of subtropical chronologies developed from *J. australis* and *Cedrela lilloi* during the 1980s has recently been updated and expanded (Villalba et al. 1998, 2006). In addition, species new in dendrochronology have been added to increase the coverage of tree-ring records including *Alnus acuminata* (Grau et al. 2003; Paolini et al. 2005) in the montane Yungas, *Polylepis tarapacana* at the higher-elevation (>4,500 m) deserts in the Puna (Morales et al. 2004), *Prosopis ferox* (Morales and Villalba 2011) in the xeric Prepuna, and *Schinopsis lorentzii* (Ferrero and Villalba 2009) in the lowland xeric Chaco forest.

In South America, variations in tree-growth responses to climate have been evaluated along elevation and latitudinal gradients in southern temperate *Nothofagus* forests (Villalba et al. 1997, Lara et al. 2005). However, climate-related variations in tree growth (between different species) have rarely been considered in subtropical forests. The objectives of this study are: (1) to determine the climatic parameters that control tree growth across altitudinal ranges, (2) to assess the relative importance of site conditions versus species responses in modulating the growth of dominant tree species, and (3) to compare the variety of growth responses to climate variations for a single species from the lowland Chaco to the montane Yungas forests in NW Argentina. In the context of future climate changes, our research is relevant to determine the differences in tree-growth responses to climate along environmental gradients. Given the large diversity of species and environments, different responses to climate variations mediated by species and/or site conditions would have profound impacts on the structure and composition of subtropical montane forests in South America.

Materials and methods

Study area: climate and vegetation

The study area embraces two subtropical formations in NW Argentina (22–28°S): the montane Yungas and the adjacent Chaco lowlands (Fig. 1). The climate in the

region is monsoonal with a large percentage (70–90 %) of total annual precipitation concentrated in the summer season from November to March. The dry season extends up to 7 months (from April to October). In the Chaco lowlands, precipitation decreases from ~1,000 mm in the eastern wetter sector to less than 450 mm at the western dry sector near the Andes. Mean annual temperature ranges between 20 and 28 °C with some frosts in winter (Sarmiento 1972). The Chaco biogeographic province is a mosaic of grasslands, shrublands and semi-deciduous forests. Tree species show low rates of growth and high specific density wood (Morello 2002). *S. lorentzii* and *Aspidosperma quebracho-blanco* are the dominant tree species at the western sector or semiarid Chaco. *Bulnesia sarmientoi* and several *Prosopis* are also present (Sarmiento 1972; Cabrera 1994).

The montane Yungas forests extend along the Andes from tropical Peru and Bolivia to 28°S in NW Argentina (Killeen et al. 1993). This montane, humid forest formation ranges in elevation between 700 and 3,000 m (Grau et al. 2003). Mountains, mostly north–south oriented, enhance orographic precipitation on east-facing slopes to c.a. 3,000 mm. The rain shadow effect of the mountain creates semiarid environments with rainfall close to 800 mm at the western intermountain valleys (Fig. 2). Mean annual temperature oscillates from 22 °C in the Andes piedmont to less than 15 °C above 2,000 m. The locations of the altitudinal vegetation belts are modulated by the interactions between precipitation and temperature. Grau et al. (2003) reported that two montane forest types can be identified along the elevation gradient in NW Argentina. The semi-evergreen montane forest extends from 400 to 600 m in the transition with the Chaco forests to 1,700 m elevation. Forests are dominated by transitional elements including *Phoebe porfiria*, *Blepharocalyx gigantea*, *Cedrela* spp., *J. australis* and *Eugenia* spp. (Pennington et al. 2000). The humid, upper-montane forest, which extends from 1,700 to 2,700 m, is largely dominated by *J. australis*, *C. lilloi*, *A. acuminata* and *Podocarpus parlatorei*. This formation, adjacent to the persistently clouded grasslands, represents the relatively most humid and coolest forest formation in the subtropics. At higher elevations, the humid montane forest changes to the dry mountain forest (Prepuna) and gradually from grasslands and shrub steppes in the Prepuna to desert above 4,000–4,500 m in the main Puna.

