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Spatio-temporal variations in *Polylepis tarapacana* radial growth across the Bolivian Altiplano during the 20th century

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A B S T R A C T

We document the dendroclimatological potential of *Polylepis tarapacana* to estimate past temporal and spatial variations in precipitation across the Bolivian Altiplano (17–23°S). The *P. tarapacana* chronologies, which presently range between 110 and 705 years in length, represent the highest altitude tree-ring records worldwide. Interannual variations in fourteen tree-ring chronologies located between 3900 and 4850 m elevation were compared using correlation and principal component analyses. There is a strong common signal among the chronologies. For the common interval AD 1890–1999, three dominant patterns of tree growth across the Bolivian Altiplano were identified. The first pattern which explains 52% of the total variance in tree growth is associated with years of above- or below-average tree growth across the whole region. The second and third patterns, which are related to significantly lower common variance (13 and 8%, respectively), are associated with contrasting positive and negative anomalies of growth between the northern and southern sectors, and between the central-western sector and the rest of the region, respectively. In order to determine the climatic significance of the spatial variations of *P. tarapacana* growth, the interannual patterns in tree growth were compared with spatial anomalies in precipitation across the region. Uniform patterns of above (below) average tree growth are associated with positive (negative) precipitation anomalies in the preceding year that are uniformly distributed across the whole Altiplano. In the westernmost areas of the Altiplano, summer rainfall accounts for more than 80% of total annual precipitation. Therefore, relationships between tree growth and summer or annual precipitation are, in most cases, similar. Contrasting patterns of tree growth are related to opposite anomalies in precipitation during the preceding year in the different sub-regions in the Altiplano (north *versus* south, central *versus* north and south). Climatic preconditioning of tree growth was also identified for individual years. For instance, extremely reduced growth in the year 1967 reflects dry conditions in the two preceding years (1965–1966). Long-term intervals (3 or more years) with reduced tree growth resulted from several consecutive years with low precipitation. Our results indicate that the network of tree-ring chronologies of *P. tarapacana* in the Bolivian Altiplano has the potential to provide annually-resolved precipitation reconstructions in this region for the past 5–7 centuries. This is a valuable source to document decadal-to-century-scale precipitation variability in the Altiplano and its relation to large-scale ocean–atmosphere circulation features.

1. Introduction

Atmospheric and oceanic variations in the tropics affect climate worldwide. Energy in the climatic system is transferred from the tropics to the extratropics along preferred pathways in the atmosphere. This transfer of energy modulates the location and strength of the storm tracks and the fluxes of heat, moisture and momentum. In response to the atmospheric alterations induced by tropical weather, regional anomalies of temperature and precipitation occur across the world. Such anomalies have direct human and environmental impacts, often being associated with droughts and floods that severely disrupt food production and modulate air and water quality, fire risk, energy production and human health.

Instrumental records of climate in the tropics are scarce. Most tropical records are short, fragmentary and heterogeneous (IPCC,

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2007). Longer records are needed to understand the nature of climate variations, and how the interannual modes of climate variability have evolved under changes in long-term background conditions. There is a need for developing climatic proxy records from natural archives such as corals, tree rings, ice cores, and others to complement the current limited nature of the instrumental record in the tropics. In consequence, the development of climate-sensitive and well-replicated tree-ring records from tropical regions represents a major challenge in our efforts to reconstruct past environmental changes at regional and global scales.

In our search of species for the development of reliable tree-ring chronologies in tropical–subtropical regions of South America south of 15°S, different sampling strategies have been applied. In the early 1980s, the effort was centered on tropical conifers, particularly on different species of the genus *Podocarpus*, widely distributed in tropical areas of Central and South America (Villalba et al., 1985; Villalba, 1987). Late in the 1980s and early 1990s, the focus turned from tropical conifers to broadleaf species with a phylogenetic distribution in temperate regions which have invaded tropical regions in Central and South America during recent geological times. Clearly marked bands in the wood of *Juglans australis* yielded the first tree-ring chronologies in the subtropical (22–28°S) montane forests of South America. Our present knowledge on climate variations across the subtropical montane South America during the past 200 years largely relies on *Juglans* chronologies (Villalba et al., 1992, 1998; Gil-Montero and Villalba, 2005).

During the past five years, we concentrated on the study of tropical–subtropical species showing well-defined tree rings at high-elevation subtropical treelines (Morales et al., 2004). A first *Prosopis ferox* chronology has been reported for semiarid inter-mountain valleys (23°S, 3800 m; Morales et al., 2001, 2004) in northwestern Argentina, and several *Polylepis tarapacana* chronologies have been developed at higher elevations on the Bolivian Altiplano (16–22°S, 4500–5000 m; Argollo et al., 2004; Morales et al., 2004; Christie et al., 2009-this issue).

Polylepis, a genus of the *Rosaceae* family, includes 28 woody species of small- to medium-size trees growing at very high altitudes in the tropical Andes of South America (Kessler, 1995; Kessler and Schmidt-Lebuhn, 2006; Schmidt-Lebuhn et al., 2006). *Polylepis tarapacana*, adapted to dryer and colder conditions than other species of the same genus, reaches the highest elevation of tree growth in the world. On the slopes of the high volcanoes in Bolivia and adjacent areas of Peru, Chile and Argentina (17–23°S), *P. tarapacana* grows between 3900 and 5200 m elevation. Previous dendrochronological studies indicate that the radial growth of *P. tarapacana* is influenced by precipitation during the summer preceding the ring formation. At the sampling sites, precipitation during the year preceding the growing season explains around 50% of the total radial growth variance. Preceding summer temperatures which increase evapotranspiration and reduced soil water supply, are negatively correlated with tree growth (Argollo et al., 2004; Morales et al., 2004).

Based on new extensive collections, we present here a detailed study of the relationships between precipitation variations and tree growth of *Polylepis tarapacana* across the Bolivian Altiplano during the 20th century. It is not the purpose of the present study to reconstruct past precipitation variations in the Bolivian Altiplano, but to explore the spatial and temporal variations in *P. tarapacana* tree-growth responses to climatic variations in order to validate further reconstructions. Annual maps of tree-growth variations have been developed for the area between 17° and 23°S for the past 100 years and are compared with precipitation variations across the region. The complexity of tree-growth responses evident in these maps is interpreted in relation to spatial climatic variations over the recent past on the Bolivian Altiplano.

2. Climate

The Bolivian Altiplano (inter-Andean plateau at 3800 m) receives precipitation almost exclusively during the austral summer (December–March) associated with the seasonal expansion of the upper-air easterlies and related near-surface moisture influx from continental lowlands to the east. Over the interior and western parts of the Altiplano, summer precipitation accounts for 70 to 90% of the total annual precipitation. On average 600 to 1000 mm of annual

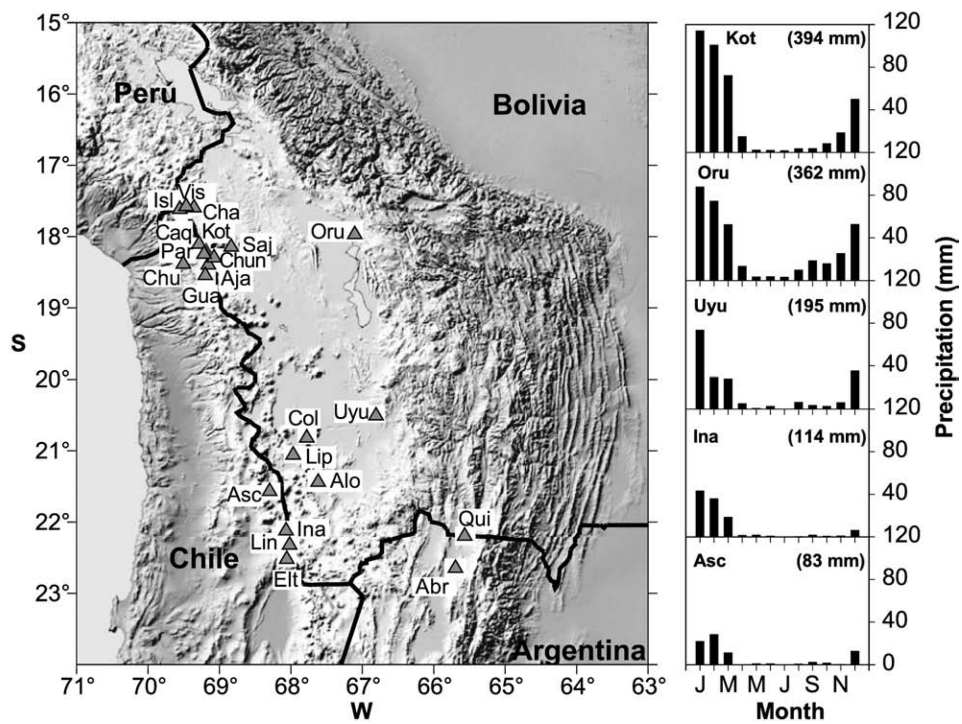


Fig. 1. Geographical locations of meteorological stations across the study area. Monthly precipitation distributions from five stations across the region are shown on the right panel. Note the reduction in precipitation in both north–south and east–west directions. See Table 2 for station code definitions.

precipitation falls along the Eastern Cordillera. Precipitation decreases to 50–400 mm in the Western Cordillera (Vuille and Keimig, 2004).

Consistent with a tropical moisture source, there is also a significant decrease in precipitation from north to south, in particular along the western slopes of the central Andes (Fig. 1).

