

RAINFALL-CONTROLLED TREE GROWTH IN HIGH-ELEVATION SUBTROPICAL TREELINES

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Abstract. It is generally assumed that tree growth in the upper limit of a forest is mainly controlled by summer temperature. This general statement is mostly based on studies from extra-tropical mountains and has been rarely evaluated in subtropical latitudes frequently characterized by drier climates. In the subtropical mountains from Northwestern Argentina (~23° S), annual precipitation decreases with elevation from >1500 mm at 1200–1500 m, to <200 mm above 4000 m. In consequence, tree growth at high elevations in the region may be seriously limited by water supply. In order to assess the influence of precipitation on tree growth, we evaluated the relationships between climatic variations and radial growth in four species growing at different altitudinal zones: *Juglans australis* from the montane cloud forest at 1800 m; *Alnus acuminata* from the montane savanna-like woodland at 2700 m; *Prosopis ferox* from the subalpine dryland at 3500 m; and *Polylepis tarapacana* from the high-elevation alpine dryland at 4750 m. Dendrochronological techniques were used to relate variations in annual ring width with instrumental climatic records. Growth rings were correctly dated to the year of formation, and the cross-dated series standardized using autoregressive models to reduce non-climatic signals present in the records. Tree-ring chronologies, ranging from 117 to 341 years, were compared, during the common period, with instrumental climatic records using correlation-function analysis. In spite of the remarkable differences in elevation and environmental conditions among the sampling sites, correlation functions with climate indicated that the radial growth of the four species is largely controlled by precipitation. In most cases, increased precipitation during the previous and current growing seasons favors tree growth, while temperatures are negatively correlated with radial growth, likely due to the negative effect on water availability. These results indicate that the generalized idea of upper-treeline growth limited by summer temperatures should be carefully evaluated in low-latitude environments and does not apply to subtropical areas with severe water deficits or strong moisture seasonalities.

Key words: *Alnus acuminata*; altitudinal range; Argentina, Northwestern; dendrochronology; *Juglans australis*; *Polylepis tarapacana*; *Prosopis ferox*; rainfall-controlled growth; subtropical trees; treeline.

INTRODUCTION

The location of treelines is expected to be controlled by the limiting factor that regulates the carbon balance of each individual plant, including the cost of producing woody tissues (Stevens and Fox 1991). Radial growth in woody plants at high-altitude treelines has been traditionally associated with temperature during the growing season (Troll 1973, Oshawa 1990, Körner 1999, Hoch and Körner 2003). Several studies coincide in assigning the positions of the alpine treelines to the isoline of mean air temperature of 10°C during the warmest month (Daubenmire 1954, Holtmeier 1974, Grace 1977, Tranquilini 1979). Ellenberg (1963) sug-

gested that the number of days with temperature above 5°C was a better estimate of the treeline positions than the 10°C isotherm during the warmest month. More recently, Körner (1999) noted that the mean temperature of the growing season is the variable better correlated with treeline elevation across different latitudes. Although the physiological and developmental mechanisms are not fully understood, the critical temperature for tree growth at upper elevations oscillates between 5.5 and 7.5°C, which is the range most commonly associated with treeline positions worldwide (Körner 1999). Jobbagy and Jackson (2000) found that almost 80% of forest-line elevation variation in extra-tropical regions is explained by mean annual temperature and seasonal thermal amplitude.

This traditional view of temperature-controlled tree growth at upper elevations is largely based on high-

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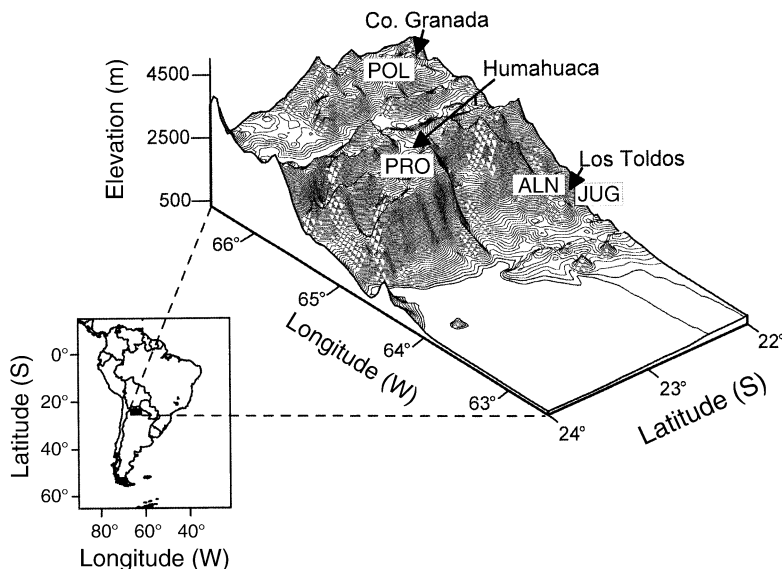


