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Source: Tree-Ring Research, 68(2):91-103. 2012.
Published By: Tree-Ring Society
DOI: http://dx.doi.org/10.3959/2011-10.1
URL: http://www.bioone.org/doi/full/10.3959/2011-10.1

TREE-RING RESEARCH, *Vol. 68(2), 2012, pp. 91–103*

ANALYSIS OF THE DENDROCLIMATIC POTENTIAL OF *POLYLEPIS PEPEI*, *P. SUBSERICANS* AND *P. RUGULOSA* IN THE TROPICAL ANDES (PERU-BOLIVIA)

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ABSTRACT

This paper reports on investigation of the dendroclimatic potential of three *Polylepis* species, *P. pepei, P. subsericans and P. rugulosa* in Peru and Bolivia in the tropical Andes, where they form the world's highest treeline forests up to 5,000 m a.s.l. In Bolivia, *P. pepei* trees were sampled close to La Paz City. In Peru, *P. pepei* and *P. subsericans* were sampled in the Vilcanota Mountains close to Urubamba City, and *P. rugulosa* in the Arequipa region on the slope of Coropuna Volcano. Chronologies span the 20th Century and all three species show intermediate values of mean sensitivity, common variance and signal-to-noise ratio. In general, correlation and response-function analyses revealed significant positive relationships with temperature during the rainy season for all three species in Peru and Bolivia. Relationships with precipitation were more difficult to interpret as positive relationships were observed between radial growth and precipitation at the beginning of the rainy season in all three species in Peru, whereas for *P. pepei* in Bolivia, the relationships with precipitation appeared to be controlled by local conditions including slope and substrate (moraine or scree slope).

Keywords: ring widths, *Polylepis pepei*, *Polylepis subsericans*, *Polylepis rugulosa*, temperature, precipitation, Peru, Bolivia.

RÉSUMÉ

Cet article étudie l'intérêt dendroclimatique de trois espèces de Polylepis, *P. pepei, P. subsericans* et *P. rugulosa* dans les Andes tropicales du Pérou et de Bolivie, où ils forment les forêts les plus hautes du monde jusqu'à 5,000 m d'altitude. En Bolivie, les *P. pepei* ont été échantillonnés près de La Paz. Au Pérou, les bois de *P. pepei* et de *P. subsericans* ont été échantillonnés dans la cordillère de Vilcanota près de la ville d'Urubamba, et les bois de *P. rugolosa* dans la région d'Arequipa sur les pentes du volcan Coropuna. Les chronologies qui couvrent le 20e siècle, montrent pour les trois espèces des valeurs modérées de sensibilité moyenne, de variance commune et de rapport signal sur bruit. Les fonctions de corrélation et de réponse ont révélé des relations positives significatives entre la température durant la saison estivale et la croissance radiale pour les trois espèces au Pérou et en Bolivie. Les relations avec les précipitations sont plus complexes. Des relations positives ont été

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observées entre les précipitations au début de la saison des pluies et la croissance radiale pour les trois espèces au Pérou, tandis que pour les bois de *P. pepei* en Bolivie, les relations avec les précipitations semblent être influencées par les conditions locales incluant la nature des dépôts de pente (moraine ou talus d'éboulis) sur lesquels les arbres poussent.

Mots clefs: largeur de cernes, *Polylepis pepei*, *Polylepis subsericans*, *Polylepis rugulosa*, température, précipitation, Pérou, Bolivie.

RESUMEN

Este trabajo investiga el potencial dendroclimático de tres especies de *Polylepis*: *P. pepei*, *P. subsericans* y *P. rugulosa* en los Andes tropicales de Perú y Bolivia, donde forman el límite arbóreo más alto del mundo, de hasta 5,000 m s.n.m. En Bolivia se colectaron muestras de *P. pepei* cerca de la ciudad de La Paz. En Perú, se colectaron muestras de *P. pepei* y *P. subsericans* en la cordillera Vilcanota cerca de la ciudad de Urubamba, y *P. rugolosa* en la región de Arequipa en la pendiente del volcán Coropuna. Las cronologías que se extienden sobre el siglo XX muestran valores moderados de sensibilidad media, varianza común y relación señal/ruido para las tres especies. En general, el análisis de correlación y función de respuesta reveló relaciones positivas significativas entre la temperatura de verano y el crecimiento radial para las tres especies en Perú y Bolivia. Las relaciones del crecimiento con la precipitación fueron más complicadas. Se observaron relaciones positivas entre la precipitación al inicio del periodo de lluvias y el crecimiento radial para las tres especies en Perú, mientras en Bolivia, la relación entre el crecimiento radial de *P. pepei* y la precipitación parecería tener alguna relación con la localización y naturaleza de los depósitos de pendiente (morrena o talud) en la que crecen los árboles.

Palabras clave: Ancho de los anillos, *Polylepis pepei*, *Polylepis subsericans*, *Polylepis rugulosa*, temperatura, precipitación, Perú, Bolivia.

INTRODUCTION

In recent decades, significant efforts have been made to model the climate during the last few centuries at different regional and temporal scales (Bradley and Jones 1992; Villalba *et al.* 2003; Jones and Mann 2004; IPCC 2007). Despite these efforts, continental climate reconstructions of the last millennium in the tropics are largely underrepresented (Jomelli *et al.* 2009). Instrumental climate records are rare and too short (usually around 40 years in length) (Vuille *et al.* 2003). Given the high elevation and sensitivity of the tropical Andes to global climate change, it is important to produce long time series of high-resolution proxy data to better understand past climatic variations in this region.

Today, high-resolution paleoclimatic information in the tropical Andes is mainly based on ice core records (Thompson *et al.* 1986; Hoffmann *et al.* 2003; Jomelli *et al.* 2009), but their interpretation is still a matter of debate (Vimeux *et al.* 2005). In this context, tree-ring records are also a promising way to retrieve past climatic information at an annual resolution. Moreover, climate reconstructions using trees growing close to former Inca towns may be of particular interest for archaeological research. *Polylepis* is a high Andean tree genus comprising around 30 morphologically distinct species that are geographically or altitudinally differentiated (Kessler 1995; Shmidt-Lebuhn *et al.* 2006). In the Andes, the first analyses of relationships between tree-ring variations and climate were developed using *Polylepis taracapana* (Argollo *et al.* 2004), which is widely distributed in the dry Altiplano of Bolivia and can live for more than 600 years. Recent studies of this tree species included relationships with El Niño events (Christie *et al.* 2009) and with summer precipitation (Soliz *et al.* 2009). *P. pepei* is another Andean tree species with proven dendroclimatic potential (Roig *et al.* 2001), whereas to date, *P. subsericans* and *P. rugulosa* have not been used for dendrochronological studies.