Summer precipitation on the Bolivian Altiplano exhibits pronounced spatial and temporal variability (Aceituno and Montecinos, 1993; Lenters and Cook, 1999; Vuille and Keimig, 2004). During the austral summer, precipitation is convective and typically occurs during afternoon thunderstorms. During the early hours of the day, the radiative heating of the land surface warms the low-level air and induces the inflow of wet air masses from the Amazon basin. Later in the day, the convergence of this air induces precipitation.

Precipitation variability is not restricted to daily and seasonal time scales. Based on instrumental records, a marked interannual variability in rainfall has also been reported by Kessler (1981), Horel et al. (1989) and Lenters (1997) among others. Composites of 200-mb geopotential height for wet and dry days during summer suggest that rainfall variability on the Altiplano is related to the position and intensity of the Bolivian High, a prominent upper-air anticyclone that develops over the Central Andes during summer (Lenters and Cook, 1997). The Bolivian High is stronger and located farther south during the wet intervals. In general, the Altiplano is dry (wet) during warm (cold) phases of the Southern Oscillation (Aceituno, 1988; Lenters and Cook, 1999; Vuille, 1999; Vuille et al., 2000). Wet summers on the Altiplano are associated with La Niña-related cooling of the tropical Pacific and the tropical troposphere. The westerly flow aloft the central Andes weakens in response to reduced meridional baroclinicity at subtropical latitudes and favors the ingression of wet air masses from the east (Garreaud and Aceituno, 2001; Vuille and Keimig, 2004). The reverse happens during El Niño events related to warming of the tropical Pacific.

3. Methods

3.1. Field collections

Collections of *Polylepis tarapacana* along the Bolivian Altiplano were undertaken from 2001 to 2004 on both sides of the Cordillera Occidental from 17 to 23°S, which so far has yielded 14 tree-ring chronologies (Table 1, Fig. 2). Four chronologies were originally reported by Argollo et al. (2004). Three of these sites, Sajama, Caquella and Soniquera, were re-visited, and the replication of the chronology was substantially improved by the addition of new samples.

Table 1
Geographical characteristics of the tree-ring chronology sites.

Sampling site	Code	Latitude (°S)	Longitude (°W)	Altitudinal range (m)	Source
Huarikunca	HUA	17°12′	69°22′	3886–4803	This study
Serke	SER	17°26′	69°20′	4429–4458	This study
Nicolás	NIC	17°54′	69°13′	4350–4377	This study
Analajchi	ANA	17°55′	68°53′	4413–4584	This study
Nasahuento	NAS	17°55′	69°21′	4300	This study
Sajama	SAJ	18°06′	68°53′	4400–4500	Argollo et al. (2004) with additional sampling
Guallatiri Norte	GUN	18°28′	69°04′	4650	Christie et al. (2009-this issue)
Guallatiri Oeste	GUO	18°27′	69°05′	4730	This study
Tunupa	TUN	19°46′	67°34′	4090–4851	Argollo et al. (2004)
Caquella	CAQ	21°30′	67°34′	4370–4672	Argollo et al. (2004) with additional sampling
Tapachilca	TAP	21°35′	67°35′	4460–4479	This study
Soniquera	SON	22°00′	67°17′	4400–4675	Argollo et al. (2004) with additional sampling
Uturuncu	UTU	22°18′	67°14′	4375–4703	This study
Granada	GRA	22°32′	66°35′	4500–4750	Morales et al. (2004)

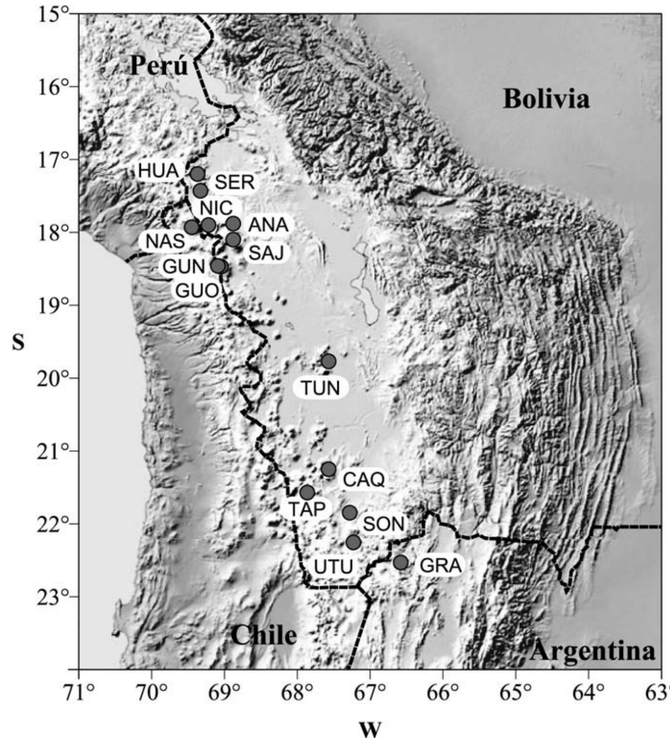


Fig. 2. Map showing sample sites for tree-ring chronologies. See Table 1 for chronology code definitions.

Tree cores were collected using increment borers. Additional samples from cross-sections and wedges were obtained from dead and living trees. Most of the collections are from open woodlands of *Polylepis tarapacana* on steep, rocky and xeric environments on the volcano slopes along the Cordillera Occidental. The sampling strategy relied on a careful selection of the sites to reduce effects of non-climatic factors on tree growth. Because evidence of logging and fire was observed at some places, cores were collected on the less-affected sectors of the stands. Insect attacks or diseases were not recorded.

3.2. Tree-ring chronologies

Standard dendrochronological procedures (Fritts, 1976; Cook et al., 1990) were used to develop tree-ring chronologies from all site collections. Cores were mounted and sanded following Stokes and Smiley (1968). For dating purposes, we followed Schulman's convention (1956) for the Southern Hemisphere, which assigns to each tree ring the date of the year in which radial growth started. The number of trees used in each chronology ranges from 9 to 40, and the number of radii ranges from 11 to 50. Ring widths were measured to the nearest 0.01mm, and the computer program COFECHA (Holmes, 1983) was used to detect measurement and cross-dating errors. Each tree's ring-width series was standardized and then averaged with the other records to produce a mean stand chronology for each site (Fritts, 1976; Cook et al., 1990). Standardization was performed using the TURBO ARSTAN program (Cook and Holmes, 1984; Cook, 1985). TURBO ARSTAN generates standard chronologies by combining standardized tree-ring series with bi-weighted robust estimation. Residual chronologies were produced in the same manner as the standard chronologies, but in this case the chronologies were residuals from autoregressive modeling of the standardized index series.

To asses the quality of the chronologies and the temporal variability in the strength of the common variation, the *Rbar* analysis (Briffa, 1995) was performed using the program TURBO ARSTAN. *Rbar* is the mean correlation coefficients for all possible pairings among tree-ring series from individual cores, computed for a specific time interval (Briffa, 1995). We used a 50-year window with an overlap of 10years between adjacent windows.

The degree of similarity among chronologies, and hence the detection of intraregional differences, was determined by measuring the inter-correlation among residual chronologies using correlation and PC analyses (Cooley and Lohnes, 1971). Residual instead of standard chronologies were used to avoid inflating the correlation coefficients due to serial autocorrelation present in the tree-ring series. The common interval 1890–1999 was used for comparing chronologies.

3.3. Climate–tree growth relationships

To identify the influence of temperature and precipitation on tree growth, residual ring-width chronologies were compared with temperature and precipitation records using correlation function analysis (Blasing et al., 1984). The ring-width index was correlated against monthly temperature and precipitation for each month separately to identify the months that best predict tree growth. As the width of an annual ring is an integration of climatically influenced processes occurring over a longer period (Fritts, 1976), the correlation coefficients must be computed between ring indices and climate variable for both the months of the growing season during which the annual ring formed, and for several months leading that growing season. In the present analysis, the relationships between ring indices and monthly climate data were examined for a sequence of 21 months starting with September of the preceding growing season and ending with May of actual growing season.

To assess the long-term relationships between climate and radial growth, we selected those climate stations with the longest available records on the Bolivian Altiplano (Table 2). The climate data were transformed to standard deviations from monthly mean temperature and total precipitation for this 21-month interval. All the correlation functions were determined for the interval 1943–1998, which was common to both the chronologies and the regional climatic records.

3.4. Climate–tree growth spatio-temporal analysis

To show the geographical variation in tree growth across the Altiplano, annual maps of tree-growth variations were produced from 1890 to 2000 using the program SURFER. Isolines of radial growth were calculated using the kriging interpolation procedure (Golden Software, 1994). The original 14 residual chronologies were normalized (i.e., the 1890–2000 long-term mean was subtracted from the value for each year and the result divided by the standard deviation) to equally weight the variance of each chronology in the resulting spatial pattern. Based on these normalized tree-ring indices, maps of annual tree-growth variations were produced. For the interval 1890–2000, replication consists of ten or more samples per year in the 14 chronologies (Table 2). Due to the site locations along the Cordillera Occidental, the spatial pattern of *Polylepis tarapacana* growth is mostly a transect in the north to south direction. Isolines of radial growth that are far distant from the sampling points of the chronologies should be interpreted with caution. The entire set of maps is included as supplementary material (Appendix A). Only selected maps are interpreted and discussed in this study.