FIG. 1. Study area in Northwest Argentina showing the location of tree-ring chronologies. For tree species code, see Fig. 2 legend.

latitude treelines (Körner 1999). At tropical and subtropical treelines, other climatic factors such as precipitation could influence tree growth. For example, the radial growth of *Pinus hartwegii* at 3600–3700 m elevation at the tropical treeline of Mexico is largely determined by year-to-year variations in summer monsoon precipitation (Biondi 2001). Leuschner (2000) showed a close association between water shortage and the presence of scleromorphic plants at the upper elevation in the tropics. Based on a leaf energy-balance model, he concluded that transpiration rates in tropical alpine environments exceed the rates recorded at low elevations in middle latitudes. Due to a high diffusion coefficient for water vapor and a high radiation load at upper elevations, the potential transpiration rates in tropical mountains are 50 to 90% higher than in mid-latitude mountains. Consequently, water shortages contribute to the observed scleromorphy of alpine tropical plants, which previously was attributed only to low temperature or high radiation (Leuschner 2000).

Increases in altitude on the eastern slopes of the subtropical Andes are accompanied by lower air temperatures and humidity (Ives 1992). In Northwestern Argentina, precipitation decreases from 1200–2000 mm at 1200–1500 m elevation to <200 mm above 4000 m. Our study examined whether the radial growth of subtropical trees in different treelines from Northwestern Argentina was more closely regulated by rainfall or temperature (Fig. 1). We hypothesized that the annual variability in tree-ring width from subtropical trees would be positively associated with variation in seasonal and/or annual precipitation.

To address this issue we utilized our previous experience working with ring-width studies of four species growing at their highest range limits in different

vegetation zones of subtropical Northwestern Argentina (Villalba et al. 1985, 1998, Morales et al. 2001, Grau et al. 2003). The relationship between tree-ring width of these four species and regional climate variables was examined using correlation functions. The strength of the relationships between tree growth and precipitation was compared along the gradient and the influence of precipitation on interannual ring variations assessed.

METHODS

Study area

Climate.—In Northwestern Argentina, temperature decreases with elevation according to local environmental lapse rates while rainfall varies in relation to the combined effect of elevation and exposure to the northeasterly winds, which bring humidity to the region (Bianchi and Yáñez 1992). Major mountain ranges are oriented in the north–south direction, generating abundant orographic rainfall on the eastern slopes and dry inter-montane valleys on the western slopes (Fig. 2). The whole region is characterized by a monsoonal rainfall pattern in which summer precipitation, depending on geographical location and elevation, represents between 80 and ~100% of the annual total (Prohaska 1976).

Mean annual temperature across the altitudinal gradient varies from 20.2 °C in Orán (357-m elevation) to 8.7 °C in Abra Pampa (3484 m, Table 1). At upper elevations (Abra Pampa and La Quiaca; 3459 m) the annual thermal range is lower than the daily range for any month in the year (Fig. 2).

Vegetation and species sampled.—Samples for this study were collected from four sites on an altitudinal