Field collection, sample preparation and chronology development

Samples were collected at seven sites along a precipitation gradient from the Chaco-Yungas transition to the humid sites at the upper montane Yungas forests (Fig. 1). At the xeric Chaco forest, trees with high-density wood limited the use of increment bores; hence cross-sections from 16 individuals of *S. lorentzii* were collected (Ferrero and Villalba 2009). Two increment cores were taken at breast height from *J. australis*, *C. lilloi* and *A. acuminata* along the elevation gradients in the Yungas. Fourteen to 39 dominant trees were sampled at each site (Tables 1, 2). Cores were mounted, sanded and visually cross-dated following the standard procedures used in dendrochronology (Stokes and Smiley 1968). Ring widths were measured with a precision of 0.001 mm, and dating quality controlled with the COFECHA program (Holmes 1983). This program detects measurement and cross-dating errors in the individual series. The cross-dated series were standardized using the ARSTAN 40 program (Cook and Krusic 2005). Standardization, which removes age-related effects and variations due to endogenous stand disturbances, enhances the common signal present in tree-ring series (Fritts 1976). This procedure resulted in 15 chronologies: 1 of *S. lorentzii*, 3 of *A. acuminata*, 4 of *C. lilloi* and 7 of *J. australis* (Table 2). Both standard and residual chronologies were developed for each of the 15 sites using the 4 aforementioned species (Table 2). Residual chronologies are computed in the same manner as the standard versions, but the serial autocorrelation present in tree-ring series is removed (Cook 1985). We assessed the quality of the chronologies using the following statistics: mean sensitivity, R-bar and expressed population signal (EPS). The mean sensitivity is a measure of the year-to-year variability in ring width (Fritts 1976); the R-bar represents the mean of all possible correlation pairings, computed over a specific window time interval, among all tree-ring series from an individual chronology (Briffa 1995); the EPS estimates the degree to which a particular chronology resembles an infinitely-replicated hypothetical chronology (Briffa 1995). For the estimation of R-bar and EPS, we used a 50-year window with an overlap of 25 years between adjacent windows. A threshold for EPS of 0.85 is considered adequate to reflect the common growth signal (Wigley et al. 1984).

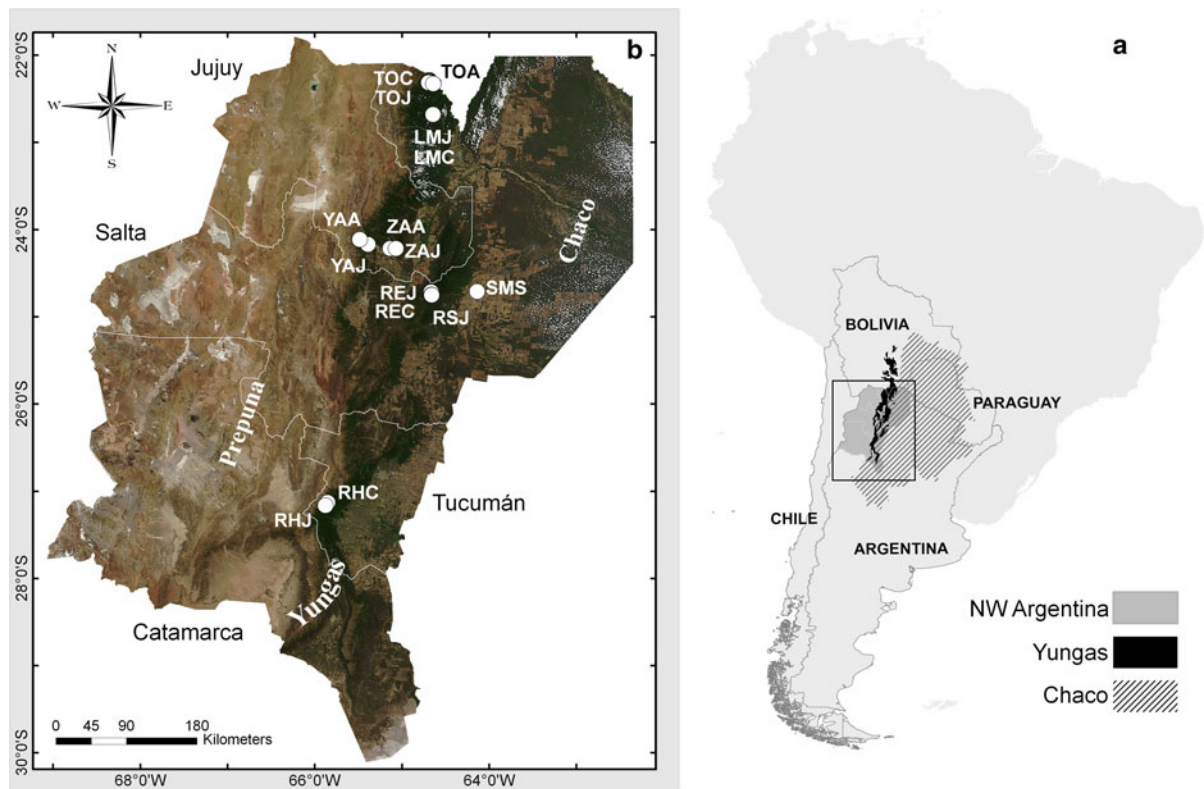
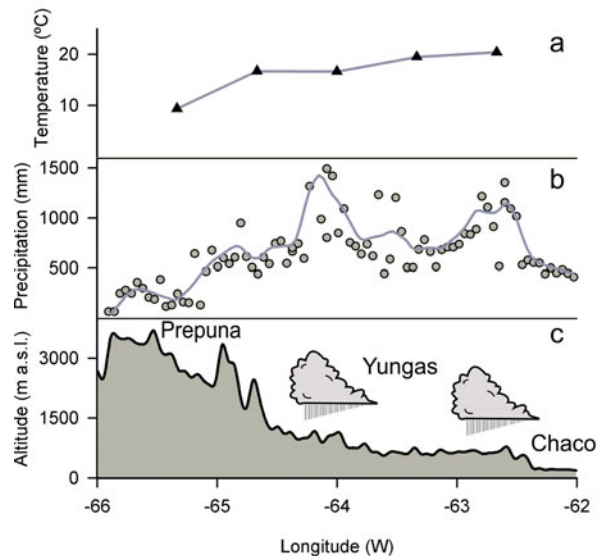


