Plant Ecol (2013) 214:11–27
DOI 10.1007/s11258-012-0141-2

Use of differential water sources by *Prosopis flexuosa* DC: a dendroecological study

María Alejandra Giantomasi ·
Fidel Alejandro Roig-Juñent ·
Pablo Eugenio Villagra

Received: 15 March 2012 / Accepted: 25 October 2012 / Published online: 4 November 2012

Abstract In central-western Argentina, there is a pronounced water deficit gradient, from semiarid climate conditions with 500-mm rainfall/year to arid climate conditions with 80-mm rainfall/year. This climatic transition, governed by the rainfall gradient, occurs between the Arid Chaco and Monte phytogeographic regions and is evidenced by differences in vegetation type, structure, dynamics and tree growth. In turn, the availability of soil moisture, particularly access to the water table, modifies water use strategies by trees along this gradient. We analyzed how water availability, expressed as differences in accessibility to the water table, influences *Prosopis flexuosa* tree rings along a precipitation gradient. In this manner, we try to interpret the growth of species according to the use of differential water sources. *P. flexuosa* showed highly varying growth reactions (tree-ring width and hydraulic anatomic parameters) with climate, depending on the ecology of the site. Along the Arid Chaco-Monte gradient, the growth of *P. flexuosa* is more dependent on variations in rainfall in those areas where water depth is greater than root spread. The climate signal was hidden in those regions where the water table is accessible to the root system.

M. A. Giantomasi (✉) · F. A. Roig-Juñent ·
P. E. Villagra
IANIGLA, CCT Mendoza-CONICET, Mendoza, CC 330,
5500 Mendoza, Argentina
e-mail: mgiantomasi@mendoza-conicet.gob.ar

Keywords Arid Chaco · Dendroclimatology · Monte · *P. flexuosa* · Water table

Introduction

Low precipitation, extreme temperature range and low relative humidity are the major limiting factors for the biological processes prevalent in desert areas (Noy Meir 1973). Precipitation in these regions is highly variable in terms of seasonality, intensity, volume and frequency (Whitford 2002). Nonetheless, besides the predominant influence of precipitation, groundwater is of particular importance in desert areas, because in some cases, it can naturally support foci of high biological activity in environments where the vegetation has deep root systems (Jobbágy et al. 2011).

Woody species play a major role in desert areas as ecosystem structuring agents and add to the maintenance of biodiversity through processes of facilitation and mitigation of environmental extremes (Karlin et al. 1997). The genus *Prosopis* in particular, because of its species diversity, distribution and ecological behavior, plays an essential ecosystem role in arid and semiarid regions. Climate, soil, water table depth, disturbances and biological interactions have been cited as the factors determining the structure and dynamics of *Prosopis* woodlands (Villagra et al. 2010). The influence of these environmental factors on tree growth can be studied by the analysis of tree-ring width and tree-ring wood anatomy, in particular vessels, which represent the wood hydrosystem (Fritts 1976; Fonti et al. 2010).

Variations in the anatomical features of growth rings on trees growing in different climate regions, or along environmental gradients, provide ecological information on the link between the particular conditions of the habitat and wood anatomy (Carlquist 1975; Baas 1986; Villar Salvador et al. 1997). In this sense, the chronological interpretation of these variations in the wood of trees broadens the grounds to enhance knowledge of the environment's influence on plant growth (Eckstein and Frisse 1982; Baas 1986). Transects along environmental gradients are natural experiments that allow the analysis of the effect of environmental variables on ecosystem function and structure. However, few studies have considered dendrochronology as a tool to analyze variability in the wood anatomy of tree rings along environmental gradients in arid and semiarid areas (Roig and Boninsegna 1990; Morales et al. 2001; Srur and Villalba 2009).

Given that climate is one of the major growth-limiting factors in arid and semiarid areas, a tree-ring chronology becomes a proxy record for annual fluctuations in climate. However, the presence of accessible water tables can mask the growth response of a species to climate. In ecosystems where precipitation does not exceed 500 mm/year, growth in plants is limited, primarily, by water availability. Under these conditions, the presence of a water table accessible to plants can represent an important water source, becoming a more stable reservoir than rainwater. *Prosopis flexuosa* can use both rain and groundwater through the horizontal (30 m) and vertical (up to 17 m) stratification of its root system (Villagra et al. 2010). Therefore, the presence of *P. flexuosa* woodlands in regions with scarce rainfall cannot be totally explained by the use of rains, but as a result of the use of phreatic water (Roig 1985; Villalba and Boninsegna 1989; Villagra et al. 2010). A study recently conducted by Jobbágy et al. (2011) in the Monte region in Argentina experimentally confirms the use of groundwater by this species. Notwithstanding, the importance of precipitation to plant growth in systems with shallow water tables has not yet been sufficiently studied.