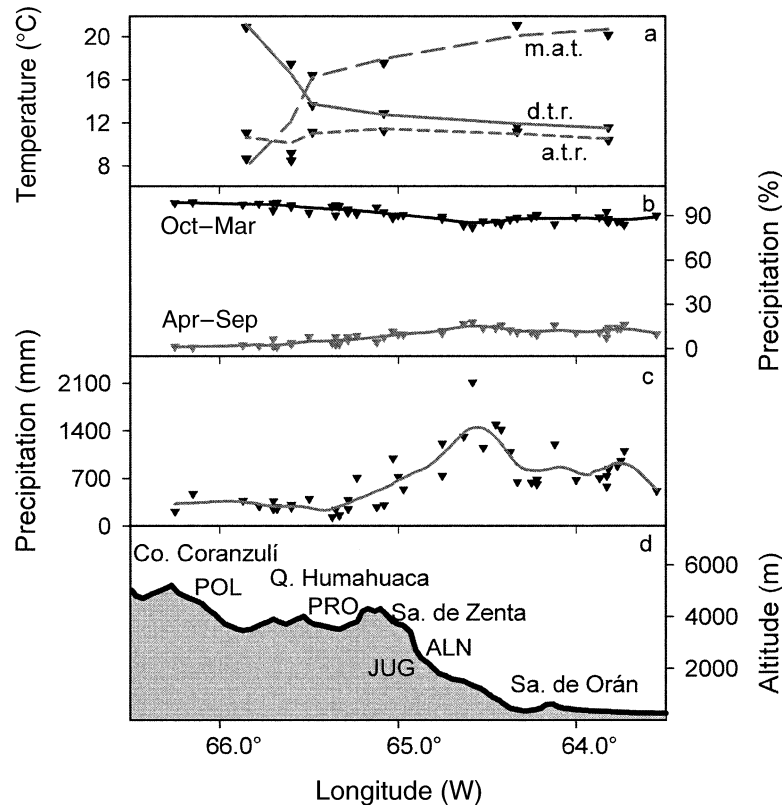


FIG. 2. Altitudinal transect across the subtropical montane forest in Northwestern Argentina between 22° and 24° S latitude, showing changes (a) in mean annual temperature (m.a.t.), in annual mean daily thermal range (d.t.r.), and in annual thermal range (a.t.r.) between the coldest and warmest month; (b) in seasonal precipitation distribution; and (c) in total annual precipitation (d) associated with topography. Locations of the meteorological stations are indicated by solid inverted triangles. Meteorological stations in the latitudinal band between 22° S and 24° S have been included in this transect. The sample sites are indicated for the four species growing at different altitudinal zones: JUG, *Juglans australis*; ALN, *Alnus acuminata*; PRO, *Prosopis ferox*; and POL, *Polylepis tarapacana*.

transect from 1800 m to 4750 m (Table 2, Fig. 1) representing different forest types. In the eastern slopes, diverse cloud forests occur below 2000 m. Sample collections for *Juglans australis* (one of the most common species of this forest type) were conducted between 1800 and 1850 m near Los Toldos, Salta (Table 2), at the upper limit of *J. australis* distribution (Fig. 1), which is also the upper limit of the montane cloud

forest at this latitude (Grau and Brown 1995, Brown et al. 2001).

Between 2100 and 2800 m elevation, vegetation is characterized by a savana-like mosaic of grasslands, shrublands, and single-species forest stands of *Alnus acuminata* (Brown et al. 2001). *A. acuminata* was sampled at Cerro Bravo and Nacientes del Río Toldos located at 2650 and 2700 m, respectively (Table 2). Due

TABLE 1. Climate data for selected weather stations along the altitudinal transect in Northwestern Argentina.

Locality	Latitude	Longitude	Altitude (m)	Precipitation (mm)	Annual temperature (°C)		
					Mean	Max.	Min.
Tartagal	22°39'	63°49'	450	835	20.2	27.2	15.6
Orán	23°09'	64°19'	357	648	21.1	27.9	16.2
Jujuy	24°23'	65°05'	1260	753	17.6	26.6	12.7
Salta	24°51'	65°29'	1221	660	16.4	24	10.3
La Quiaca	22°06'	65°36'	3459	249	9.2	18.4	0.9
Abra Pampa	22°50'	65°51'	3484	292	8.7	18.5	-2.4

Note: Data are from Servicio Meteorológico Nacional Argentino.



PLATE 1. Upper-range distribution of *Prosopis ferox* in the dry valley of El Angosto, located at 3500 m elevation in the subtropical mountains of Northwestern Argentina. Patches of small *Prosopis* trees (2–4 m tall) grow in a xerophytic shrubland with abundance of cacti. Photo credit: R. Villalba.

to the topographic and floristic similarities between sites, we merged the samples in a single collection.

Dry intermontane valleys between 2500 and 4000 m are dominated by xerophytic shrublands (Puna and Pre-puna biogeographic provinces) with some patches of *Prosopis ferox* woodlands (Ruthsatz and Movia 1975; see Plate 1). The *P. ferox* samples were collected at Churquiaguada and Quebrada de Sapagua, at 3500 m in the Quebrada de Humahuaca, Jujuy (Table 2, Fig. 1). Scattered *Polylepis tarapacana* woodlands occur in the alpine grasslands between 4000 and 4800 m (Braun-Wilke et al. 1999). Samples from *P. tarapacana* were

collected at 4750 m on the northeastern slope of the Cerro Granada, Jujuy (Table 2, Fig. 1).

Sample collection and processing

Tree cores were collected using manual and mechanical increment borers and the *Prosopis ferox* and *Polylepis tarapacana* collections were complemented with cross sections and wedges from dead and living trees. Growth rings were correctly dated to the year of formation following standard dendrochronological procedures (Stokes and Smiley 1968). The rings were measured with 0.01-mm accuracy under a microscope with

TABLE 2. Characteristics of the study sites in Northwestern Argentina.