To facilitate comparison with tree-growth maps, isolines on the precipitation maps were drawn using the same interpolation procedure described for the maps of tree growth (i.e., the kriging method, Golden Software, 1994). Precipitation variations for each of the 21 weather stations listed in Table 3 were normalized (zero mean and one standard deviation). As a consequence of using normalized standard deviations, each station, independent of its particular values, has the same weight in the spatial representation. Because the length and time period of each precipitation record are different, the number of precipitation records used in each map changes over time. The set starts with four stations in 1948, increases to eight stations in 1962 and to 10 or more stations between 1969 and 1998, and decreases to six stations after 2001.

Monthly, seasonal, and annual maps for precipitation variations were produced for the 1948–1998 period. The complete set of precipitation maps is included as Supplementary Information (Appendix B). For the purpose of this study, only a few of these maps will be considered.

4. Results

4.1. Tree-ring chronologies

Trees severely limited by climate exhibit greater relative variability in ring widths than those for which growth is less affected by climate (Fritts, 1976). Mean sensitivity is a measure of the relative change in

Table 2
Meteorological records used for comparison with tree-ring records.

Station	Code	Latitude (°S)	Longitude (°W)	Elevation (m)	Period record	Parameter	Source
Visviri	Vis	17°37′	69°03′	4070	1974–1993	P	Vuille et al. (2000)
Charana	Cha	17°35′	69°26′	4059	1948–1998	P	Vuille et al. (2000)
Isla Blanca	Isl	17°36′	69°36′	4540	1970–1988	P	Vuille et al. (2000)
Oruro	Oru	17°57′	67°08′	3706	1943–1998	P, T	SENAMHI
Caquena	Caq	18°05′	69°20′	4400	1970–2002	P	Vuille pers. com. 2002
Sajama	Saj	18°06′	68°53′	4220	1975–1984	P	Vuille et al. (2000)
Kota Kotani	Kot	18°11′	69°13′	4550	1960–2005	P	Vuille pers. com. 2002
Parinacota	Par	18°14′	69°12′	4390	1952–2003	P	Vuille pers. com. 2002
Chungara reten	Chun	18°17′	69°07′	4570	1962–2003	P	Vuille pers. com. 2002
Chucuyo	Chu	18°22′	69°33′	4400	1961–2003	P	Vuille pers. com. 2002
Ajata	Aja	18°23′	69°01′	4570	1983–2003	P	Vuille pers. com. 2002
Guallatire	Gua	18°29′	69°09′	4240	1969–2003	P	Vuille pers. com. 2002
Uyuni	Uyu	20°28′	66°48′	3660	1975–1998	P	SENAMHI
Colcha	Col	20°47′	67°47′	3700	1980–1996	P	Vuille et al. (2000)
Calcha de Lipez	Lip	21°01′	67°58′	3670	1984–1994	P	Vuille et al. (2000)
Alota	Alo	21°24′	67°37′	3609	1986–1997	P	Vuille et al. (2000)
Ascotan	Asc	21°32′	68°18′	4000	1975–1992	P	Vuille et al. (2000)
Inacalliri	Ina	22°01′	68°05′	4100	1970–1993	P	Vuille et al. (2000)
La Quiaca	Qui	22°07′	65°36′	3442	1903–1993	P, T	Ser. Met. Arg.
Linzor	Lin	22°13′	68°01′	4096	1975–1992	P	Vuille et al. (2000)
El Tatio	Elt	22°25′	68°04′	4320	1979–1992	P	Vuille et al. (2000)
Abra Pampa	Abr	22°42′	65°41′	3484	1934–1989	P	Bianchi and Yáñez (1992)

Table 3
Descriptive statistics for the 14 residual tree-ring chronologies from *Polylepis tarapacana* used in this study (see Table 1 for chronology code definitions).

Chronology code	No. of trees	No. of radii	Record period	Mean tree-ring width (mm)	No. of radii in year 1890	Missing rings (%)	Mean sensitivity	Variance in first eigenvector (%)	Rbar	
									Mean	SErr
HUA	24	24	1850–2002	0.434	6	0.000	0.268	37.52	0.281	0.019
SER	13	15	1890–2002	0.271	2	0.000	0.226	36.46	0.262	0.030
NIC	16	17	1794–2001	0.446	7	0.000	0.300	44.07	0.404	0.016
ANA	32	34	1876–2002	0.735	34	0.000	0.181	27.81	0.234	0.012
NAS	16	25	1761–2002	0.491	11	0.000	0.258	37.86	0.352	0.025
SAJ	35	37	1664–2003	0.438	25	0.000	0.226	32.24	0.246	0.013
GUN	36	50	1737–2001	0.389	38	0.012	0.277	52.20	0.500	0.005
GUO	18	28	1467–2002	0.401	28	0.000	0.255	56.13	0.483	0.018
TUN	37	40	1768–2002	0.542	39	0.070	0.263	29.96	0.257	0.012
CAQ	18	26	1660–2000	0.368	26	0.076	0.279	49.88	0.460	0.013
TAP	09	11	1618–2000	0.352	11	0.000	0.304	47.25	0.355	0.027
SON	38	38	1430–2003	0.426	38	0.000	0.268	40.63	0.368	0.013
UTU	37	43	1297–2003	0.400	43	0.000	0.234	37.90	0.321	0.012
GRA	47	26	1659–1999	0.848	46	0.017	0.368	35.62	0.339	0.007

ring-width variations from year to year and is calculated as the absolute difference between adjacent indices divided by the mean of the two indices (Fritts, 1976). The mean sensitivity of the residual chronologies ranges from 0.181 in Analajchi to 0.368 in Granadas (Table 3). In general, the chronologies with lower mean sensitivities are from relatively more humid sites in terms of mean annual precipitation (Analajchi, Serke and Sajama, Fig. 1). Drier sites yielded chronologies with higher mean sensitivity values (Granadas, Caquella, Soniquera).

The *Rbar* values for the different chronologies varies between 0.23 and 0.50 (Table 3). In general, higher *Rbar* values are associated with chronologies from drier and more southern-located sites, which also include a larger proportion of older trees in the chronologies. For most chronologies, lower *Rbar* values are consistent with reduced mean sensitivity values (Table 3).

Another informative parameter for evaluating the quality of a chronology is the common variance among trees that are included in a chronology (Fritts, 1976; Briffa and Jones, 1990). Higher common variance is believed to indicate a greater climatic influence on tree growth. Principal component (PC) analyses on the individual samples from each chronology for the period 1890 to 1999 (i.e. the last 110-year period common to all the chronologies) show that the variance accounted for by the first component ranges from 30 to 60% (variance first eigenvector in Table 3). On average most chronologies show values of common variance higher than 35%. The Analajchi and Tunupa chronologies show lower values of common variance among trees, which is interpreted to reflect human-induced impacts such as browsing, fire and/or logging in the woodlands.

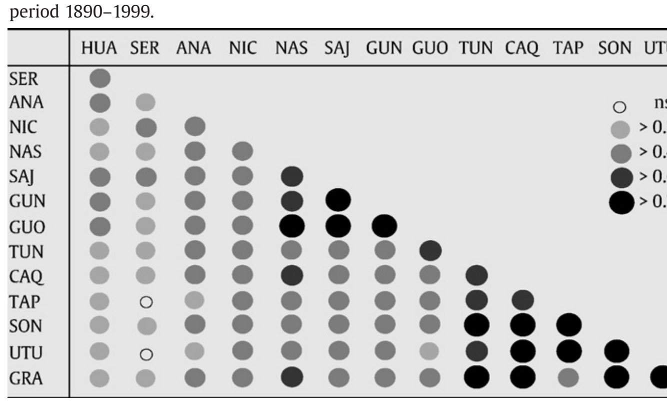
4.2. Spatial patterns of tree-ring variations across the Altiplano

Correlation patterns among the 14 ring-width chronologies over the common interval 1890–1999 indicate similar patterns of growth variations over the entire region (Table 4). In general, correlation coefficients between chronologies decrease as the distance between sites increases. This pattern of slowly decreasing correlation with distance may correspond to regional differences in climatic conditions along the Cordillera Occidental between Huarikunca (17°12′S) and Granadas (22°32′S). However, most of the correlation coefficients remain significant over the entire latitudinal range, reflecting the high percentage of common variance among the tree-ring series and a relatively homogeneous response to large-scale climatic conditions. Correlation coefficients are higher among southern chronologies, which might reflect more extreme growing conditions (i.e. drier sites) and less human impact on woodlands in the southern sector of the Altiplano.

Results from a Principal Component Analysis (PCA) of the residual tree-ring chronologies also indicate high similarities in tree-growth variations across the region. The three first principal components accounted for 52, 13, and 8% of the total variance, respectively, or cumulatively for 73% of the total variance. Due to the similarity in tree-ring variations along the western Altiplano, all the factor loadings (eigenvalues) in the first component have the same sign. Consequently, the first component does not provide a clear way of separating chronologies by site location (Fig. 3). Geographical differences in tree-growth variations only become evident when higher order components with less associated-variance are considered. The second component clearly discriminates the northern- from the southern-located chronologies (Fig. 3). The records in the northern part of the study area (SER, HUA, NIC, ANA, SAJ, NAS, GUN and GUO) all have positive loadings on the second factor axes, whereas those in the southern sector (TUN, CAQ, SON, TAP, UTU and GRA) have negative values. The chronologies located in the northern Altiplano are characterized by progressive changes in loadings on the third component axis, with records on the northern (SER, HUA, NIC and ANA) and southern sector (NAS, SAJ, GUN and GUO), showing negative and positive contributions, respectively (Fig. 3). The two nearby chronologies (GUN and GUO) on the Chilean side of the Cordillera Oriental show both more extreme positive values in the third component axis than NAS and SAJ in the same group.