In general, the distribution of all *Polylepis* species is highly fragmented and most of the species are currently endangered (IUCN 2010).

P. pepei is one of the species with a relatively wide distribution in the humid or semi-humid eastern side of the Andes, from central Peru to central Bolivia, where it forms an upper tree line above the continuous mountain forest belt that extends from approximately 4100 m to 4400 m a.s.l. *P. rugulosa* grows in arid regions in southwestern Peru and northwestern Chile in a narrower altitudinal range 3500–4200 m a.s.l. *P. subsericans* has the most restricted distribution and can only be found in a relatively small area near Cuzco in the semi-dry part of southeastern Peru at elevations from 4200 up to 5000 m a.s.l. (Fjeldså and Kessler 1996; Toivonen *et al.* 2011). The aim of this paper is to explore the dendroclimatological potential of these three high-Andean tree species sampled from different regions in the eastern and western Andes.

MATERIAL AND METHODS

Sampling Sites

Sampling was carried out at five sites in Bolivia and Peru in 2005–2007. Samples were obtained by cutting cross-sections of the main stem, one from each individual tree. The Bolivian sites were located in the Zongo Valley 30 km north of La Paz, on the western slope of Cerro Llampu (16°12′S; 68°07′W) (Sites 1–2 in Figure 1). Eleven *P. pepei* trees were selected at the base of a scree slope and on a gentle ridge of a late-glacial lateral moraine located at 4130 m a.s.l. The Peruvian Sites (3–5 in Figure 1) were located in the Cordillera Vilcanota near the former Inca towns of Ollantaytambo (Site 3; 13°08′S; 72°17′W) and Urubamba (Site 4; 13°12′S; 72°05′W), 40–50 km northeast of Cuzco, and on the western slope of Coropuna Volcano, 150 km northeast of the city of Arequipa, Peru (Site 5; 15°40′S; 75°48′W). At these sites, 17 *P. pepei* trees (Site 3), 15 *P. subsericans* trees (Site 4) and 23 *P. rugulosa* trees (Site 5) were sampled at 4310 m, 4450 m and 4240 m a.s.l., respectively. At Sites 3–4, *P. pepei* and *P. subsericans* trees were growing on an old (probably dating from the late glacial) steep southwest-facing lateral moraine, whereas at Site 5, *P. rugulosa* trees were growing on the ignimbrite plateau of Coropuna Volcano.

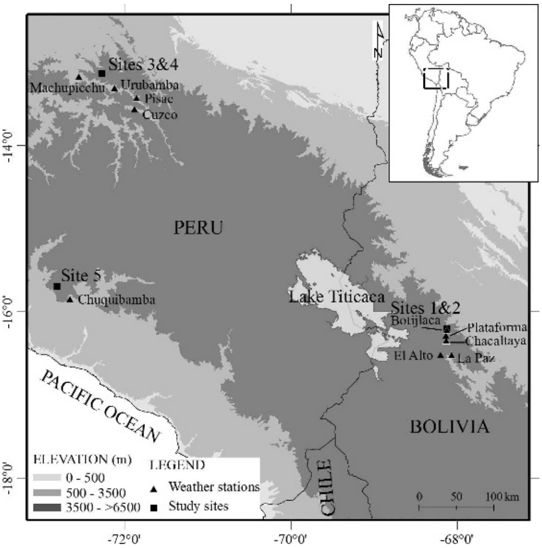

Figure 1. Map showing the different tree-ring sampling sites and meteorological stations.

Tree-Ring Dating

The surfaces of the discs were sanded to prepare the wood for microscopic analysis. Ring boundaries were clearly visible between the small thick-walled latewood and large thin-walled earlywood with a gradual transition of cell sizes within the rings.

Each ring was dated to the calendar year using crossdating techniques (Stokes and Smiley 1968). The ring widths of each disc were measured with a magnifying glass along a ruler to the nearest tenth of a millimeter from the pith towards the bark along 3–4 radii of each disc. The quality of the tree-ring series was checked using the computer program COFECHA (Holmes 1983). Radii showing errors in dating were re-examined and corrections were made. Each ring-width series was standardized and then averaged with the others to produce a mean site chronology (Fritts 1976; Cook *et al.* 1990). Standardization was performed using the ARSTAN program (Cook and Kairiukstis 1990) and a negative exponential curve was fitted to remove the biological growth trend of each series.

A residual chronology was computed by performing autoregressive modeling (AR) on the de-trended ring measurement, resulting in a chronology in which low-order autocorrelations (at time lags of 1–2 years) were removed. The order of the AR model is based on the Akaike Information Criterion (AIC).

The degree of similarity among chronologies, and hence the detection of intraregional differences, was determined by measuring the inter-correlation among residual chronologies. We also calculated the Expressed Population Signal (EPS) for the entire interval of each chronology, which measures the confidence of the chronology, to quantify how well the site chronology represented the population chronology (Wigley *et al.* 1984; Briffa 1984). It is based on an average inter-sample correlation coefficient and varies from 0 to 1. A value of 0.85 for EPS is suggested by Wigley *et al.* (1984) as a reasonable threshold for an acceptable statistical quality of the chronology. All the statistics used for the evaluation of tree-ring chronology are listed in Table 1 (Fritts 1976).

Climate-Growth Analysis

Climate-growth relationships were explored using correlation and response-function analyses from residual chronologies. The analyses were conducted using the DendroClim program (Biondi *et al.* 2003; Biondi and Waikul 2004). Coefficients of correlations are univariate estimates of the Pearson's product moment correlation, whereas coefficients of response functions are multivariate estimates from a principal component regression model. The predictor variables for correlation and response-function analyses were monthly temperature and precipitation data. Variables were considered significant at the 95% level. Principal component analyses were performed to avoid the problem of intercorrelation among climatic variables (Briffa and Cook 1990; Guiot 1985, 1990). Afterwards, a regression model was applied. A bootstrap method was used to compute response and correlation coefficients (Guiot 1991). Here, the predictor variables for response-function analysis were monthly mean temperatures and total monthly precipitation for a period of 24 months (12 months from the previous year and 12 of the present year of growth). The relationship between climate and tree-ring width chronologies was based on these climate-growth models.