Locality	Species	Altitude (m)	Lat. S	Long. W	Precip. (mm)	Climate	Vegetation
Los Toldos	<i>Juglans australis</i>	1800–1850	22°19'	64°40'	1200	mild–humid	cloud montane forest
Los Toldos	<i>Alnus acuminata</i>	2650–2700	22°15'	64°46'	800	mild–drier	open montane forests
Humahuca	<i>Prosopis ferox</i>	3400–3500	23°10'	65°20'	170	mild–cold–drier	subalpine drylands
Cerro Granada	<i>Polylepis tarapacana</i>	4500–4750	22°32'	66°35'	475	cold–drier	alpine drylands

TABLE 3. Characteristics and descriptive statistics of the four tree-ring chronologies.

Species	Chronology			Data			Statistics		
	Period	Total no. years	No. adequate replicated years	No. trees	No. cores	No. rings	Mean sensitivity	SD	<i>r</i> -bar
<i>Juglans australis</i>	1814–1994	181	156	15	20	1263	0.25	0.21	0.24
<i>Alnus acuminata</i>	1849–2001	153	71	35	65	2674	0.30	0.42	0.29
<i>Prosopis ferox</i>	1883–1999	117	100	23	38	2537	0.28	0.26	0.27
<i>Polylepis tarapacana</i>	1659–1999	341	199	27	47	5753	0.34	0.19	0.33

a Bannister-type measuring machine connected to a computer (Robinson and Evans 1980).

The cross-dating and measuring qualities were checked with the program COFECHA (Holmes 1983). COFECHA calculates correlation coefficients between individual series of ring widths to identify the location of absent or false rings. The cross-dated series were standardized using the program ARSTAN to produce standard and residual chronologies (Cook 1985). Standardized series were averaged to obtain a mean standard chronology from each of the four sampled sites. Consequently, the final chronologies constitute temporal series representing annual variations in the radial growth of *J. australis*, *A. acuminata*, *P. ferox*, and *P. tarapacana* at the respective sampled sites.

Residual chronologies were produced in the same manner as the standard chronologies, but in this case the chronologies were residuals from autoregressive modeling (Cook 1985). The use of residual chronologies is recommended in dendroecological studies requiring the removal of the serial autocorrelation present in the tree-ring series to determine the correct level of significance of some statistical analyses (e.g., correlation functions). Similarities between the chronologies were evaluated using correlation coefficients. We evaluated the quality of each chronology using the mean sensitivity, the standard deviation (Fritts 1976), and *r*-bar statistics (Briffa 1995); *r*-bar is the mean correlation coefficient for all possible pairings among tree-ring series from an individual chronology, computed for a specific common time interval. We used a 50-year window with an overlap of 25 years between adjacent windows.

Climate and radial growth

Correlation-functions analysis (Blasing et al. 1984) was used to determine the influence of macroclimatic factors on tree growth. The statistical relationship between standard and residual chronologies and monthly temperature and precipitation was examined over the common interval between the chronology and the instrumental climatic record for each region. As radial growth is influenced by climatic conditions several months before ring formation (Fritts 1976), we examined relationships over a 22-month period starting in July of the prior growing season to May in the current growing season.

Climate data from Jujuy (Table 1), located at 1260 m elevation, are the longest (1930–1990) and most homogeneous records available for comparison with the *J. australis* and *A. acuminata* chronologies in the cloud-montane and subhumid-montane forests. La Quiaca records, at 3490 m elevation, are similarly the longest (1903–1993) and most representative records of climate conditions for the Argentinean sector of the Puna. Climate data for Jujuy and La Quiaca were taken from Bianchi and Yáñez (1992) and Vose et al. (1992). Precipitation and temperature records were also integrated in a moisture index, which represents the difference between the departures (positive or negative standard deviations) from total precipitation and temperature means (Villalba and Veblen 1997). In general, tree-ring variations in subtropical regions are better correlated with seasonal climate than with climate from a particular month (Villalba et al. 1987, 1998). Therefore, seasonal temperature and precipitation records were also correlated with tree growth.

We also evaluated differences in the strength of the relationships between climate and tree growth for each species along the elevational gradient. Tree-ring variations for each species were regressed against seasonal precipitation and moisture indices, and the differences in regression slopes tested between species.