Variations in the amplitudes for the first three PCs over the period 1890–1999 are presented in Fig. 4. Given the regional uniformity in tree growth associated with the first PC, negative or positive values of its amplitude indicate opposite tree-growth conditions across the Altiplano. For the second PC, years with large amplitudes reflect opposite trends in tree growth in the northern *versus* the southern

Table 4
Correlations matrix between the 14 residual tree-ring chronologies over the common period 1890–1999.



Sites are arranged from north (left) to south (right) along the *X*-axis. All correlations >0.2 are statistically significant at the 99% confidence level except TAP *versus* HUA and CAQ *versus* SER, which are significant at 95% confidence level. ns = not significant. Chronology codes and locations are indicated in Table 1.

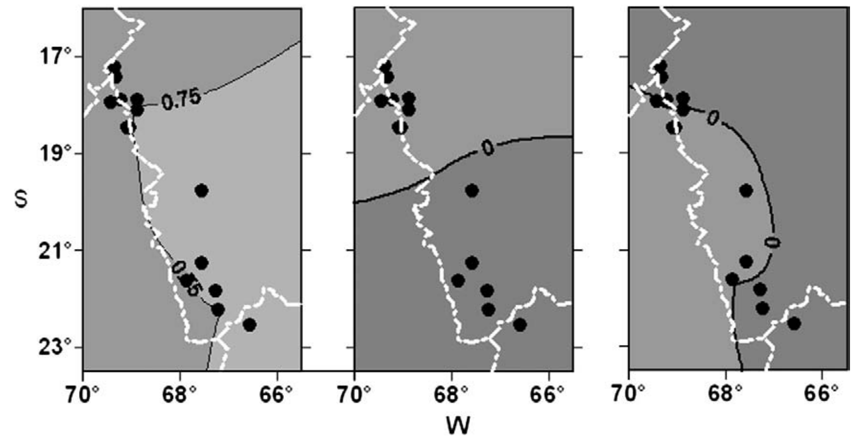


Fig. 3. Dominant spatial patterns of tree growth for 14 *Polylepis tarapacana* chronologies across their geographical range in the Bolivian Altiplano, over the 1890–1999 common period. Chronologies, represented by black dots are plotted in their longitudinal (*x*) and latitudinal (*y*) locations. Isolines represent the factor scores for the first three principal components for radial growth (left box: PC1-growth, centre box: PC2-growth and right box: PC3-growth), which account for 52%, 13% and 8% of the total variance, respectively.

areas. Years with large amplitudes on the third PC correspond to opposite patterns of tree growth between the western (Chilean) and the eastern sites.

To facilitate the interpretation of the three main spatial patterns of *Polylepis tarapacana* growth shown in Fig. 3, the spatial eigenvector patterns were compared with spatial plots of the original tree-ring data. Based on the amplitudes of the first PC for the interval 1890–1999 (Fig. 5), we selected five years that had the lowest and highest amplitude values. Tree growth was below the long-term mean throughout the Altiplano region in 1998, 1983, 1967, 1964 and 1916. Conversely, tree growth was above the mean at most of the sites in 1997, 1987, 1972, 1963, and 1925 (Fig. 5).

The maps for the years 1999, 1975, and 1906, representing the largest positive departures on the second PC, are characterized by higher and lower growth in the southern and northern parts of the Cordillera Oriental, respectively (Fig. 6a). In contrast, the largest negative departures from the second PC, occurring in the years 1965, 1970 and 1982, are associated with relatively lower and higher growth in the southern and in the northern areas, respectively (Fig. 6a). Finally, those maps related to positive departures in the third PC (1913 and 1914) are characterized by having high tree growth in the Chilean area (western sites) with a slight tendency towards lower growth in the northeastearn and eastern sites (Fig. 6b). Conversely, the maps for the years 1943 and 1944, which correspond to the largest negative amplitude in the third PC, show the opposite pattern (Fig. 6b).

4.3. Climate–tree growth relationships

Fig. 7 summarizes the results of the correlation functions between the 14 tree-ring chronologies and climate across the Altiplano.

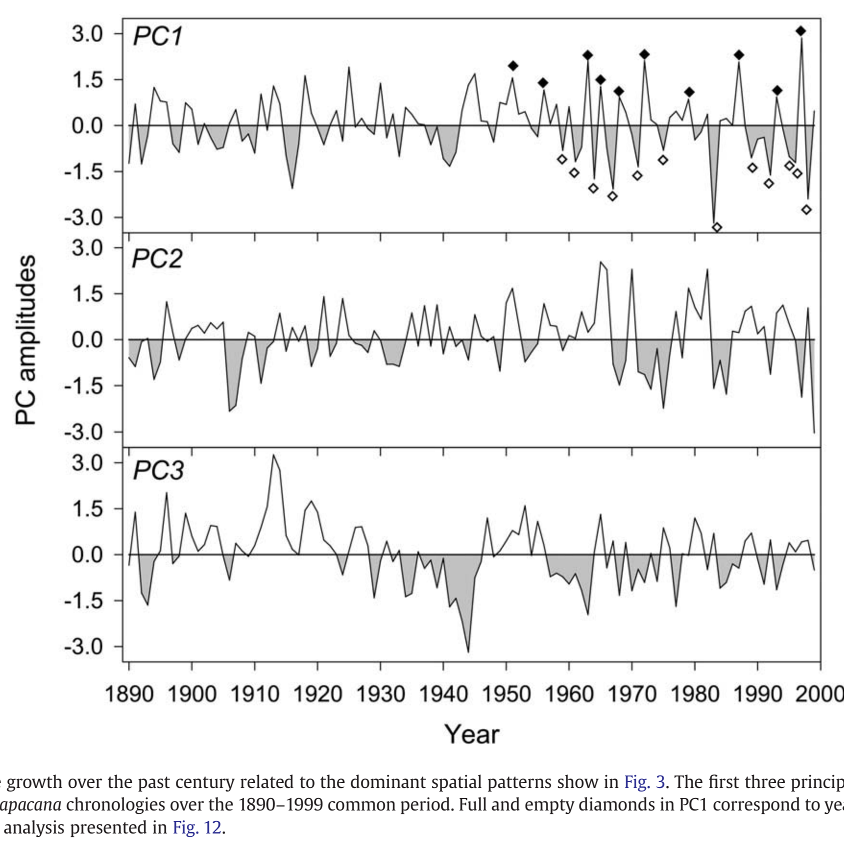


Fig. 4. Temporal variations of tree growth over the past century related to the dominant spatial patterns show in Fig. 3. The first three principal components of tree growth were extracted from the 14 *Polylepis tarapacana* chronologies over the 1890–1999 common period. Full and empty diamonds in PC1 correspond to years with relatively high and low tree growth, respectively, used for the analysis presented in Fig. 12.

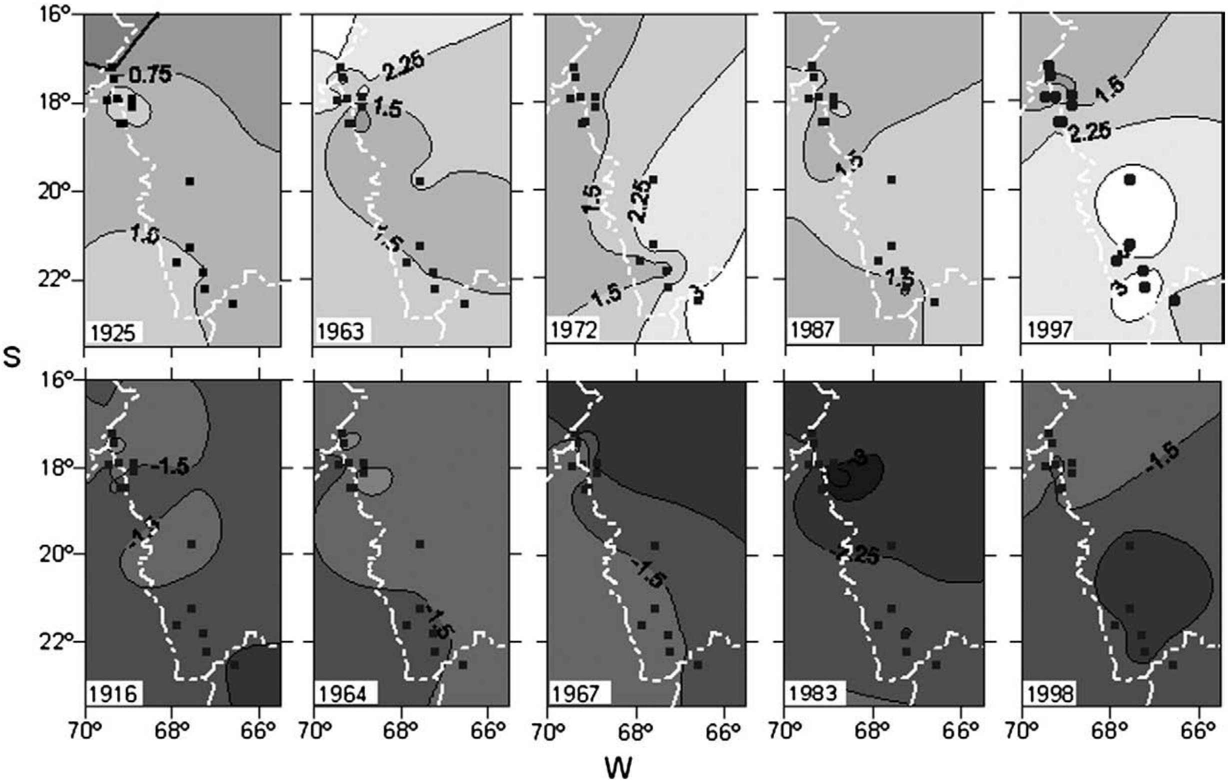


Fig. 5. Maps of regional spatial variation in tree growth for the five years with the most extreme high (upper) and low (bottom) mean growth during the 1890–1999 interval as determined by the amplitudes on PC1 in Fig. 4. Chronological dates are indicated for each map in the lower left corner.