Fig. 1 Distribution of the Yungas and Chaco forest and location of NW Argentina in South America (**a**); MODIS satellite image of the study area showing major forest formations and sampling sites for tree-ring chronologies (**b**).

For chronology codes and description, see Tables 1 and 2. Digital classification of Yungas and Chaco forest formations from S. Pacheco, Fundación ProYungas <http://www.proyungas.org.ar>

Fig. 2 Transect across subtropical NW Argentina including Chaco, Yungas and Prepuna forests, showing changes in (**a**) mean annual temperature, (**b**) total annual precipitation, and (**c**) topography. Data correspond to meteorological stations (triangles temperature; dots precipitation) drawn from Bianchi and Yáñez (1992). Sampling sites include (**d**) Chaco-Yungas transitional forests, (**e**) mid-elevation and (**f**) higher altitude Yungas montane forests



Statistical analysis of tree-ring chronologies

We used a Principal Components Analysis (PCA), based on covariance matrix with Varimax rotation, to analyze patterns of growth variability. The PCA is an ordination technique, which reduces the number of original variables to a set of new uncorrelated new variables (principal components, PC) that capture a large percentage of the total variance in the original data set (Cooley and Lohnes 1971). In a first step, we applied PCA to the 15 residual chronologies for the common interval 1890–1994 to identify common patterns in growth within chronologies. Various criteria have been proposed to judge how many PCs should be retained. We selected those components showing eigenvalues larger than one; in our case we retained the first three principal components.

Climate and tree growth

Standard tree ring-width chronologies were compared with precipitation and temperature records using correlation analysis (also called “correlation functions”; Blasing et al. 1984), determining the series of correlation coefficients between a tree-ring chronology and

each of several sequential monthly temperature and precipitation variables. Since tree growth is influenced by climate conditions occurring prior to the period of ring formation (Fritts 1976), correlation coefficients were computed for a sequence of 23 months starting in July of the previous growing season and ending in May of the year in which the ring was formed (i.e. at the end of the current growing season). A positive value indicates that above-average growth is related to an above-average value of the climate variable; conversely, a negative value indicates an inverse relationship between climate and tree growth.

Monthly temperature and precipitation records were used to estimate correlations with tree growth (Table 3). Temperatures records in the region are scarce. We used mean monthly temperature variations from Tucumán weather station, which provides the longest and most homogeneous record in the region. In contrast to temperature, 32 homogeneous, coherent precipitation records are available for our study area. Previous studies indicate that composite records, based on two or more series, reflect spatial variations in precipitation better than a single station record (Barry 1981). Given the large variability induced by the complex mountain topography in NW Argentina, we

Table 1 Location of study sites, species collected and geographical characteristics of the stands, listed by sampling site and increasing elevation

Site	Code	Species sampled	d.b.h. ^a (cm)	Latitude (S)	Longitude (W)	Altitude (m a.s.l.)	Climate
San Martín	SMS	<i>Schinopsis lorentzii</i>	37–54	24°42′	64°08′	458	Xeric-warm
Río Sala	RSJ	<i>Juglans australis</i>	40–91	24°44′	64°40′	935	Xeric-warm
La Mesada	LMJ	<i>Juglans australis</i>	50–95	22°20′	64°38′	1,460	Mesic-mild
La Mesada	LMC	<i>Cedrela lilloi</i>	45–110	22°19′	64°38′	1,600	Mesic-mild
El Rey	REJ	<i>Juglans australis</i>	39–70	24°45′	64°39′	1,700	Mesic-cool
El Rey	REC	<i>Cedrela lilloi</i>	45–75	24°45′	64°39′	1,700	Mesic-cool
Los Toldos	TOJ	<i>Juglans australis</i>	70–90	22°19′	64°40′	1,875	Mesic-mild
Los Toldos	TOC	<i>Cedrela lilloi</i>	70–110	22°19′	64°41′	2,025	Mesic-mild
Los Toldos	TOA	<i>Alnus acuminata</i>	16–37	22°15′	64°46′	2,100	Mesic-cool
Yala	YAJ	<i>Juglans australis</i>	50–70	24°10′	65°23′	1,660	Mesic-mild
Yala	YAA	<i>Alnus acuminata</i>	32–85	24°07′	65° 29′	2,000	Mesic-mild
Río Horqueta	RHC	<i>Cedrela lilloi</i>	55–95	27°07′	65°50′	1,650	Wet-cool
Río Horqueta	RHJ	<i>Juglans australis</i>	50–90	27°10′	65°53′	1,902	Wet-cool
Zapla	ZAJ	<i>Juglans australis</i>	33–66	24°13′	65°08′	1,893	Wet-cool
Zapla	ZAA	<i>Alnus acuminata</i>	26–70	24°13′	65°08′	2,004	Wet-cool