Oscillation modes in local climate records

A visual inspection of summer temperatures at La Quiaca suggests the presence of a persistent biennial mode in the record. We use the Blackman-Tukey (BT) spectral analysis (Jenkins and Watts 1968) to assess biennial oscillation modes in the temperature records from La Quiaca and Jujuy. In our analysis, the BT spectrum was estimated from 25- (La Quiaca) and 15-year (Jujuy) lags of autocorrelation. With lags $\sim 25\%$ of the series length, we set a reasonable balance between high resolution and moderate stability. The number of degrees of freedom per spectral estimate is 10. The 95% confidence level of the spectrum was estimated from a “red noise” first-order Markov null continuum based on the lag-1 autocorrelation of the time series (Mitchell et al. 1966).

RESULTS

Tree-ring chronologies

The statistics used to measure the quality of the chronologies indicate a common signal in the interannual

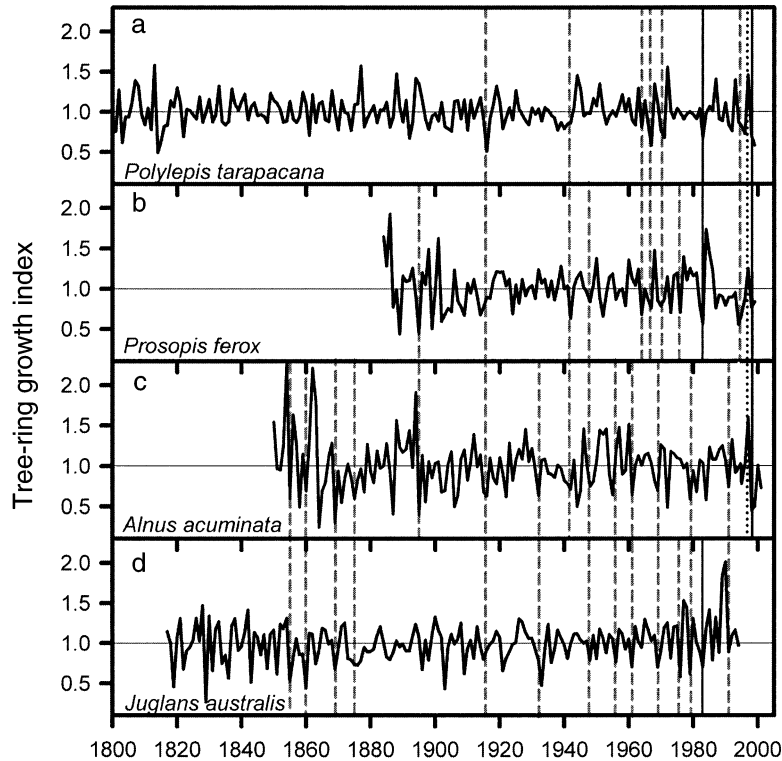


FIG. 3. Tree-ring chronologies for the four species growing at different altitudinal zones. The vertical solid line indicates the very strong El Niño events (EN) in 1982–1983 and 1997–1998, whereas the vertical dotted line indicates the La Niña event in 1996–1997 (LN). The vertical short dashed lines indicate coincidence in growth reduction between two or more chronologies.

variations of radial growth among the individual samples that integrate each chronology (Table 3). The highest mean sensitivity is for *Polylepis tarapacana* (0.34), followed by *Alnus acuminata* (0.30), *Prosopis ferox* (0.28), and *Juglans australis* (0.22) chronologies. The \bar{r} statistic varies between 0.24 and 0.33.

Summary characteristics of the chronologies and time-series plots are presented in Table 3 and Fig. 3, respectively. *P. tarapacana* is the longest chronology (350 years) and well replicated since 1800. Four of the seven largest growth reductions in that chronology since 1800 are coincident with strong and very strong ENSO (El Niño–Southern Oscillation) events (Quinn 1992), namely 1803 (strong plus ENSO), 1814 (strong ENSO), 1916, 1967, 1971, 1983 (very strong ENSO)

and 1998 (very strong ENSO). The severe ENSO events of 1982–1983 and 1997–1998 caused a significant decrease in regional precipitation in Northwestern Argentina, and a remarkable growth reduction in the *P. ferox* and *P. tarapacana* chronologies. Below-average growth during the year 1983 was also observed for *J. australis*, but the reduction was more subdued than in *P. ferox* and *P. tarapacana*. Although there is no reduction in growth for *A. acuminata* in 1983, there is a decrease in growth in the following year (Fig. 3).

A correlation matrix (Table 4) between the four chronologies shows that the two western and higher-elevation chronologies from *P. tarapacana* and *P. ferox* are significantly correlated ($r = 0.29$, $n = 85$ -yr period, $P < 0.01$), but they are not related to the *A. acuminata* chronology. The *P. tarapacana* chronology is also well correlated with the *J. australis* chronology, at the lower border of the our elevation transect ($r = 0.24$, $n = 85$ -yr period, $P < 0.05$).