Consistent with the large percentage of common variance between chronologies, there are large similarities among sites in their responses of tree growth to climate. For precipitation, the most conspicuous pattern is the large number of sites showing significant positive responses from November to March during the preceding growing season, January being statistically significant at most sites.

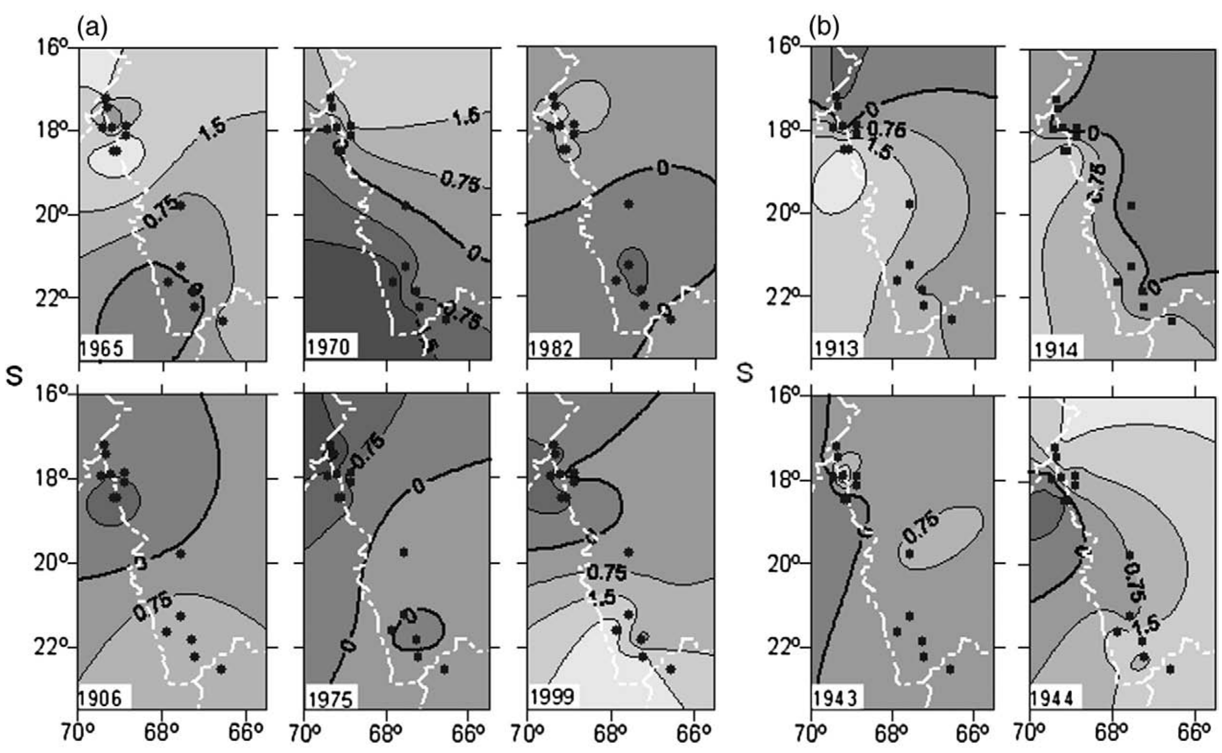


Fig. 6. Maps of regional spatial variation in tree growth for (a) the six most extreme years of tree growth from 1890 to 1999 as indicated by the amplitudes on PC2 in Fig. 4 and (b) four extreme years of tree growth as indicated by the amplitudes on PC3 in Fig. 4. Chronological dates are indicated for each map in the lower left corner.

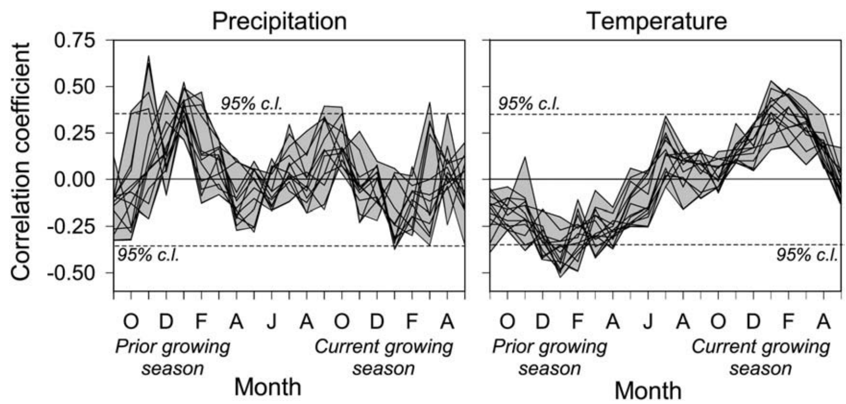


Fig. 7. Correlation functions, based on residual chronologies, showing the correlation coefficients between the ring width indices from each of the 14 *Polylepis tarapacana* chronologies, total monthly precipitation (left) and mean monthly temperatures (right). Correlation coefficients are for residual ring width against the average of normalized departures of monthly total precipitation and mean temperatures from meteorological stations across the Bolivian Altiplano, for the period 1943–1998. Positive correlation indicates that above-average tree growth is associated with above-average values of the climatic variable. Coefficients greater than 0.35 (dotted lines) are significant at the 95% confidence level.

During the actual growing season, negative correlations with December rainfall are registered at few sites (Fig. 7). This indicates that the radial growth of *Polylepis tarapacana* along the Cordillera Occidental is favored by above-average summer precipitation during the preceding growing season. Indeed, the average correlation coefficient between the 14 chronologies and January precipitation is $r = 0.40$, with some correlation coefficients between individual chronologies and precipitation during the preceding growing season as high as $r = 0.66$ ($n = 56$, $p < 0.001$).

Contrasting responses of *Polylepis tarapacana* to temperature during the preceding and actual growing season are registered at most sites. Above-average temperatures during the preceding growing season increase evapotranspiration, reduce soil water supply, and consequently are negatively correlated with tree growth (Fig. 7). During the actual growing season, temperatures from January to March are positively related to radial growth.

In addition to the documented monthly responses to precipitation variations, the growth of *Polylepis tarapacana* is also highly correlated with seasonal variations in climate, particularly total summer (December to March) precipitation. For some sites, correlation coefficients as high as $r = 0.60$ ($n = 56$, $p < 0.001$) occur when total summer precipitation is compared with tree-ring variations during the 1943–1998 interval (Argollo et al., 2004). These results indicate that tree-ring records of *P. tarapacana* along the western Altiplano can also be used to estimate fluctuations of seasonal precipitation during the past centuries. This is a valuable feature considering that summer (December to March) precipitation represents more than 80% of the total annual precipitation in the western Bolivian Altiplano (Vuille and Keimig, 2004).

4.4. Climatic significance of spatial tree-growth patterns

The most common spatial patterns of tree growth (Figs. 3, 5, 6) account for a large part of the total variance of tree growth across the Bolivian Altiplano. However, an examination of the tree-growth maps from 1890 to 2000 reveals a large degree of interannual variability (see supplementary information, Appendix A). In this section, we evaluate if the observed high variability in tree growth across the Cordillera Occidental is related to regional climate or to local features.

Correlation function analysis (Fig. 7) shows that growth of *Polylepis tarapacana* across the Bolivian Altiplano is significantly correlated with precipitation variations during summer (November to March) of the preceding growing season. Within summer, the growth of *P. tarapacana* is strongly related to January precipitation (Fig. 7). In addition, at some sites significant correlation with precipitation variations are recorded during other months. Consequently, January, summer (November to March) and annual (July to June) precipitation variations were compared with annual tree growth.

Visual examination of the spatial variations in tree growth and precipitation indicates the existence of some important patterns (see supplementary information, Appendixes A and B). The most common pattern consists of spatial tree-growth variations resembling annual precipitation variations during the preceding year. The highest correlation coefficients between ring-width variations and precipitation are recorded during the preceding growing season (Fig. 7). However, as summer precipitation represents in most sites more than 80% of the annual precipitation, for most years there are no substantial differences between the maps for summer and annual precipitation variations.

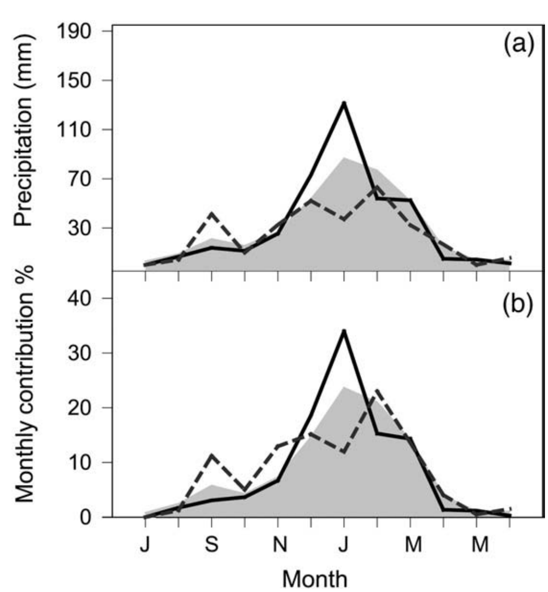


Fig. 8. Mean patterns of monthly total precipitation (a) and monthly precipitation contribution to the annual hydrological cycle (b) from the years previous to those shown in Fig. 5. The grey area represents the mean monthly precipitation pattern for the period 1943–1998. The solid and short-dashed lines represent the mean values from the four previous years with the most extreme above- (1962, 1971, 1986 and 1996) and below-average (1963, 1966, 1982 and 1997) tree growth across the Bolivian Altiplano, respectively. Since representative meteorological records in the region started in 1943, the years 1915 and 1924 corresponding to the maps of 1916 and 1925 (shown in Fig. 5), respectively, were not included in the estimation of precipitation mean patterns.