The two first letters in the code refer to the site and the third one to species. *S* *Schinopsis lorentzii*, *J* *Juglans australis*, *C* *Cedrela lilloi*, *A* *Alnus acuminata*

^a Diameter at breast height range of sampled trees

Table 2 Characteristics and descriptive statistics of tree-ring chronologies

Chronologies						Statistics					
Code	Period	No. of years	No. of trees	No. of series	Absent rings (%)	Mean ring width (mm)	SD	Series inter-correlation	Mean sensitivity ^a	R-bar ^b	Mean EPS ^c
SMS	1829–2004	176	15	29	0	1.561	1.065	0.581	0.587	0.521	0.97 (1860)
RSJ	1849–2002	154	21	33	0.001	2.370	1.700	0.582	0.482	0.457	0.96 (1870)
LMJ	1709–1999	291	14	20	0	2.100	1.148	0.541	0.442	0.296	0.79 (1821)
LMC	1793–1999	207	15	24	0	2.154	1.324	0.615	0.402	0.383	0.93 (1815)
REJ	1740–2002	263	7	14	0	1.791	1.300	0.583	0.424	0.351	0.77 (1820)
REC	1810–2002	193	32	58	0	2.146	1.442	0.569	0.459	0.369	0.94 (1870)
TOJ	1814–1994	181	14	19	0	2.380	1.746	0.509	0.336	0.282	0.85 (1835)
TOC	1752–1994	243	13	24	0	2.048	1.252	0.611	0.471	0.411	0.87 (1780)
TOA	1849–2001	153	39	65	0	2.307	1.575	0.585	0.397	0.368	0.94 (1924)
YAJ	1889–2001	113	13	25	0	3.134	1.687	0.550	0.372	0.417	0.88 (1900)
YAA	1888–1999	112	14	21	0	3.964	3.842	0.655	0.402	0.331	0.91 (1915)
RHC	1729–1982	254	17	24	0	2.217	1.104	0.451	0.424	0.307	0.85 (1830)
RHJ	1646–1994	349	36	65	0	1.910	1.405	0.610	0.382	0.502	0.92 (1665)
ZAJ	1883–2003	121	12	26	0	1.702	1.149	0.597	0.392	0.445	0.95 (1905)
ZAA	1867–2003	137	16	31	0	3.232	2.158	0.483	0.439	0.303	0.89 (1907)

SD standard deviation

^a Mean sensitivity is the measure of the relative changes in ring-width variations from year to year (Fritts 1976)

^b Mean correlation coefficient for all possible pairings among tree-ring series from individual cores at a site

^c Mean expressed population signal; the year at which each chronology reaches the 0.85 threshold, is given in parentheses

compared each standard chronology with all precipitation records located at distances <100 km from the sampling site (Table 3). Based on the three records better correlated with tree-ring indices, a composite record was developed for comparison with each chronology. Precipitation variations from these three stations were standardized and merged in a single composite precipitation record. The MET program of the Dendrochronological Program Library (DPL; Holmes 1994), which produces records based on the standard deviations of each series, was used to develop the composite precipitation records. Since MET used the standard deviations, each station contribute similarly to the composite record regardless of the total precipitation registered at each stations. Composite records of rainfall were estimated over the 1935–1990 common period among records (Table 3), and this interval was used for the comparison with tree growth. Climate data were taken from Bianchi and Yáñez (1992) and the Argentinean Meteorological Service.

Similar to the PCA on tree-ring chronologies (see above), we applied PCA to the correlation analyses (the 15 sets of 46 correlation coefficients between each

chronologies and temperature [23] and precipitation [23] records) to identify the dominant patterns in tree-growth responses to climate. The contribution of each correlation analysis to the three dominant PCA component (PCA loadings), provide a measure of the similarities in tree growth to climate responses among chronology sites. In addition, the PCA amplitudes, representing the contribution of each PC to the sequence of 23 months starting in July of the previous growing season and ending in May of the current growing season, were plotted for temperature and precipitation to evaluate month-to-month fluctuations in the main modes of tree growth responses to climate.