Table 1. Statistical properties of tree-ring chronologies.

Site Name	Latitude (°N)	Longitude (°W)	Elevation (m)	A*	Series Mean Sensitivity	Total Series Length	Number of Trees	Number of Radii	Mean Correlation Among All Radii	Mean Correlation Between Trees	Signal-to-Noise Ratio	EPS
Cordillera Real-1	16°12 S	68°07 W	4130	0.68	0.37	71	11	36	0.54	0.50	0.25	0.91
Cordillera Real-2	16°12 S	68°07 W	4130	0.70	0.33	70	9	32	0.52	0.45	0.24	0.91
Vilcanota-3	13°08 S	72°17′W	4310	0.55	0.39	137	17	68	0.65	0.52	0.28	0.89
Vilcanota-4	13°12 S	72°05′W	4450	0.59	0.38	115	15	36	0.64	0.51	0.28	0.90
Coropuna-5	15°40 S	75°48′W	4240	0.61	0.31	66	23	49	0.51	0.43	0.23	0.90

*Series mean first-order autocorrelation.

Meteorological Data

The climate of the tropical Andes is defined by the position of the Inter-tropical Convergence Zone (ITCZ), which controls the variability of seasonal rains in the eastern Andes (Aceituno 1988; Roche *et al.* 1990; Ribstein *et al.* 1995; Vuille *et al.* 1998; Garreaud 1999) (Figure 2). To explore tree ring and climate relationships, we only used climate records covering more than 30 years, which were available from meteorological services in Bolivia and in Peru. In Bolivia, the climate data were obtained from five weather stations: La Paz (16°31′S; 68°04′W) at 3516 m a.s.l., El Alto (16°13′S; 68°07′W) at 4049 m a.s.l., Chacaltaya (16°21′S; 68°08′W) at 5325 m a.s.l., Plataforma (16°16′S; 68°07′W) at 4750 m a.s.l., and Botijlaca (16°22′S; 68°12′W) at 4497 m a.s.l. (Figure 1, Table 2). The precipitation regime at Sites 1 and 2 is related to the elevation and the orientation of the valley. During the rainy season in the morning, clouds come up from the Amazon plain (Wagnon *et al.* 1999). This phenomenon results in decreasing rainfall along the valley, with intensities of less than 10 mm/h above 3500 m a.s.l. Hydrological observations estimated water transfer velocities (subsurface and ground water flow) to moraine and scree slopes at between 24 m/day and 260 m/day, respectively (Caballero *et al.* 2002). In La Paz, the average temperature is about 9°C in the warm season (DJF) and about 5°C in the cold season (JJA). The 0°C isotherm remains above 4900 m all year round. Total annual precipitation ranges from 350 mm to 800 mm per year with more than 82% falling in the rainy season (Nov-March) (Figure 2a).

In Peru, the climate data were obtained from the five weather stations located closest to the forest sites sampled: Cuzco (13°33′S; 71°53′W) at 3219 m a.s.l., Urubamba (13°18′S; 71°53′W) at 2883 m a.s.l., Pisac (13°25′S; 71°51′W) at 2980 m a.s.l., Machu Pichu (13°10′S; 72°33′W) at 2481 m a.s.l., and Chuquibamba (15°51′S; 72°39′W) at 2895 m a.s.l. (Figure 1, Table 2). The average temperature varies from 12°C to 14°C during the warm season and from 9°C to 11°C during the cold season in Cusco. Total annual precipitation ranges from 550 mm to 850 mm with more than 80% falling in the rainy season (Figure 2b). Meteorological observations for the year 2006–2007 near Sites 2 and 3 reported a mean annual air temperature of 2.8°C, a mean growing-season (Oct—Mar) air temperature of 3.6°C and a mean annual soil temperature of 4.6°C (Toivonen and Hertel, unpublished data).

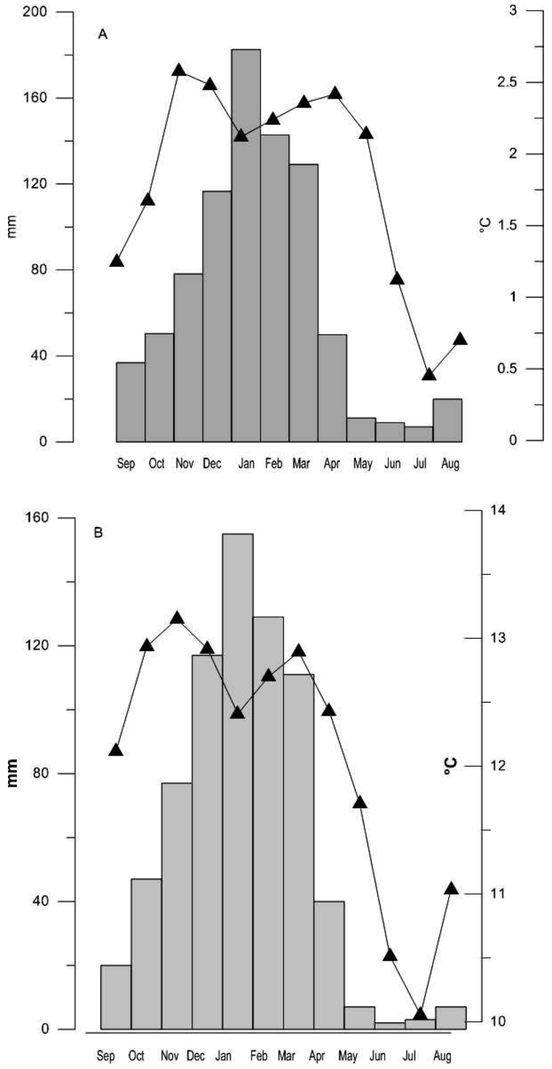

Figure 2. Mean monthly precipitation (bar) and temperature (curve) at (A) Plataforma rain gauge station (Bolivia) (1970–2007), and (B) Cusco (Peru) station (1969–2006).

RESULTS

Bolivian Sites

The tree-ring chronology on the scree slope (Site 1) spanned the period AD 1934 to 2004

Table 2. Location of meteorological stations.