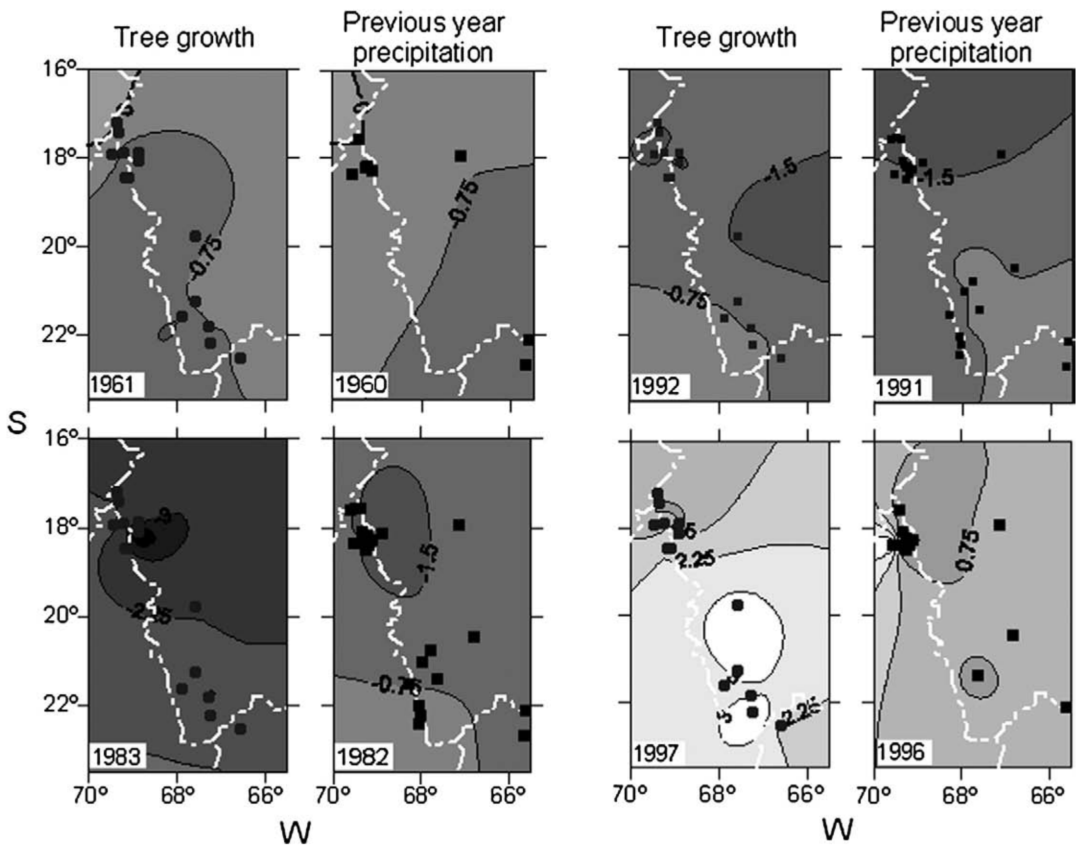


Fig. 9. Comparison of regional spatial patterns of variation in tree growth (left) and previous year annual precipitation (right) for the years 1961, 1983, 1992, and 1997. Chronology and meteorological station locations are indicated by circles and squares, respectively.

Fig. 8 compares the precipitation anomalies, with reference to the interval 1943–2000, during the four years with the lowest and highest tree growth across the Altiplano (as taken from Fig. 5). Precipitation variations are taken from Oruro, the longest record in the central sector of the Altiplano starting in 1943. In consequence, the years 1916 and 1925 listed in the sets of the five extremes (Fig. 5) were not included in this comparison. The most remarkable feature in Fig. 8 is the large difference in January precipitation between above- and below-mean growth patterns. On average, January precipitation in Oruro during the preceding (lead 1year) summer was three times larger during the years with the highest *versus* the years with the lowest tree growth across the Altiplano.

Fig. 9 shows the spatial patterns in tree growth and the annual precipitation (preceding year: from preceding July to actual June) for the years 1961, 1983, 1992 and 1997. For the year 1997, both tree growth and preceding annual precipitation show large positive departures in the central part of the study area and gradual decreases towards the north (Fig. 9). For the years 1992 and 1983, lower tree growth in the northwestern sites was concurrent with larger negative departures of annual precipitation in this zone (Fig. 9). In both years, the radial growth increases to the south, consistent with reduced negative departures in precipitation in the same direction. Extremely reduced radial growth at Analajchi and Sajama is consistent with the largest negative precipitation departures in the same area. Larger tree growth at the northwestern sites during the year 1961 coincides with positive annual rainfall departures at the stations in the northern sector of our latitudinal transect (Fig. 9).

Changes in the dominant patterns of climate–tree growth relationships occur in years with anomalous monthly precipitation distribution. For instance, December–January precipitation at Oruro during the years 1955 and 1959 represented 71 and 58% of the total annual precipitation (from preceding July to actual June) respectively. These percentages

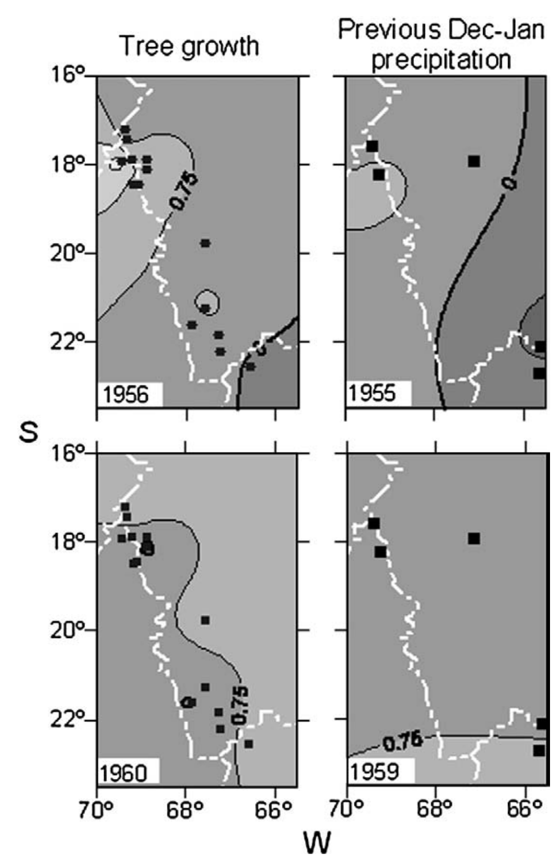


Fig. 10. Comparison of regional spatial patterns of variation in tree growth (left) and previous December–January precipitation (right) for the years 1956 and 1960.

largely exceed the mean value of 39% for the interval 1943–1998. During these years, the wet December–January period at the beginning of the growing season was followed by extremely dry conditions in February. On average (1943–1998) February precipitation in Oruro constitutes 21% of the total annual. However, February precipitation in the years 1955 and 1959 accounted only for 11 and 1% of the total precipitation of that year, respectively. In response to these anomalies in monthly precipitation, the spatial patterns of tree growth in the following years (1956 and 1960) are more similar to December–January than to total annual precipitation patterns (Fig. 10).

Another spatial pattern between growth and climate results from climatic preconditioning in preceding years and is associated with the formation of extremely narrow or wide rings of *Polylepis tarapacana*. The abrupt reduction in tree growth in the year 1967 corresponds to extremely dry conditions not only in 1966, but also in 1965 (Fig. 11a). Similarly, the largest positive departures of tree growth in 1987 are better explained if climatic conditions during the preceding two years (1985 and 1986) are taken into account (Fig. 11a).