Results

Tree-ring chronologies

Chronology lengths range from 112 to 349 years (Table 2). Mean sensitivity, characterizing the year-to-year variability in tree ring records, vary from 0.336 to 0.506 (mean of 0.422). The *Juglans*' chronologies

Table 3 Meteorological records used in this study

Name	Data period	Latitude (S)	Longitude (W)	Elevation (m a.s.l.)	Total annual precipitation (mm)
La Quiaca	1903–1992	22°10'	65°60'	3,442	328
Abrapampa	1935–1990	22°42'	65°40'	3,484	283
Humahuaca	1934–1990	23°12'	65°19'	2,939	176
Jujuy	1934–1990	24°12'	65°19'	1,259	830
Puerta Tastil	1935–1990	24°31'	65°48'	2,675	67
Cerrillos	1934–2001	24°54'	65°28'	1,250	642
Tobantirenda	1934–1990	22°09'	63°43'	529	929
Tartagal	1931–2001	22°31'	63°48'	502	931
Senda Hachada	1934–1990	23°03'	63°55'	329	741
Orán	1915–1993	23°07'	64°19'	362	816
Urundel	1934–1990	23°33'	64°24'	349	928
Ledesma	1928–2002	23°49'	64°46'	457	735
Chaguaral	1934–1990	24°03'	64°01'	388	717
Río Piedras	1934–1990	25°16'	64°54'	723	812
Tala	1934–1990	26°06'	65°15'	820	480
Vipos	1916–2002	26°28'	65°21'	786	473
Monteros	1934–1990	27°10'	65°30'	352	1126
Tucumán	1874–2002	26°49'	65°12'	447	983
Tucumán ^a	1889–1990	26°49'	65°12'	447	19.4

The time interval used for tree growth-climate comparisons was 1935–1990. Precipitation data from Bianchi and Yáñez (1992)

^a Mean annual temperature (°C), provided by the Argentinean Meteorological Service

showed greater sensitivity values at low- and high-elevation sites, which is not evident for the other three species (partially due to the lower number of other species' chronologies). R-bar statistics range from 0.282 to 0.521 (*J. australis* has a mean R-bar of 0.397; *C. lilloi*, 0.366; *A. acuminata*, 0.334; and *S. lorentzii*, 0.521). For the last 100–150 years of high-sample replication, most chronologies have EPS values above the threshold of 0.85, an indication of good quality and a strong signal in the records. Due to the low number of series included in early portions, La Mesada (LMJ) and El Rey (REJ) chronologies show mean values below this threshold. However, EPS is over the 0.85 threshold since the 1821 and 1820 for LMJ and REJ, respectively (Table 2).

Statistical analysis of tree-ring chronologies

We assessed the common variations in the annual growth of the four studied species over the common period 1890–1994 (104 years). Three major principal components extracted from the 15 residual chronologies

accounted for 43 % of the total variance in interannual variations (Fig. 3). The arrangement of chronologies with respect to the first three PC-CH (CH for chronology) axes reflects different patterns in relation to species and habitat characteristics. Based on the PC-CH loadings, the 15 chronologies were spatially arranged into two major groups, with the *Juglans* and *Cedrela/Alnus* chronologies displaying higher loadings in PC-CH1 and PC-CH2, respectively (Fig. 3). A third group, including the low-elevation RSJ and SMS chronologies had high values on the third principal component axis. Although the 15 chronologies were initially arranged by species, they were also grouped by location along the moisture gradient associated with altitude (related to PC-CH3), with chronologies from xeric sites displaying the higher loadings and with a progressive decrease in the contribution of the rest of the chronologies as site elevation (and precipitation) increases (Table 1). Similarities between tree-ring chronologies from different species growing at extreme environments are consistent with significant relationships between these records over the common interval (Fig. 4).

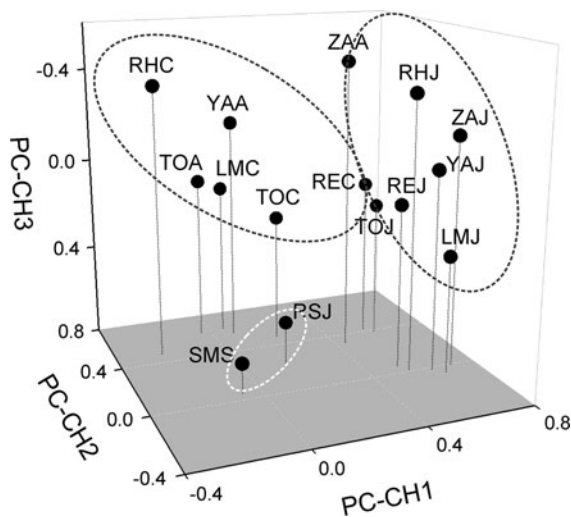


Fig. 3 Relative contributions of the 15 residual chronologies to the first three PC axes resulting from the principal components analysis, over the common period 1890–1994. The *PC-CH1* (21.32 %), *PC-CH2* (11.43 %) and *PC-CH3* (10.27 %) cumulatively account for by 43 % of total variability in tree ring variations. Dotted groups are related to similar patterns in tree-growth variations

Tree-ring and climate relationships

Figure 5 shows the correlation coefficients between standard chronologies and climate (precipitation and temperature) from previous-to-current growing seasons over the period 1935–1990 (55 years). Correlation patterns varied between sites and species, with different responses to climate along the altitudinal gradient. The correlation coefficients of the chronologies from low and xeric locations (RSJ, SMS) showed persistent month-to-month positive relationships with rainfall and negative with temperature. On the other hand, trees at higher-elevation sites (RHJ, RHC, ZAJ, ZAA; Figs. 1, 5) displayed opposite responses to climate variations. Temperature at these cold and moist sites is the limiting factor; hence tree growth was related positively to temperature and negatively to precipitation variations during the growing period (October to April). Beyond these two well-defined groups, correlation analyses for sites in between the altitudinal extremes were more complex and difficult to interpret, since the responses to climate varied between stands and species.