Location	Country	Elevation (m)	Period of Observation	
			Precipitation	Temperature
Cusco	Peru	3219	1969–2006	1969–2002
Urubamba	Peru	2883	1963–2005	1963–2005
Machu Pichu	Peru	2481	1969–2000	1969–2000
Pisac	Peru	2980	1964–2000	-
Chuquibamba	Peru	2895	1963–2003	1963–2003
La Paz	Bolivia	3516	1952–2006	1952–2006
El Alto	Bolivia	4049	1943–1997	1943–1997
Chacaltaya	Bolivia	5325	1953–1997	1953–1997
Plataforma	Bolivia	4750	1970–1997	1970–2007
Botijlaca	Bolivia	4497	1970–2007	1970–2007

(Figure 3). Mean sensitivity, which is a measure of the relative difference in widths between adjacent rings, was 0.37 (Table 1). The first-order autocorrelation was 0.68, suggesting that *Polylepis pepei* tree-ring growth in one year is influenced by the preceding year. The average correlation among tree-ring series (all radii) was 0.54 and the signal-to-noise ratio was 0.25, indicating that the tree-ring chronology reflects a common growth-limiting signal. The EPS score was 0.91.

Correlation-function analyses revealed significant relationships with climate conditions during the preceding year and the growth year (Table 3). Total monthly precipitation exhibited negative correlations during the rainy season and positive correlations during the dry season, whereas mean monthly temperature exhibited positive correlations during the rainy season and negative correlations during the dry season.

Narrow and wide rings of *P. pepei* in excess of two standard deviations were frequently observed. For example, in 1992, 1981, 1980, 1976, 1973 and 1949 the rings were narrow and synchronous with narrow rings at Site 2. In 2002, 2001, 1990, 1972, 1969, 1966, 1962 and 1938 the rings were wide (Table 4) synchronously with those recorded at Site 2. Generally, reduced growth was better explained if the climatic conditions of the preceding year were taken into account. Cooler temperatures than the average during the rainy season in both the preceding and the current growth year were associated with narrow rings.

Response-function analysis revealed a positive relationship between temperature and radial growth at the beginning of the rainy season. The relationships were significant in October of the preceding and current year. A non-significant negative relationship was also observed at the end of the rainy season. Precipitation and radial growth showed a more complex pattern. Growth was not significantly correlated with precipitation in the preceding growth year (except in April) (Figure 4a). During the growth year, growth was negatively correlated with precipitation at the beginning of the rainy season with a significant value in October, and positively correlated with precipitation at the end of the rainy season and at the beginning of the dry season (with significant values in January and April).

Tree-ring chronology on the talus slope (Site 2) also covered the period AD 1935 to 2004 (Figure 3). Statistics suggest that, like the trees on the scree slope, these trees exhibited moderate sensitivity (0.33), with an autocorrelation value of 0.70 and an EPS value of 0.91.

Correlation analyses revealed significant relationships between radial growth and climate conditions similar to those observed in trees growing on the scree slope (Table 3; Figure 3). Both chronologies were significantly correlated and revealed synchronous narrow and wide rings (Table 4). Four years of recorded wide rings were synchronous with Site 3. Response-function analysis revealed that radial growth was poorly correlated with precipitation during the rainy

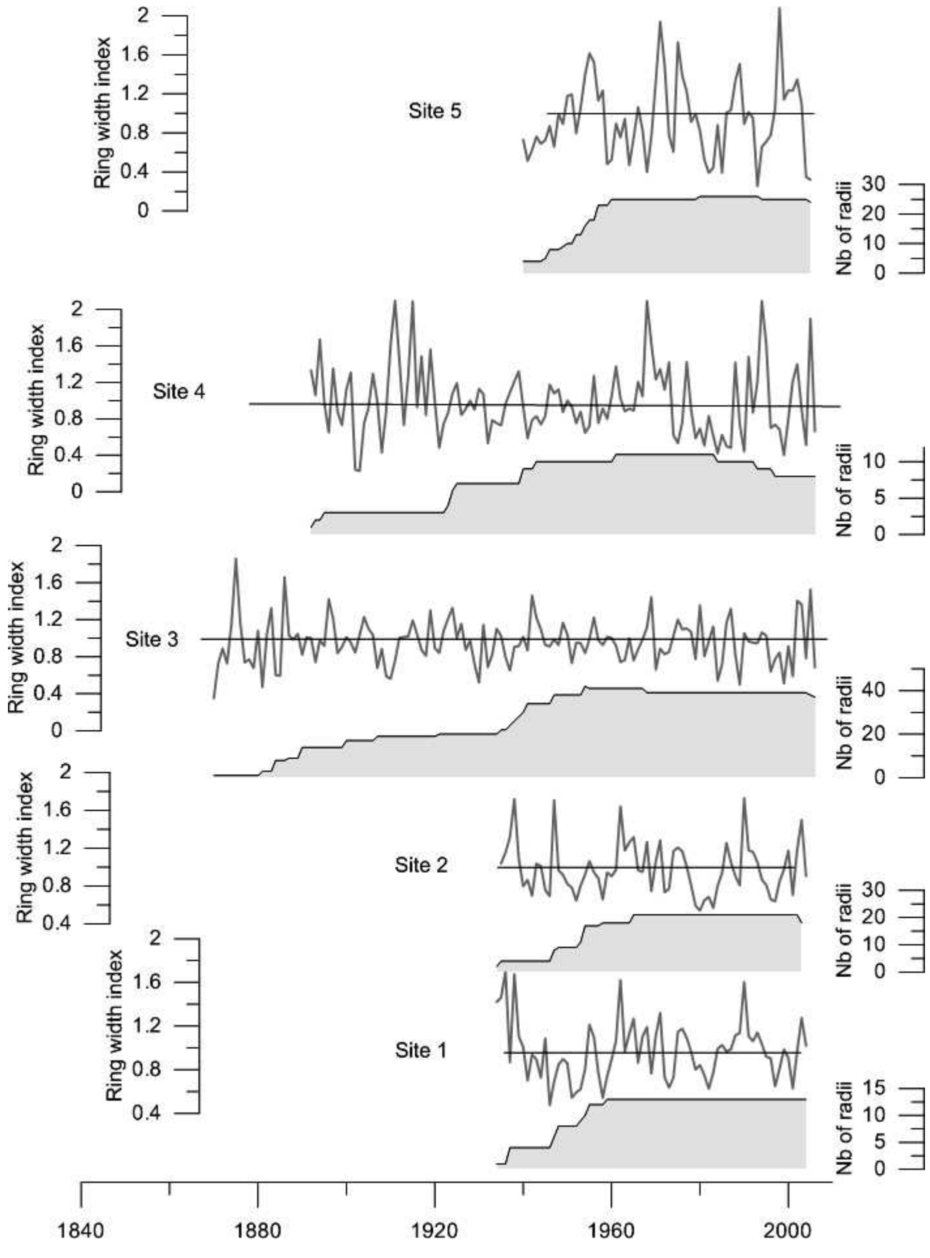

Figure 3. Standard ring-width chronologies (Sites 1–2 for *P. pepei,* in Zongo Valley Bolivia, Site 3 for *P. pepei,* in Cusco region Peru, Site 4 for *P. subsericans* in Cusco region Peru and Site 5 for *P. rugolosa* Arequipa region Peru).