For years with normal or above-average precipitation following one or more extremely dry years, the radial growth of *Polylepis tarapacana* during the following growing season is normally lower than expected if only the preceding year is considered in terms of climate conditions. For example, after the severe drought of 1982, tree growth in 1984 was around the long-term mean at almost all sites

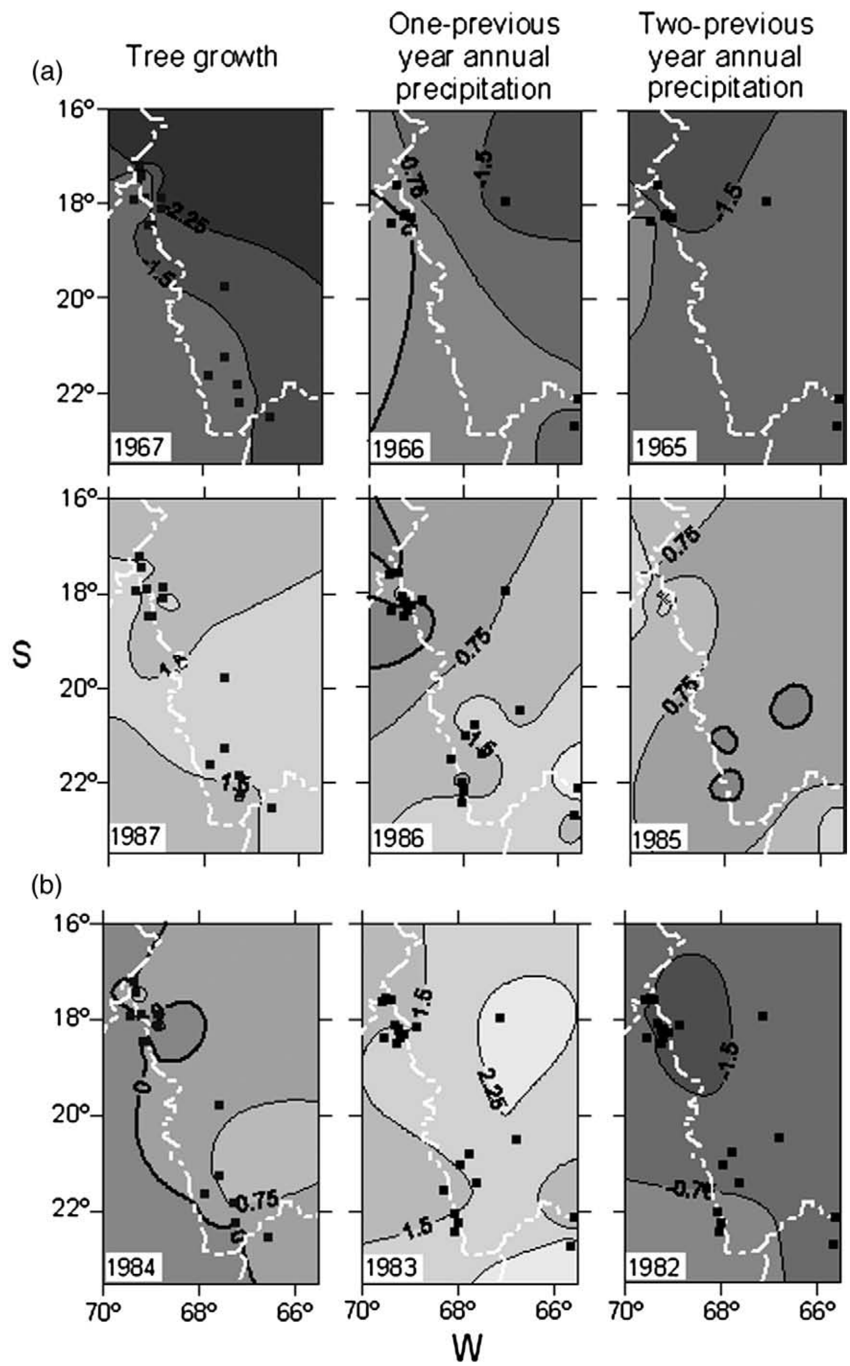


Fig. 11. Comparison of regional spatial patterns of variation in tree growth (left), previous year (July–June) precipitation (center), and two-previous year (July–June) precipitation. a) Influences of two consecutive previous years of below-average (1967) and above-average precipitation (1987). (b) Influences on tree growth of two consecutive years with contrasting abundant-reduced (1984) precipitations. Tree growth of *P. tarapacana* is normally lower than expected in years that follow annual periods with above-average precipitation preceded by one or more extremely dry years as shown for 1984.

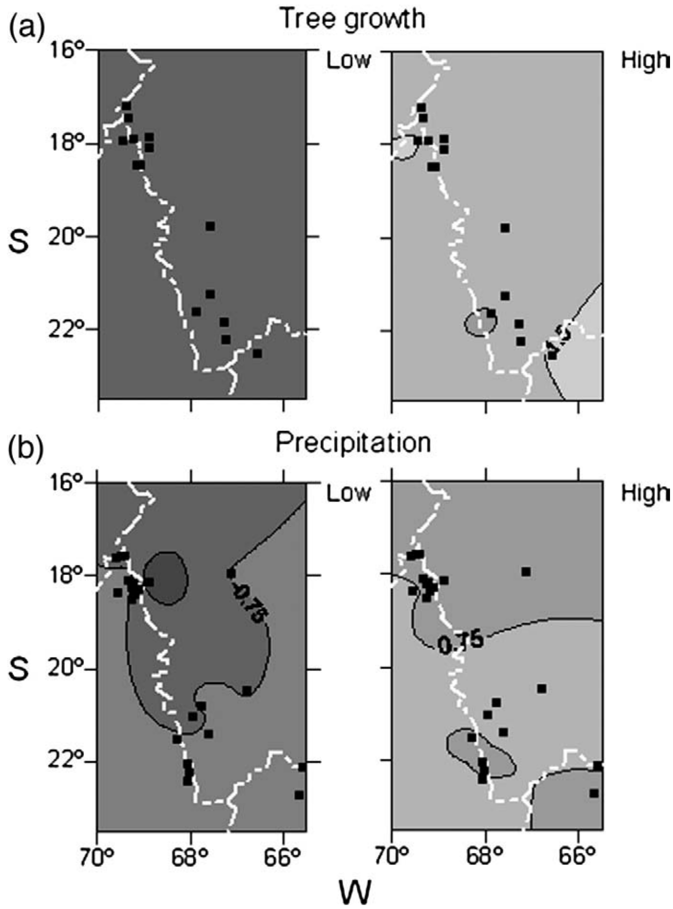


Fig. 12. a) Regional spatial variations in tree growth for years of low (left) and high (right) tree-growth anomalies derived from grouping all the years with amplitudes below −0.75 and above 0.75 on the first PC axis shown in Fig. 4. For the interval 1948–1998, the years allocated to the low and high growth patterns are shown as empty and full diamonds, respectively, in Fig. 4. b) Regional spatial variation in total annual (July–June) precipitation anomalies corresponding to each of the previous years allocated to the low and high growth patterns shown above.

despite the consistently higher annual precipitation during the preceding 1983 (Fig. 11b). Following a severe drought, trees require a year or more to recuperate to an average growth rate. The opposite situation, although less frequent, was also observed.

4.5. Multi-year growth patterns and climate

In previous sections, the three most important spatial modes of variability of tree growth of *Polylepis tarapacana* across the Bolivian Altiplano were identified (Fig. 3). The most significant type, related to the first component, is characterized by homogeneous tree-growth variations throughout the study area. Based on the amplitudes of the first PC, tree-growth spatial patterns from 1948 to 1999 (51years common to meteorological data) were discriminated into two groups. The first group includes all the patterns from years with positive amplitudes > 0.75 (10years; Fig. 4), and the second group includes all patterns from years with amplitudes < −0.75 (12years). The mean tree-growth patterns corresponding to each of the two groups are shown in Fig. 12a. As expected, the patterns of average growth anomalies show contrasting patterns of low (mean = − 1.15, SD = 0.16) and high tree growth (mean = 1.19, SD = 0.25) throughout the region, being statistically different at the 99% confidence level.

To identify the climatic signal associated with these mean tree-growth patterns (Fig. 12a), annual precipitation maps were produced for the corresponding years (Fig. 12b). The mean spatial patterns of tree growth above and below the long-term average are clearly associated with precipitation above and below average, respectively. At the 99% confidence level, the mean precipitation pattern associated with high tree growth is significantly wetter than the mean precipitation pattern corresponding to low tree growth (the means and standard deviations of precipitation were 0.65 and 0.41 for the mean wet pattern and − 0.74 and 0.40 for the mean dry pattern, respectively). Consequently, our results show that mean tree-growth patterns derived from the PC1 amplitudes can be considered as a reliable proxy for precipitation variations on the Bolivian Altiplano.

Based on the amplitudes of the first PCs for the period 1890 to 1999, we identified periods of three or more consecutive years showing negative or positive amplitudes (Fig. 13). The cumulative sum of the amplitudes during these periods provides an estimate for the intensity of the tree-growth anomalies. The most negative anomaly was observed 1915–17, the most positive 1943–45, respectively (Fig. 13). During the common interval between precipitation and tree-ring records, patterns of tree-growth variations for the most significant intervals with negative (1989–92 and 1994–96) and positive (1976–79 and 1984–87) departures are also shown in Fig. 13. Although the tree-growth patterns related to positive and negative departures show above- and below-growth across the entire region, respectively, there are some differences in the geographical distribution of the growth anomalies. For example, the 1915–17 and 1994–96 growth reductions were more severe in the south, whereas the 1989–92 reduction was stronger in the central Altiplano. Except for the 1943–45 interval, the spatial representation of periods with positive departures show a more uniform pattern of high tree growth across the Altiplano (Fig. 13).

Composite maps of annual (July to June) precipitation were produced for the intervals of below- and above-average tree growth along the Bolivian Altiplano (Fig. 13). Due to the one-year lag in the response of *Polylepis* tree growth to rainfall, precipitation maps were produced for intervals shifted one year ahead in relation to the tree-growth composites. The intervals of below-average growth during 1989–92 and 1994–96 were concurrent with below-average precipitation across the region. The spatial pattern of precipitation distribution for the interval 1975–77, associated with a period of above-average growth during 1976–79, is characterized by a gradual north-to-south decrease in above-average precipitation. During this interval, *Polylepis* growth also showed a gradual decrease in the north–south direction, with tree growth in Granada, the southernmost site, below the long-term 1890–2000 mean. The relationships between tree growth and climate in these maps indicate that multi-year (> 3years) changes in tree growth during the 20th century can be related to multi-year changes in precipitation. Indeed, the instrumental meteorological record for the region shows that multi-year periods of low and high tree growth during the 20th century were concurrent with dry and wet periods in the Altiplano, respectively.