TABLE 4. Correlation coefficients between residual tree-ring chronologies.

Species	<i>Prosopis ferox</i>	<i>Alnus acuminata</i>	<i>Juglans australis</i>
<i>Polylepis tarapacana</i>	0.29†	−0.08	0.27†
<i>Juglans australis</i>	0.14	0.24‡	
<i>Alnus acuminata</i>	−0.2		

Notes: Period used for the analysis: 1910–1994 (85 years).

† Significant at the 99% confidence level.

‡ Significant at the 95% confidence level.

Climate–tree growth relationships

Across the altitudinal gradient, the radial growth of all four species is positively associated with precipitation (Fig. 4) but there are differences in the timing of the response between species. The *J. australis* chronology is positively correlated with monthly precipi-

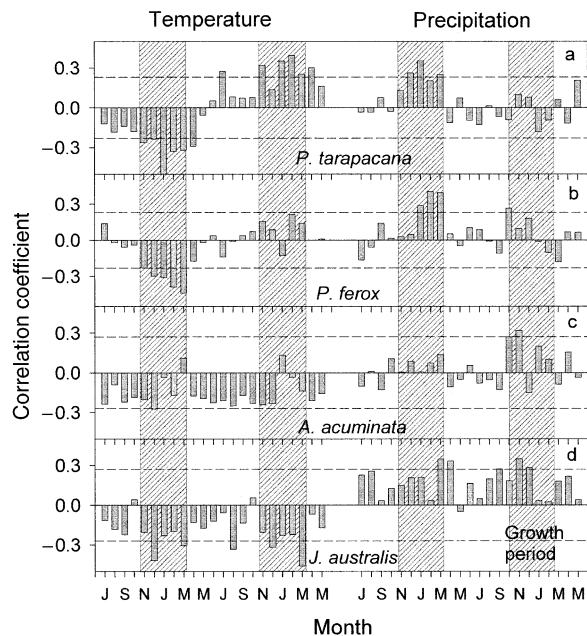


FIG. 4. Correlation functions for the four tree-ring chronologies. Precipitation and temperature records from La Quiaca were used for comparison with the (a) *Polylepis tarapacana* and (b) *Prosopis ferox* chronologies, whereas the Jujuy records were compared with (c) *Alnus acuminata* and (d) *Juglans australis* chronologies. The four wide vertical bars (diagonally hatched) represent the 95% confidence level for the correlation coefficients.

tation during the previous and current growing seasons, whereas the *A. acuminata* growth is affected only by current-growing season precipitation (Fig. 4). The radial growth of the high-elevation chronologies (*P. ferox* and *P. tarapacana*) showed a strong positive response to precipitation during the previous growing season.

The correlation-function analysis over the 1934–1980 interval indicates that the radial growth of *J. australis* at Los Toldos is positively correlated with precipitation throughout the year. However, statistically significant correlations between rainfall and tree growth are observed for March and April (late summer) in the previous year, and for September, November, and December (spring) during the current growing season (Fig. 4d). The inverse relationships between tree growth and temperatures between the previous and current year probably likely reflect the negative effect of

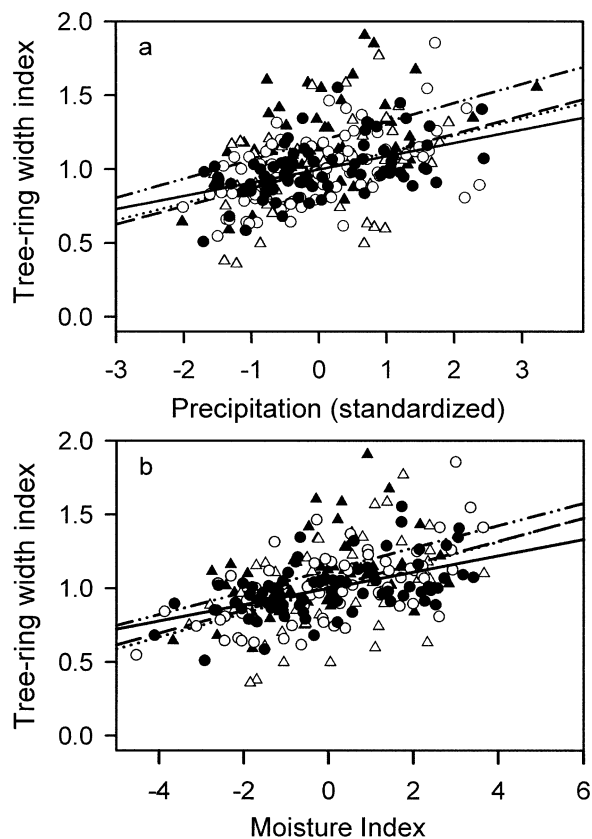


FIG. 5. Relationships between the tree-ring width indexes for *Juglans australis* (▲; dash-dot-dot line), *Alnus acuminata* (△; dotted line), *Prosopis ferox* (○; long dashed line), and *Polylepis tarapacana* (●; solid line), with (a) seasonal standardized precipitation and (b) the moisture index.

higher temperatures on water availability, particularly during the growing seasons.