season (Figure 4b) in both the preceding and current growth year. In contrast, a positive relationship was observed with precipitation during the dry season with a significant value in June in both the preceding and current growth year (Figure 4b). As for trees on the talus slope, during the rainy season, temperatures had a significant influence on tree growth with a positive significant correlation in October in the preceding and current growth year and a negative correlation at the end of the rainy season (Figure 4b). During the dry season, temperatures were poorly

Table 3. Months significantly correlated with climate data based on correlation coefficient analysis; bold = preceding year.

	Temperature	Precipitaton
Site 1	**Oct**; Oct	**April;** Jan., April
Site 2	**Oct;** Oct	**June;** June
Site 3	**Jan**; Feb	**Nov** ., Nov., Dec., Aug
Site 4	**May**; Jan., May	**Oct., Nov**; Oct., Nov
Site 5	June	**March**; March

correlated with radial growth and values were not significant.

Peruvian Sites

A 137-year-long ring-width chronology from AD 1870 to 2006 was built at Site 3 (Figure 3). The mean sensitivity was 0.39 and the first-order autocorrelation was 0.55 (Table 3), suggesting that, as at sites in Bolivia, at this site *P. pepei*, tree-ring growth is also influenced by growth in the preceding year. The average correlation among tree-ring series (all radii) was 0.65 (0.95 level), and the signal-to-noise ratio was 0.28. The EPS value was 0.89. Analyses revealed several narrow rings in 1992, 1977, 1973, for example, that were synchronous with Site 1, or wide rings in 2004, 2002 and 2001 that were synchronous with those at Sites 1 and 2. Generally drier and/or cooler conditions than average were responsible for a reduction in tree growth and vice versa at this site. However, these features were better explained if climatic conditions during the preceding year were taken into account as with at the other sites. Correlation-function analysis revealed significant positive correlations with monthly temperature and precipitation during the rainy season of the growth year and negative correlation with the dry season (Table 3).

Response-function analysis revealed a positive relationship with total precipitation in November in the preceding year and in November-December in the growth year (Figure 4c). A negative correlation was also observed during the dry season, which was significant in August in the growth year. Relationships with temperature were significant in February in the growth year and in January in the preceding year (Figure 4c).

At Site 4, a 115-year-long ring-width chronology from AD 1892 to 2006 was built (Figure 3). Chronology statistics showed that the tree species sampled, *P. subsericans,* exhibited intermediate mean sensitivity, and a common variance and signal-to-noise ratio. The average correlation among tree-ring series (all radii) was 0.64 and the signal-to-noise ratio was 0.28, indicating that the tree-ring chronology contained a common growth-limiting signal. The Expressed Population Signal (EPS) was 0.90 (Table 1).

Correlation-function analysis revealed significant positive correlations both with temperature and precipitation during the wet season in the growth year (Table 3). Narrow and wide tree rings that were synchronous with other sites were frequently observed (Table 4), and as for previous sites, this pattern was better explained if climate conditions in the preceding year were also considered. For example, the abrupt reduction in tree growth in 1998 corresponded to drier and cooler conditions than average not only in 1998, but also

Table 4. Synchronous narrow and wide rings in the different chronologies.

Narrow/wide	Site 1	Site 2	Site 3	Site 4	Site 5
Site 1		2002, 2001, 1990, 1972, 1969, 1966, 1962, 1938	2002, 1969, 1951	-	1990, 1975, 1941
Site 2	*1992, 1981, 1980, 1976, 1973, 1949*		2004, 2002, 1996, 1969	1996	2004, 1990, 1947
Site 3	*1992, 1977, 1973, 1952, 1935*	*1995, 1992, 1973, 1960, 1946*		2006, 2005, 1989, 1988, 1920, 1912, 1911	2004, 1984, 1970
Site 4	*1987, 1980, 1943, 1935*	*1997, 1980, 1975, 1965, 1964, 1951, 1944*	*1998, 1939, 1935, 1928, 1901, 1889*		1993, 1969
Site 5	*1996, 1992, 1987, 1974, 1956, 1949*	*1995, 1992, 1960, 1951, 1949*	*1995, 1992, 1991, 1960*	*1987, 1951*	

Dates in italics indicate narrow rings; non-italics indicate wide rings.