Principal component analysis of the correlation analysis allowed us to characterize the dominant patterns of growth responses to interannual climate

variations. The PCA of the 15 sets of correlation coefficients (Fig. 6) revealed that first three principal components (indicated as PC-CO, CO for correlation coefficients) explained 72 % of the total variance in tree-growth responses to climate. The spatial representation of PC-CO loadings (Fig. 6) showed a grouping pattern substantially similar to that based on tree-ring chronologies (Fig. 3), separating correlation coefficients according to a rising elevation gradient, and discriminating climatic responses from different species. PC-CO1, which explained 50 % of the variability, was consistent with previous analysis separating low- from high-elevation sites: SMS and RSJ correlation coefficients displayed larger values in the first component axis in opposition to ZAJ, RHJ, RHC and ZAA, which had the lower values. PC-CO2 explaining 12.66 % of the variability, showed that correlation coefficients with higher loadings were those pertaining to YAA, ZAA, YAJ and TOJ chronologies. These chronologies showed a marked response to precipitation in summer season and early autumn (January to May) in the year prior to growth (Fig. 5). Finally, PC-CO3, which explained 9.32 % of common variability, was represented by RHC, TOC and LMC, which were the major contributors to this component. In this case, and according to Fig. 5, the climate responses were somewhat variable, but generally showed higher correlation with climatic variations during late spring and summer of the current year of growth.

The amplitudes of the first three components of the correlation coefficients (hereafter PC-COam, for amplitudes) were analyzed to determine the main modes of monthly tree growth and its relation to climate variability. The first dominant mode PC-COam1 exhibited a strong positive correlation with precipitation and a persistent negative correlation with temperature variations during the previous and current periods of tree growth (Fig. 7). The SMS and RSJ correlation coefficients largely contributed to this pattern (0.41 and 0.53, respectively; Fig. 6). The correlation functions from the ZAJ, RHJ and RHC chronologies showed opposite contributions (−0.42, −0.37 and −0.25, respectively) to this pattern, consistent with previous analyses separating both groups. The second pattern (PC-COam2), with large contributions from ZAA (0.37), YAJ (0.34) and TOJ (0.27) chronologies, displayed a positive response to precipitation and a weak response to temperature. Precipitation markedly affected tree growth in the

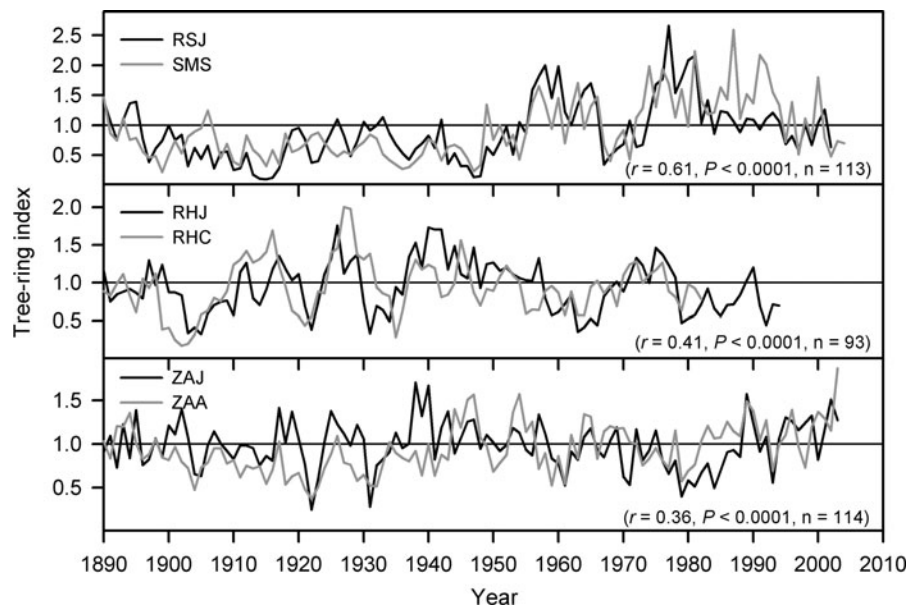


Fig. 4 Tree-ring chronologies of four species growing at different elevations in subtropical forests from NW Argentina. At lower elevations, in the transitional Chaco-Yungas forests, variations in radial growth of *Juglans australis* (RSA) are significantly related to those of *Schinopsis lorentzii* (SMS). At