The radial growth of *A. acuminata* is influenced by precipitation at the beginning of the current growing period (October–November). Inverse relationships between *A. acuminata* tree growth and temperature are recorded throughout the year, although these correlations do not exceed the confidence intervals (Fig. 4c).

As elevation increases, precipitation diminishes and is more concentrated during the summer months (Fig. 2). The correlation-function analysis showed that the growth of *P. ferox* is strongly controlled by previous

TABLE 5. Correlations of tree-ring width indexes with seasonal standardized precipitation and the moisture index from Jujuy and La Quiaca (Argentina) weather stations.

Species	Weather station	n	Precipitation		Moisture index	
			r	P	r	P
<i>Juglans australis</i>	Jujuy	47	0.38	0.01	0.43	0.01
<i>Alnus acuminata</i>	Jujuy	47	0.37	0.01	0.43	0.01
<i>Prosopis ferox</i>	La Quiaca	79	0.52	0.00001	0.60	0.000001
<i>Polylepis tarapacana</i>	La Quiaca	79	0.49	0.00001	0.54	0.000001

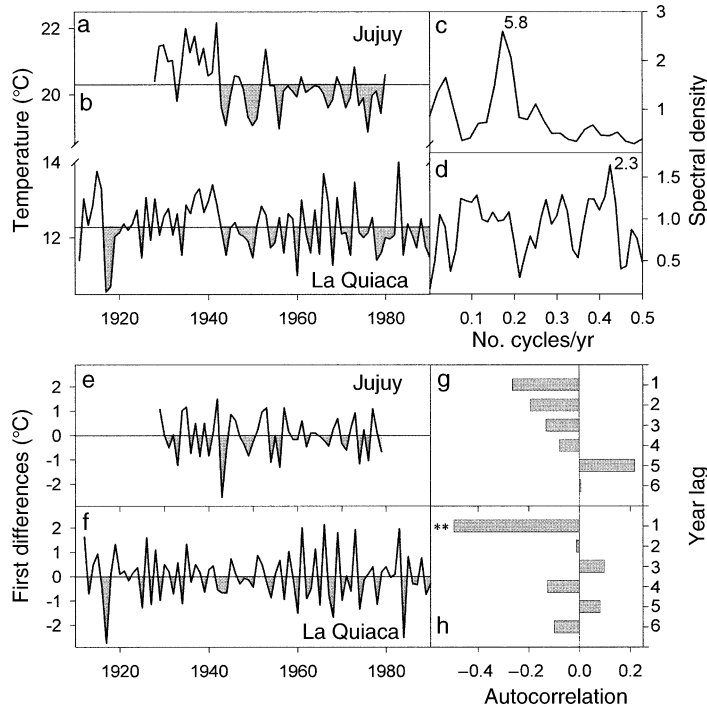


FIG. 6. Temperature variations at Jujuy (1260 m) and La Quiaca (3459 m) and their most relevant oscillatory modes. Summer (January–March) temperatures at (a) Jujuy and (b) La Quiaca. Blackman-Tukey spectral analyses for (c) Jujuy and (d) La Quiaca summer temperature variations. The periods are given in years for each significant peak (5.8 yr and 2.3 yr) at the 95% confidence level (Mitchell et al. 1966). First-difference temperature series for (e) Jujuy and (f) La Quiaca and their respective autocorrelation functions (g and h).

** $P \leq 0.01$; autocorrelation values statistically significant at the 99.0% confidence level.

summer climatic conditions (Fig. 4b). Below-average temperature and above-average precipitation during the previous growing season (January to March) favor radial growth. Climate records from elevations similar to our sampling site (3400 m) indicate that the humid period from January to March is coincident with warmer temperatures ($>12^{\circ}\text{C}$) and relatively smaller amplitudes in daily temperature range ($<15^{\circ}\text{C}$) across the year.

The radial growth of *P. tarapacana* is positively correlated with precipitation from December to March of the previous growing season. A negative relationship with temperature occurs from November to April in the previous summer. In contrast to the other species, positive relationships occur between the *P. tarapacana* radial growth and temperature during the current growing season (November–April; Fig. 4a).