5. Discussion

This study provides a dendroclimatic perspective on spatial and temporal patterns of *Polylepis tarapacana* radial growth across the Bolivian Altiplano (17–23°S). Located in the tropical–subtropical domain of South America at a mean elevation of 4000 m, the Bolivian Altiplano is characterized by a moderate seasonality in temperature but a marked seasonality in annual precipitation. The rainfall season from November to March coincides also with the season of higher temperature and reduced daily temperature amplitudes. Precisely these environmental conditions lead to cambium activation in *P. tarapacana* and the formation of annual rings (Argollo et al., 2004).

Several tree-ring studies have shown the dominant influences of site conditions on tree-growth responses to climate variations (Fritts, 1976; Schweingruber, 1988). In other regions of subtropical South America, differences in site conditions (e.g., aspect and elevation) over short distances account for major differences in growth responses to climate variations (Villalba et al., 1992, 1998). In contrast, the results of this study

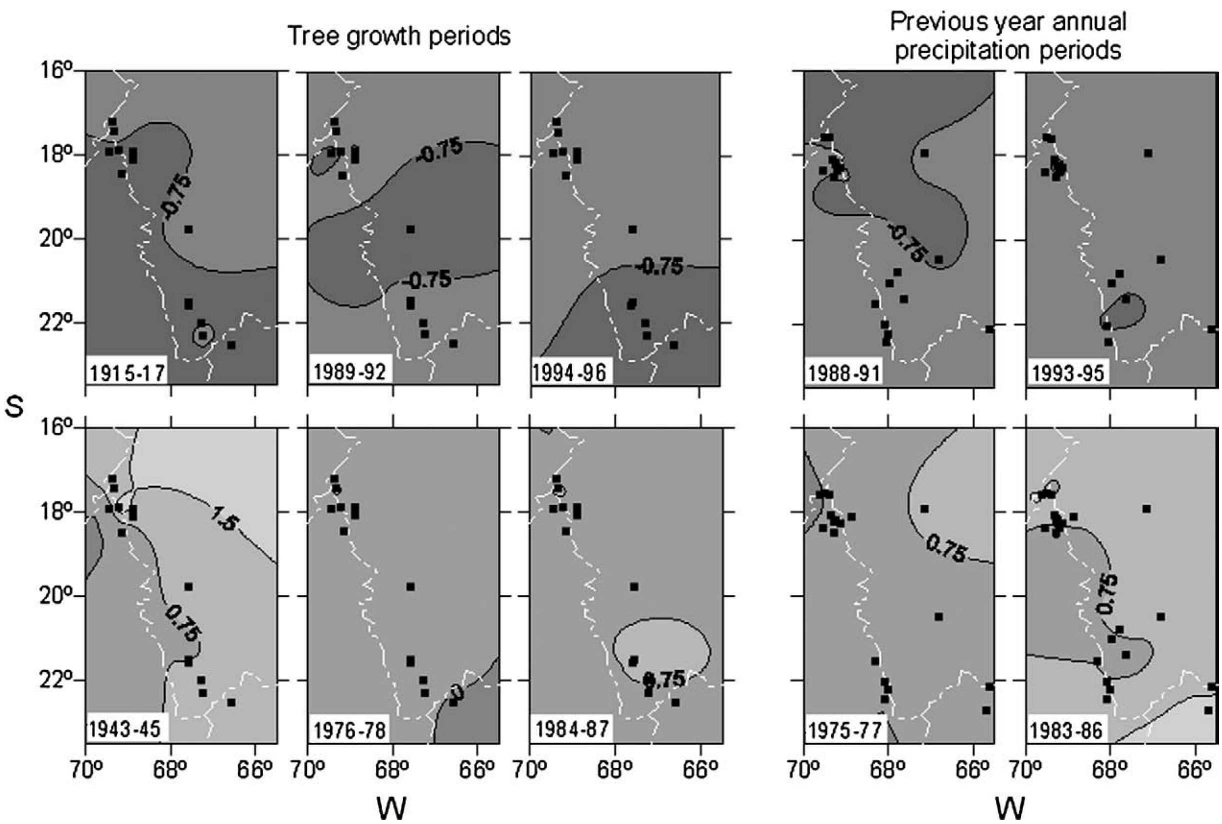


Fig. 13. Regional spatial variations in *Polylepis tarapacana* tree growth for intervals of years of low and high tree-growth anomalies derived from grouping years with amplitudes below and above average on the first PC axis shown in Fig. 4. The regional spatial anomalies in total annual (July–June) precipitation corresponding to each of the periods allocated to the low and high growth patterns during the interval 1948–1998 of instrumental records are shown on the right.

show large similarities in tree-ring variations across the Bolivian Altiplano. Tree-ring variations recorded over the region appear to reflect largely macroclimatic signals rather than local site factors.

Residual chronologies were used to properly evaluate the statistical significance of the comparisons between tree-ring records. However, due to the removal of serial autocorrelation in the residual chronologies, long-term changes and persistence associated with climatic variations were also removed from the chronologies (Cook et al., 1990), largely restricting the comparisons between climate and tree growth to the high-frequency components of variability presented in both records.

For the 14 chronologies scattered throughout the region, the first principal component accounts for more than 50% of the total variance in tree-growth variations over the interval 1890–1999. These similarities in tree growth are partially due to a careful selection of sampling sites (i.e., open woodlands at xeric sites free or with reduced human intervention) intended to maintain homogeneity in environmental conditions and due to the use of a single species as the source of the tree-ring chronologies. However, the similarity in tree growth across the Altiplano largely relies on the existence of a regional precipitation signal common to all sites. Intraregional differences in tree-growth variations correspond to slight differences in site conditions (e.g., aspect) as well as minor regional differences in climatic conditions within the study area.

Based on a network of precipitation records along the region, we related the dominant modes of radial growth with variability in seasonal and interannual rainfall. Spatial variations in tree growth in a particular year reflect to a large degree the annual precipitation during the preceding year (Fig. 9). The spatial relationships between *Polylepis tarapacana* growth and precipitation are more evident in years with extreme climatic conditions during the preceding (lead 1year) year. However, variations in ring widths of *P. tarapacana* also reflect climatic conditions during several preceding years (lead 2–3years; Figs. 11 and 12). This observation, which is valid for most of the species used in dendroclimatological studies, is an indication of the complexity of the tree-growth responses to climate.

Based on the statistics used to assess the quality of the tree-ring chronologies (Table 3) and the sensitivity to inter- and multi-annual variations in climate, we conclude that *Polylepis tarapacana* is a highly suitable species for dendroclimatological studies in tropical–subtropical South America. The good dendrochronological characteristics of *Polylepis* reflect its ability to tolerate drier conditions than those tolerated by tree species from rain forests in tropical and subtropical South America. For example, variations in ring widths of subtropical species in northwestern Argentina reflect the enormous diversity of environmental conditions imposed by the steep topography of the subtropical montane forests, which produces in this area a wider array of responses to climate compared with the Altiplano (Villalba et al., 1992, 1998). Recently, some tree-ring chronologies have been developed from tropical trees in the Amazon basin (Dünish et al., 2003; Brienen and Ziudema, 2005). Nevertheless, it is still problematic to determine whether growth increments in the xylem of tropical trees are formed annually as a rule (Worbes, 1999). Bauch and Dünisch (2000) reported that the formation of increment zones in the xylem of some neotropical *Meliaceae* species often did not correspond to the annual increment of the trees. In addition, shorter periods of dormancies, the formation of non-annual increment zones, and false rings are reported for tropical trees from regions where precipitation is distributed more equally over the year. This indicates that the annual pattern of cambial growth of tropical tree species has to be analyzed separately on each site before master chronologies can be established (Dünish et al., 2003; Brienen and Ziudema, 2005).

Although the results presented in this study point to a more direct and simple relationship between *Polylepis* growth and climate than those for other species in tropical and subtropical South America as indicated above, our study explicitly reveals the complexity of the climatic influences on *Polylepis* radial growth. A companion study by Christie et al. (2009-this issue) takes advantage of this complexity in the response of *Polylepis* tree growth to climate for evaluating the relationships between tree growth variability, actual growing season temperature on the Altiplano and the Southern Oscillation in the tropical Pacific. The opposite relationships between temperature and radial growth during two consecutive growing seasons is a particular feature of *Polylepis tarapacana* response to climate (Fig. 7). Argollo et al. (2004) and Morales et al. (2004) argued that this response is, to some extent, a function of the particular characteristics of temperature oscillations rather than a consistent response of trees to climate in the Altiplano. Spectral analysis of summer (January to March) temperature variations at La Quiaca reveals a persistent oscillation centered at 2.3years during the past 80years (Argollo et al., 2004; Morales et al., 2004). In consequence, if cool (warm) summers are, in most cases, followed by warm (cool) summers, opposite relationships between radial growth of *P. tarapacana* and the Altiplano temperature may be expected between consecutive growing seasons. However, this contrasting year-to-year response of *P. tarapacana* to temperature is still a topic of controversy (see Hoch and Körner, 2005; Kessler et al., 2007; Christie et al., 2009-this issue). Additional long-term ecophysiological studies are needed to support our results.

The detailed analysis presented here enhances our understanding of the possible climatic interpretations of *Polylepis* growth variations. The *Polylepis* records offer the unique opportunity for reconstructing precipitation variations during the past 5–7 centuries in the Bolivian Altiplano. However, careful considerations of the spatially and temporally complex relationships between tree growth and climate, as it is shown here, is a necessary step before attempting any quantitative estimation of past climate from tree rings in the region.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.palaeo.2008.07.025.

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