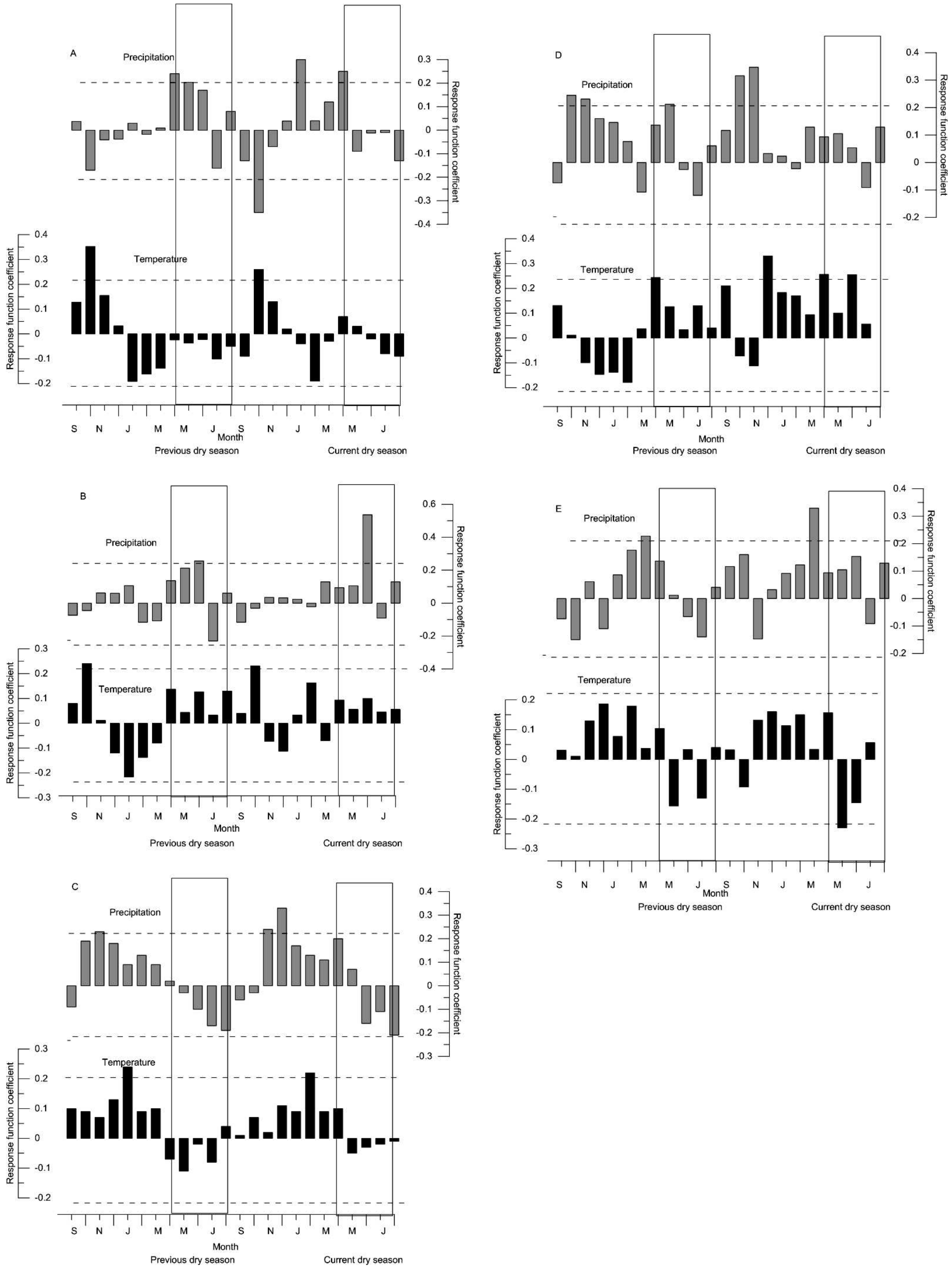

Figure 4. Tree response-function coefficients from September of the preceding growth year to August of the current growth year and monthly precipitation and temperature. (A) Site 1, (B) Site 2, (C) Site 3, (D) Site 4, (E) Site 5.

in 1997. Such a narrow ring was synchronous with one at Site 3.

Response-function analysis revealed that the radial growth of *P. subsericans* at Site 4 was positively correlated with precipitation during the rainy season in the preceding and current growth year (Figure 4d). Significant relationships were obtained with precipitation in October and November in the preceding and current growth year.

Temperature also plays a significant role in the radial growth of *P. subsericans*. Positive relationships were observed during the rainy season in the preceding and the current growth year with a significant value for the monthly mean temperature in April in the preceding year and December and April in the current growth year (Figure 4d). Positive correlations were observed during the dry season, which were significant in June in the growth year.

A 66-year-long ring-width chronology from AD 1940 to 2005 was built for *P. rugulosa* at Site 5 (Figure 3). Chronology statistics showed intermediate mean sensitivity and common variance values and signal-to-noise ratio for ring width, confirming the suitability of the chronology for further climate reconstruction despite lower values than the other chronologies (Table 1). The formation of narrow rings, for example in 1995, 1992 and 1991, synchronously with Site 3 or wide rings in 2004, 1990 and 1947 synchronously with Site 2 is a common feature among trees at this site. Correlation-function analysis revealed a positive relationship between the tree-ring index and temperature during the dry season in the growth year, which was significant in June. A positive relationship was also observed with precipitation during the wet season in the preceding and growth year, and this relationship was significant for March.

Response-function analysis revealed that at Site 5, radial growth of *P. rugulosa* was positively correlated with precipitation during the rainy season in the preceding and growth year with a significant value for the monthly mean precipitation in March (Figure 4e). Relationships between variations in ring width and temperature were more complicated. A negative relationship was observed during the dry season in the preceding and current growth year and a positive relationship during the rainy season. However, values were mostly non-significant except for monthly mean temperature in June in the growth year.

DISCUSSION

Polylepis pepei, P. subserican and P. rugulosa grow at mean elevations between 4000 and 4500 m a.s.l. in the semi-humid and semi-dry high-Andean regions (Fjeldså and Kessler 1996; Körner 1998, 2003; Toivonen *et al.* 2011). At these elevations, temperature variations are limited over the year. Nevertheless, some marked seasonal changes can be observed as temperatures are higher in the rainy season (Sicart *et al.* 1998). The rainy season, which lasts from October to March, thus coincides with a season of higher temperatures and reduced daily temperature amplitudes. The dry period coincides with the lowest temperatures in the year and greater daily thermal amplitudes (Francou *et al.* 2001). Even if temperature variations are limited over the year, temperature appears to be an important parameter in the regulation of tree-ring growth. Therefore, *Polylepis* chronologies investigated in this paper may be a useful indicator of variations in temperature in the past.

Our results point to a positive correlation between temperatures in the rainy season and tree growth at all our study sites in Peru and Bolivia. This can be explained by the physiological importance of temperature for tree growth. Favorable temperatures are required for several physiological activities of trees (such as photosynthesis, mineral uptake and transport) to enable tree growth, and these favorable temperatures prevail during the rainy season. The relationships were significant at the beginning of the rainy season in Bolivia, and in the middle of the rainy season in Peru. Such a difference may reflect possible climate differences between these regions as well as local effects (shadow made by rock wall above the site). At Sites 1–2 (Bolivia), changes from the dry season to the wet season are slightly more progressive than at Sites 3–4 (Peru). This may result in stronger correlation between the temperature at the beginning of the rainy season and tree growth in Bolivia. The higher the temperatures at the beginning of the rainy season, the earlier tree metabolic activity and growth can start, meaning stronger annual tree growth. However, despite direct meteorological measurements at these sites, this interpretation should be considered with caution.

Strong dependence of the annual tree-ring formation in *Polylepis* trees on the variability of austral summer temperatures was also observed by Roig *et al.* (2001) for *P. pepei* in southern Bolivia. These authors found significant response-function coefficients between tree-ring growth and temperatures in January and February in the current growth year, but summer temperatures in the preceding growth year were not significant. However, in our case, the response-function coefficients indicate that the temperatures in the preceding growth year are at least as important as the temperatures of the current growth year in explaining variations in tree-ring formation.