upper montane forests, variations in radial growth of *J. australis* (RHJ, ZAJ) are significantly related to *Cedrela lilloi* (RHC) and *Alnus acuminata* (ZAA), respectively. Correlation coefficients (r), significance levels (P), and lengths of the correlation period (n) are given for each comparison

previous growing season, although both precipitation and temperature slightly influenced growth at the end of the current growing season. In contrast, REJ (-0.56) showed a correlation negatively related to this component (Fig. 5); responses of tree growth to precipitation and temperature were negative at the end of both previous and current growing periods, while the positive correlation with precipitation in the current period of growth seemed to be significant for tree development at this site. Finally, the third dominant pattern (PC-COam3) had a moderate but persistent positive correlation with temperature variations during both growing seasons; precipitation affected differentially the two growing periods with stronger relationships during the previous year of growth. For this component, *Cedrela* chronologies (RHC, TOC, and LMC; -0.45 , -0.41 and -0.41) provided the largest contributions.

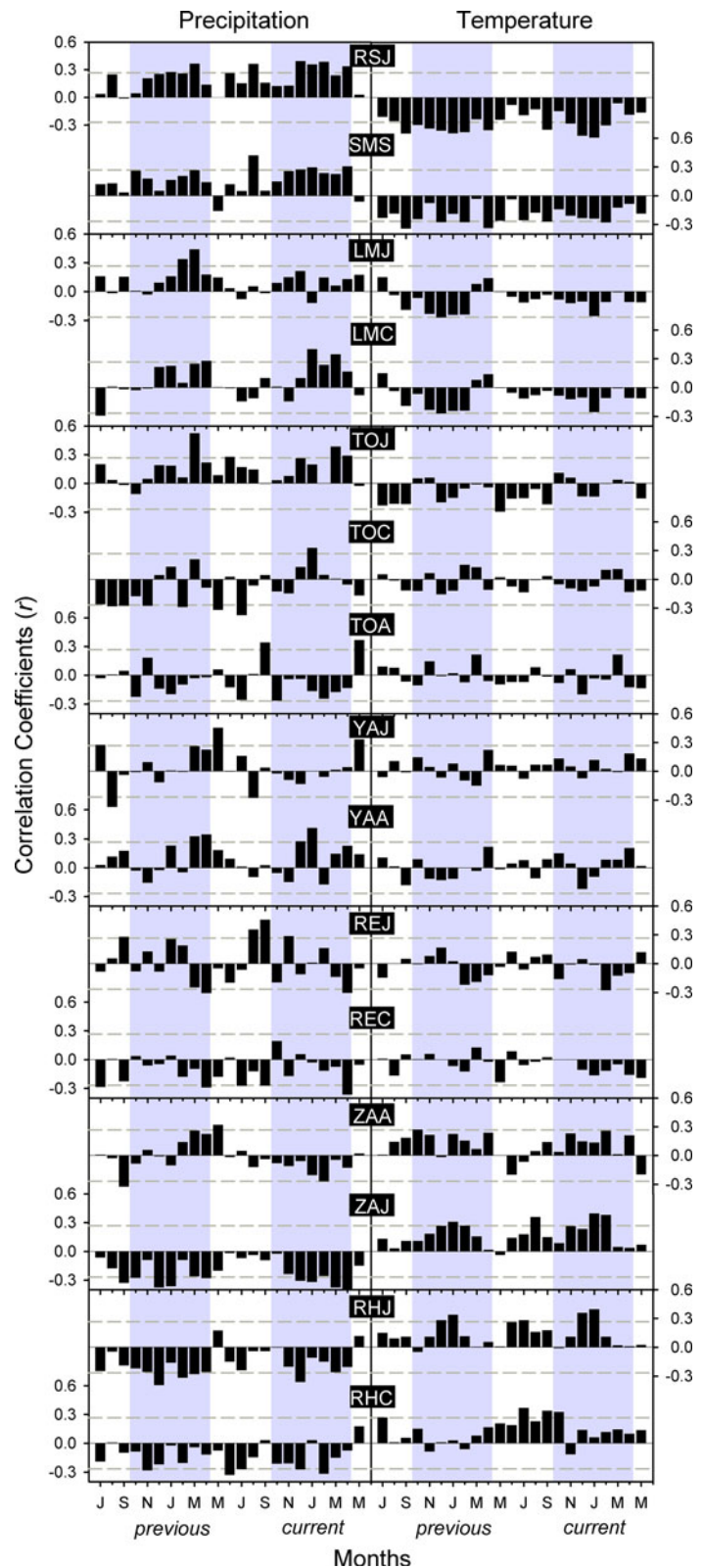
Discussion

Differential responses to climate variations might have important consequences regarding future species' distribution and forest composition, due to the individualistic growth responses within a community (Hansen

et al. 2001). In our study, we observed that the degree of similarity in growth responses to climate of two species depends on the strength with which environmental parameters control their growth. In this sense, tree-ring series provide continuous records useful to evaluate the interactions between environmental conditions and climate variability (Tardif et al. 2003).