The anatomy, ecology and productivity of *P. flexuosa* woodlands have been the object of research during the last 18 years through analysis of their tree rings (e.g., Castro 1994; Giantomasi et al. 2009, 2012; Villagra et al. 2010; Alvarez et al. 2011). Because of the ecological breadth of *P. flexuosa*, some of these studies have been carried out in the Monte region, others in the Arid Chaco, but no comparative analyses of tree growth among these regions have been performed thus far, in terms of their temporal variability in tree-ring growth or of their wood hydrosystem structure.

In the central-western region of Argentina, there is a marked hydric gradient, from a semiarid climate on the west of Córdoba (500 mm/year rainfall) to an arid climate on the northwest of Mendoza (150 mm/year rainfall). Such climatic transition, governed by the rainfall gradient, occurs between the phytogeographic regions of Arid Chaco and Monte and is evidenced by differences in vegetation type, structure and dynamics and in tree growth (Cabido et al. 1993). In turn, water availability along this gradient could be modified by different levels of accessibility to groundwater.

In this context, the overall objective of this study is to analyze, through the study of the characteristics of annual growth rings, the way in which water availability, expressed within a precipitation gradient, influences the growth of *P. flexuosa* trees with different accessibility to the water table. We expect that in areas with accessible groundwater, the rainfall signal contained in the growth rings of *P. flexuosa* trees will be not as clear as in those areas with deeper water tables. Thus, we claim that it is possible to interpret this species' growth in terms of use of differential water sources.

Materials and methods

Study sites

This study encompasses three forest sites lying along a 500-km long transect from 31° to 33° S and from 65° to 68° W (Fig. 1), and reflecting three different water conditions. On the eastern side of the transect, we sampled at the El Álamo site (Arid Chaco, 31°36′S and 65°30′W 296-m elevation), in Córdoba Province. The climate is semiarid with 500-mm annual rainfall, originated from the activity of the semipermanent South Atlantic subtropical anticyclone (as at the other sites), and a mean annual temperature of 20 °C (Capitanelli 1979). Soils are Entisols (Soil Survey