According to our response-function analysis, winter austral temperatures appear to be less important than summer temperature for tree growth. Earlier studies based on physiological analyses on *P. tarapacana* showed that cold dry conditions during the dry season can induce a period of inactivity of the vascular cambium, and the frozen plant tissues may take a long time to thaw before metabolic activity can begin (Rada *et al.* 2001). Such inactivity is a limiting factor for the growth of the trees (Körner 2003).

The influence of precipitation on tree growth is more complicated to interpret and may be influenced by local conditions. In general, precipitation during the rainy season was positively correlated with ring width in both countries (except at Site 1 in Bolivia). During the rainy season, rains are frequent and monthly mean temperatures reach their maximum. Increased precipitation along with higher temperatures during the summer are beneficial for tree growth because of accelerated CO_2 assimilation and photosynthesis in these conditions. Complicated patterns between tree growth and precipitation at Site 1 may be related to the nature of the slope deposit. Hydrological analyses carried out on talus slopes and moraines during the rainy season in Zongo valley (Bolivia) revealed that the hydrological behavior of these slope deposits depends on the season (Caballero *et al.* 2002). During the wet season, part of the water soaks in and gives rise to springs further down the slope. Local throughflow close to the talus slope responsible for the local saturation of the soil could explain the negative correlation between tree growth and precipitation during the rainy season. In the dry season, all the water infiltrates and there is no visible outlet.

The specific relationship between tree growth and precipitation during the dry season could reflect the location of the trees. The shape and setting of the tropical Cordilleras make them a barrier to the dominant and persistent easterly atmospheric flow separating the wet Amazon side from the dry Pacific side and producing pronounced windward and leeward effects. Fewer rainy days in the dry season from May to September in Zongo Valley (Bolivia) than in the Urubamba region (Peru) could explain different responses of tree growth to precipitation between these two areas. Rare rainy events during the dry season might be critical for the growth of *Polylepis pepei*, which prefers humid growing conditions. Faster throughflows in the talus slope than in the moraine (Caballero *et al.* 2002) could explain the higher sensitivity of trees on talus slopes to these climate conditions.

In summary, the growth season of the three species of *Polylepis* analyzed in this paper stretches from October to March, which corresponds to the warm wet season in the tropical Andes. Warmer summer temperatures favor earlier tree metabolic activity. The role of winter temperatures is difficult to understand without specific physiological analyses. Rain during the warm growth season favors tree growth, but the permeability of the substrate may alter such a positive relationship. Winter precipitation has a stronger impact on the growth of the trees located on the western dry cordillera than on the eastern wet cordillera.

CONCLUSIONS

The aim of this study was to investigate the dendroclimatological potential of three high-Andean *Polylepis* tree species, *P. pepei, P. subsericans and P. rugolosa,* which have different ranges in eastern and western parts of the Andes. Trees were sampled near Cuzco and Arequipa (Peru) and La Paz (Bolivia) on high altitude moraines and talus slopes. Despite the low amplitude of monthly temperature variations over the year, response-function analyses revealed positive correlations between temperature and tree-ring growth during the rainy season in the current and preceding year in all these regions. Such significant relationships open interesting perspectives for further climate reconstructions.

ACKNOWLEDGMENTS

This research was carried out as part of the ANR-ESCARCEL program of the Ministry of Research and the Prix la Recherche. Field work was conducted in collaboration with SENAMHI (Servivio Nacional de Meteorología e Hidrología) in Bolivia and with INRENA (Ministerio del Medio Ambiente) in Peru. Special thanks to Jaime Argollo who enabled us to work at the lab. We would like to thank two anonymous reviewers for their helpful comments. This work was partly supported by the Inter-American Institute for Global Change Research (IAI) CRN II # 2047 supported by the US National Science Foundation.

REFERENCES CITED

Aceituno, P., 1988. On the functioning of the southern oscillation in the South American Sector: Part I. Surface climate. *Monthly Weather Review* 116:505–524.

Aniol, R. W., 1983. Tree-ring analysis using CATRAS. *Dendrochronologia* 1:45–53.

Argollo, M., C. Soliz, and R. Villalba, 2004. Potencialidad dendrocronológica de *Polylepis tarapacana* en los Andes centrales de Bolivia. *Ecología en Bolivia* 39:5–24.

Biondi, F., I. G. Estrada, J. C. Gavilanes Ruiz, and A. E. Torres, 2003. Tree growth response to the 1913 eruption of Volcan de Fuego de Colima, Mexico. *Quaternary Research* 59:293–299.

Biondi, F., and K. Waikul, 2004. DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. *Computers & Geosciences* 30:303–311.

Bradley, R. S., and P. D. Jones, 1992. *Climate since A.D. 1500*. Routledge, London; 704 pp.

Briffa, K. R., 1984. *Tree-Climate Relationships and Dendroclimatological Reconstruction in the British Isles*. Ph.D. thesis, University of East Anglia, Norwich, UK.

Briffa, K. R., 1995. Interpreting high-resolution proxy climate data – the example of dendroclimatology. In *Analysis of climate variability. Applications of Statistical Techniques*, edited by H. von Storch, and A. Navarra, pp. 77–94. Springer, Berlin.

Briffa, K. R., E. R. Cook, 1990. Methods of response function analysis. In *Methods of Dendrochronology: Applications in the Environmental Sciences*, E. R. Cook, and L. A. Kairiukstis, pp. 165–178. Kluwer/IIASA, Dordrecht.

Caballero, Y., V. Jomelli, P. Chevallier, and P. Ribstein, 2002. Hydrological characteristics of slope deposits in high tropical mountain (Cordillera Real, Bolivia). *Catena* 47(2):101–116.

Cook, E. R., K. Briffa, S. Shiyatov, V. Mazepa, P. D. Jones, 1990. Data analysis. In *Methods of Dendrochronology: Applications in the Environmental Sciences*, E. R. Cook, and L. A. Kairiukstis, pp. 97–162. Kluwer/IIASA, Dordrecht, Netherlands.

Cook, E. R., and L. A. Kairiukstis (Eds.), 1990. *Methods of Dendrochronology: Applications in the Environmental Sciences*. Kluwer Academic Press, Dordrecht, The Netherlands: 394 pp.