Correlation analyses based on the common intervals 1934–1980 between the *J. australis* and *A. acuminata* chronologies and Jujuy precipitation, and 1912–1990 between the *P. ferox* and *P. tarapacana* chronologies and La Quiaca precipitation, indicate that the radial growth for the four species is linearly and positively related to rainfall (Fig. 5a). These relationships are stronger for the highest chronologies of *P. ferox* and *P. tarapacana*, where precipitation is less (<500 mm) than in the *J. australis* and *A. acuminata* sites (>1200 mm, Fig. 5a, Table 5). Tree growth shows similar relationships to both precipitation and the moisture index. The regression slopes of these four species using either precipitation or the moisture index are not significantly different (Fig. 5a and b, Table 5).

The BT spectrum analysis for the observed summer (January–March) temperature variations in La Quiaca show that a large component of the spectral power is concentrated at cycles 2.3 years in length (Fig. 6d). This oscillation is not present at Jujuy (Fig. 6c) and appears to be limited to high-elevation sites on the Puna. This remarkable quasi-biennial oscillation in summer temperatures is more evident in the first-difference (year t minus year $t + 1$) temperature series from La Quiaca. Indeed, the autocorrelation function of the first-difference series shows a significant 1-year lag inverse relationship in temperature over time (Fig. 6h), which is not present at Jujuy (Fig. 6g).

DISCUSSION

The altitudinal environmental gradient in Northwestern Argentina (from 1800 m to 4750 m) introduces differences in the radial growth patterns of the species growing in the montane forests, the open woodlands, and the high-elevation deserts. Changes in the length and timing of the growing season and distinct species autoecology contribute to differences in tree growth response recorded among the four species (Table 4). However, despite these differences, radial growth of the four species is largely regulated by precipitation. The radial growth of *Juglans australis* is influenced by precipitation during both the previous and current growing season (Fig. 4d), whereas spring precipitation is the control on *Alnus acuminata* (Fig. 4c) and prior summer dominates the response of *Prosopis ferox* and *Polylepis tarapacana* (Fig. 4b and a). Temperature is negatively correlated with growth for those months

with positive relationships with precipitation. In North-western Argentina warm summers are mostly dry, which increases evapotranspiration, reduces water availability, and enhances the inverse relation between summer temperatures and radial growth. At La Quiaca, summer temperatures are negatively correlated with precipitation at a 99% confidence level ($r = -0.60$; $n = 80$ years; $P < 0.001$).

At 4750-m elevation on the Volcan Granada, the positive relationships between monthly temperature and radial growth recorded for *P. tarapacana* during the growing season could indicate that the extreme low temperatures during the growing season overtake the role of water scarcity as a major control of *P. tarapacana* tree growth. However, the contrasting responses of growth to temperature in the previous (negative) and the current (positive) growing seasons is, to some extent, a function of the characteristics of the temperature series rather than a consistent response of trees to climate in the Puna. Spectral analysis of summer (January to March) temperature variations at La Quiaca reveals a persistent oscillation centered at 2.3 years during the past 80 years (Fig. 6d). In consequence, if cool (warm) summers are consistently followed in most cases by warm (cool) summers, opposite relationships between radial growth of *P. tarapacana* and La Quiaca temperature are expected for consecutive growing seasons. Based on this analysis, we believe that the positive relationship between tree growth and temperature during the current growing season arises from the biennial oscillation of the temperature at high elevations in the region. Consequently we rule out any positive effect of summer temperatures on *P. tarapacana* radial growth at these high elevation in the subtropics.

Temperature variations during the growing season are the major environmental factor regulating the growth of trees at upper elevations in the Alps (Körner 1999), in the Canadian Rockies (Luckman et al. 1997), in the New Zealand Alps (Wardle 1974), and in the Southern Andes (Villalba et al. 2003) of South America. Water limitation has rarely been considered an important limit factor to tree growth at higher elevations in temperate and cold regions, however, our work suggests that these observations should not be generalized to upper treelines worldwide. Our studies in subtropical Northwestern Argentina clearly show that the radial growth of some species at their upper altitudinal range limits can be strongly regulated by water availability. On the other hand, our study does not imply that temperature has no effect on subtropical treelines. Previous studies indicated that the growth of *J. australis* at wetter sites on the cloud montane forest is positively related to summer temperatures (Villalba et al. 1992, 1998). Future research should assess the effects of both temperature and rainfall in controlling tree growth at different environments in the subtropics, which, in addition to the decrease in precipitation with elevation,

have to consider precipitation variations across the range of distribution for each species. The dendro-chronological methods as used in this study provide a valuable tool for this task.

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