Our results provide evidence that tree growth responses to climate vary according to site and species differences. In NW Argentina, differences in tree-growth responses of *S. lorentzii*, *C. lilloi*, *J. australis* and *A. acuminata* to climate variations are modulated by site environmental conditions and species traits. Important similarities in year-to-year variations in the radial growth of species within sites (Figs. 4, 5) are driven by a common forcing associated with the climate variability at both extremes of the elevation gradient. Based on interannual variations in ring width, the PCA isolates the chronologies located at lower elevations from those located at mid- to high-elevation sites (Fig. 3). The marked gradient of precipitation from the xeric-warm lowlands in the Chaco to the moist-cool mountain ridges in the Yungas creates contrasting environmental conditions. Along this gradient, similarities in species responses to

Fig. 5 Correlation coefficients between 15 standard chronologies and monthly records of precipitation and temperature over a 2-year interval including the previous and current growing seasons (1935–1990 common period of analysis). Correlations larger than $r = 0.268$ (grey dashed lines) are statistically significant ($P < 0.05$). Grey vertical bars highlight tree growth–climate relationships during previous and current growing in the austral summer period (October–April)



lower evapotranspiration. In consequence, at high and humid elevation sites the growth of *Juglans*, *Alnus* and *Cedrela* responds positively to temperature during the growing season. Consistent with studies by Díaz et al. (2004) and Pavoine et al. (2011), our results suggest that limiting factors lead to convergent ecophysiological traits, where plants of different lineages adapt to overcome these environmental constraints including the protection of tissues (photosynthetic, hydraulic conductance) to extreme weather agents.

In between the two extremes, the complex topography (slope and orientation) of NW Argentina originate a variety of intermountain habitats, where the interaction between precipitation and temperature is reflected in a diverse range of tree-growth responses to climate (Fig. 5). Principal components analysis applied to the chronologies and the climatic responses emerging from these intermediate sites, separate *Cedrela* from *Juglans* records. This species' grouping reveals that the diversity in responses to climate variations in mild environments may be related to differences in physiology between species in processes such as tree growth (Reich 1995).

Comparative studies of tree phenology at hyper-humid (low seasonality) and marked dry-season sites conducted in the Cordillera Real from Ecuador (Günter et al. 2008), revealed that species, including *Alnus*, *Cedrela* and *Juglans* at the drier sites show a highly synchronized seasonality both in flowering and fruiting not recorded in the same species growing at hyper-humid sites. Variations in tree phenology across moisture gradients are also strongly associated with the diversity in leaf life spans (Reich 1995). Individuals of the same species growing on different sites may display different patterns of adaptation to the particular environmental conditions. Pacheco and Yapur (2006) recorded differences in leaf production patterns of *Cedrela balansae* and *C. lilloi* across an altitudinal gradient in the Argentinean Yungas. Both species display a similar phenological pattern within a narrow altitudinal belt; *C. balansae* in the lower elevations (700 m) is deciduous without leaves during the three-month dry season, whereas *C. lilloi* in the upper montane forest (1,600 m) is a semi-deciduous species without leaves during 2 months in the cold season. However, in the mid-elevation belt (1,100 m), both species maintain mature and senescent foliage until leaf flushing, hence having short or no deciduous period. The authors argue that at 700 and 1,600 m,

water deficit and low temperature limit foliage retention, respectively, while at intermediate sites, rainfall and temperatures are less contrasting between seasons. Results from our study account for similar patterns of variability in *Juglans*, a species present throughout NW Argentinean Yungas, and widely distributed along the cloud-montane forests in South America. The variety of growth responses of this species emphasized the plasticity of subtropical trees to adapt to differential climatic and environmental situations.

Differences in phenology between species and therefore, their behavior under climate variables, could explain the differential clustering of *Juglans* and *Cedrela* at sites climatically intermediate of our environmental transect. When comparing across moisture gradients, species may display from asynchronous to highly synchronized behaviors (Reich 1995). Tree attributes tend to be similar among species in constrained environments, but when climatic conditions become ameliorated, growth of each species result from different physiological tolerances to the physical environment. Our results underline the differential behavior of species under different environmental situations: similar growth responses appear in those places where climate conditions are limiting, whereas distinct growth responses occur in not so extreme environments where differences between species prevail.

Species-specific responses to environmental variability imply that tree growth may not be synchronized among species, which would translate into changes in structure and composition of future forest communities (Drobyshev et al. 2012). Differential growth behavior or how species respond individually may lead to temporary assemblages of species (non-analogue communities) whose components would dissociate as they respond individualistically and would form new associations under novel environmental conditions (Huntley 1991). Since the last decades of the twentieth century, significant increases in precipitation rates have been observed in large regions of subtropical South America, including northwestern Argentina (IPPC 2007). These changes in the magnitude and intensity of the climatic patterns should be eventually examined since, given the results of the present work, may potentially alter the dynamics of the species and the future composition of tree communities in subtropical South America.

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