Christie, D. A., A. Lara, J. Barichivich, R. Villalba, M. S. Morales, and E. Cuq, 2009. El Niño southern Oscillation signal in the world's highest-elevation tree-ring chronologies from the Altiplano, Central Andes. *Palaeogeography, Palaeoclimatology, Palaeoecology* 281:309–319.

Fjeldså, J., and M. Kessler, 1996. *Conserving the Biological Diversity of* Polylepis *Woodlands of the Highlands of Peru and Bolivia. A Contribution to Sustainable Natural Resource Management in the Andes*. NORDECO, Copenhagen.

Francou, B., N. Le Mehauté, and V. Jomelli, 2001. Factors controlling spacing distances of sorted stripes in a low-latitude, Alpine Environment (Cordillera Real, Bolivia, 16°S). *Permafrost and Periglacial Processes* 12:367–377.

Fritts, H. C., 1976. *Tree rings and Climate*. Cambridge University Press, Cambridge, London; 567 pp.

Garreaud, R. D., 1999. Multi-scale analysis of the summertime precipitation over the Central Andes. *Monthly Weather Review* 12:3157–3171.

Guiot, J., 1985. The extrapolation of recent climatological series with spectral canonical regression. *Journal of Climatology* 5: 325–335.

Guiot, J., 1990. *Methods and Programs of Statistics for Paleoclimatology and Paleoecology*. Quantification des changements climatiques: Méthodes et programmes, Monographie n. I; 253 pp.

Guiot, J., 1991. The bootstrapped response function. *Tree-Ring Bulletin* 51:39–41.

Hoffmann, G., E. Ramirez, J. D. Taupin, B. Francou, P. Ribstein, D. Delmas, H. Dürr, R. Gallaire, J. Simoes, U. Schotterer, M. Stievenard, and M. Werner, 2003. Coherent isotope history of Andean ice cores over the last century. *Geophysical Research Letters* 30(4):10.1029/2002GL014870.

Holmes, R. L., 1983. Computer-assisted quality control in tree-ring dating and measurements. *Tree-Ring Bull* 43:69–75.

IPCC, 2007. *Fourth Assessment Report: Climate Change 2007 (AR4)*. Intergovernmental Panel on Climate Change, Cambridge University Press.

IUCN, 2010. IUCN Red List of Threatened Species. Version 2010.1. International Union for Conservation of Nature, www.iucnredlist.org.

Jomelli, V., J. Argollo, D. Brunstein, D. Grancher, V. Favier, G. Hoffmann, M. P. Ledru, and J. E. Sicart, 2009. Multiproxy analysis of climate variability for the last millennium in the tropical Andes. In *Climate Change Research Progress*, edited by L. N. Peretz, pp. 127–159. Nova Science Publishers.

Jones, P. D., and M. E. Mann, 2004. Climate over past millennia. *Reviews of Geophysics* 42:1–42.

Kessler, M., 1995. The genus *Polylepis* (Rosaceae) in Bolivia. *Candollea* 50(1):131–171.

Körner, C., 1998. A re-assessment of high elevation treeline positions and their explanations. *Oecologia* 115:445–459.

Körner, C., 2003. *Alpine Plant Life: Functional Plant Ecology of High Mountain Ecosystems*. Springer, Berlin.

Körner, C., and G. Hoch, 2006. A test of treeline theory on a montane permafrost island. *Arctic, Antarctic and Alpine Research* 38:113–119.

Montes de Oca, I., 1997. *Geografia y Recursos Naturales de Bolivia*. Edobol, La Paz; 613 pp.

Rada, F., C. Gacia-Nunez, C. Boero, M. Gallardo, M. Hilal, J. Gonzales, F. Prado, M. Liberman-Cruz, and A. Azocar, 2001. Low temperature resistance in *Polylepis tarapacana*, a tree growing at the highest altitudes in the world. *Plant, Cell, and Environment* 24:377–381.

Ribstein, P., E. Tiriau, B. Francou, and R. Saravia, 1995. Tropical climate and glacier hydrology: A case study in Bolivia. *Journal of Hydrology* 165:221–234.

Roche, M. A., A. Aliaga, J. Campos, J. Penna, J. Cortes, and A. Rocha, 1990. Heterogeneite des precipitations sur la Cordillere des Andes boliviennes. In *Hydrology in Mountainous Regions*, edited by A. Lang, and A. Musy, pp. 381–388. IAHS Publication 193, Wallingford, UK.

Roig, F., M. Fernandez, E. Gareca, S. Altamirano, and S. Monge, 2001. Dendrochronological studies in the Humid Puna environments of Bolivia. *Revista Ecologia en Bolivia* 9: 9–13.

Schmidt-Lebuhn, A. N., M. Kessler, and M. Kumar, 2006. Promiscuity in the Andes: Species relationships in *Polylepis* (Rosaceae, Sanguisorbeae) based on AFLP and morphology. *Systematic Botany* 31(3):547–559.

Sicart, J. E., P. Wagnon, R. Gallaire, B. Francou, P. Ribstein, B. Pouyaud, and H. Baldiviesco, 1998. Mesures meteorologiques, hydrologiques et glaciologiques sur le glacier du Zongo. Annee Hydrologique 1996–1997. Orstom Bolivie, Rapport no. 57, 119 pp.

Solíz, C., R. Villalba, J. Argollo, S. Mariano, M. S. Morales, D. A. Christie, J. Moya, and J. Pacajes, 2009. Spatio-temporal variations in *Polylepis tarapacana* radial growth across the Bolivian Altiplano during the 20th century. *Palaeogeography, Palaeoclimatology, Palaeoecology* 281:296–308.

Stokes, M. A., and T. L. Smiley, 1968. *An Introduction to Tree-Ring Dating*. University of Chicago Press, Chicago; 73 pp.

Thompson, L. G., E. Mosley-Thompson, W. Dansgaard, and P. M. Grootes, 1986. The Little Ice Age as recorded in the stratigraphy of the tropical Quelccaya Ice Cap. *Science* 234: 361–364.

Vuille, M., R. S. Bradley, M. Werner, and F. Keimig, 2003. 20th Century climate change in the tropical Andes: Observations and model results. *Climatic Change* 59:75–99.

Wagnon, P., P. Ribstein, B. Francou, and B. Pouyaud, 1999. Annual cycle of energy balance of Zongo Glacier, Cordillera Real, Bolivia. *Journal of Geophysical Research* 104(D4): 3907–3924.

Wigley, T. M. L., K. R. Briffa, and P. D. Jones, 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology* 23:201–213.

Received 21 July 2011; accepted 14 May 2012.