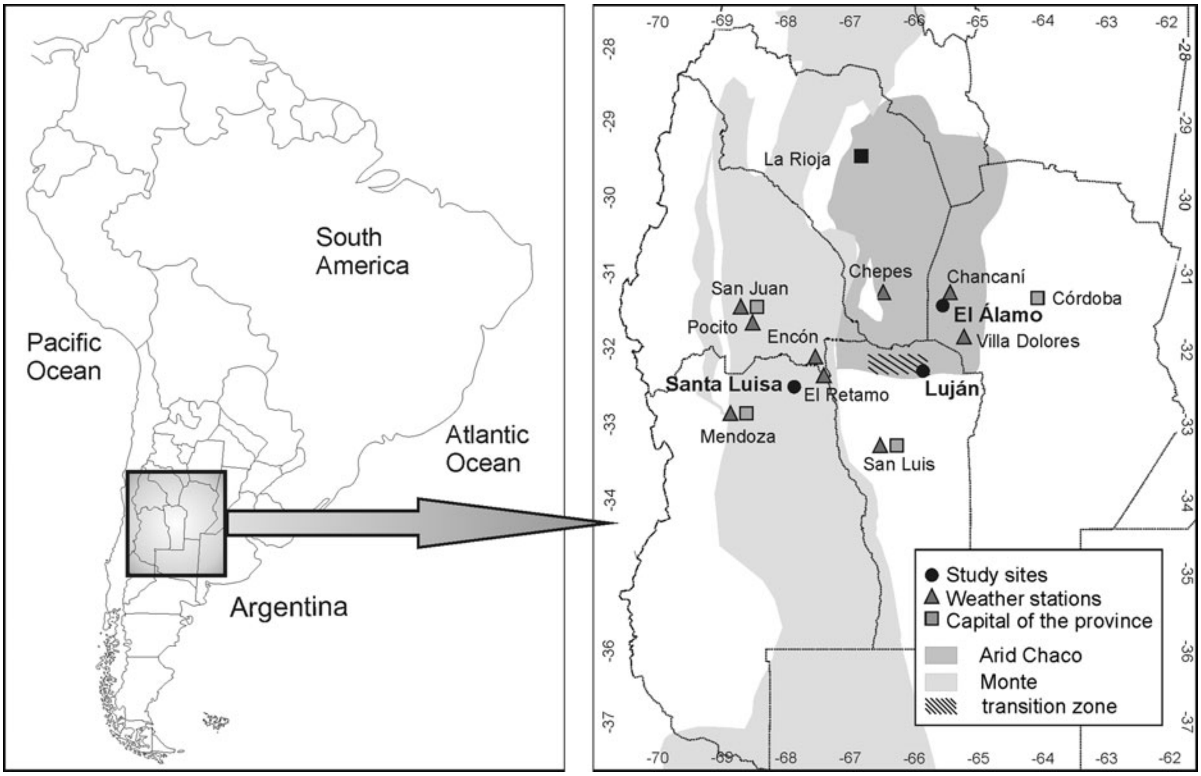

Fig. 1 Geographical location of the study sites from which chronologies were developed (represented with *circles*) and of meteorological stations (represented with *triangles*)

Staff 1999), of brown color, loam texture, a granular structure, high alkalinity at depth and of high permeability and water retention (Coirini 1992; Lorenz 1995). All soils are similar along the transect gradient. At this site, the water table occurs at 12–15 m depth (Carranza pers. comm.). The vegetation corresponds to the Western Chaco Forest (Luti et al.1979).

At the transect midpoint, we sampled at the Luján locality (Arid Chaco transition to Monte, 32 21′S, 65 58′W, 593-m elevation) in San Luis Province. The climate is semiarid with annual rainfall ranging between 250 and 300 mm/year (Capitanelli and Zamorano 1972). Mean temperature is 26 C in summer and 16 C in winter (Karlin et al. 1994). The soils are predominantly sandy. The water table approximately occurs at a depth between 18 and 25 m (Tissera pers. comm.). Although the area is included in the Arid Chaco Region, from an ecological point of view, the vegetation is defined as a transition zone between the *Aspidosperma quebracho-blanco* woodland from Arid Chaco and the *Prosopis* woodland from the Monte desert (Cabido et al. 1993).

The study site located on the western side of the transect corresponds to Santa Luisa site (Monte, 32 30′S, 67 57′W, 556-m elevation), in the northwest of Mendoza Province. This site lies in the driest sector of the study transect, with wide daily and annual temperature ranges, with maximum temperatures of 40–42 C in summer (the mean being 27 C) and minimum temperatures of −10 C in winter (the mean being 9.3 C). Mean annual temperature is 18 C. Precipitations are very variable, between 50 and 200 mm/year, with an average of 150 mm (Capitanelli 1967). Both potential evapotranspiration and water deficit are high. The soils have little development, are composed of inorganic sediments carried by the rivers, are slightly saline, in some cases sodic and may present calcium carbonate and gypsum on the surface (Regairaz 2000). Most of the water tables occur at depths of 8–15 m (Villagra et al. 2010). The vegetation growing in the area corresponds to the Monte phytogeographic region (Morello 1958; Villagra et al. 2004).

Sample collection

Cross-sections of *P. flexuosa* wood were obtained from both Arid Chaco and the transition site, taking advantage of clearings made in lands destined for future agricultural and range uses. In both cases, cross-sections were taken from the base of the trunk of one-stemmed trees. A total of 55 samples were collected at the Arid Chaco site. A total of 78 samples, which had been collected for a previously published study (Giantomasi et al. 2009), were used at the transition site. In the case of the Monte site, radial wood samples were obtained from standing trees with a mechanical increment borer (1.2 cm in diameter). The use of this instrument is necessary because of the high density of the wood of *P. flexuosa* (0.73 g/cm^3, Iglesias 2010). Like at the previous sites, all individuals sampled were one stemmed, so as to eliminate the effect of disturbance on growth that might be shown by multi-stemmed individuals, probably originating from logging, browsing, etc. A total of 61 samples were collected at this site.

Tree-ring width measurement

Once in the laboratory, the samples were mechanically sanded with sandpaper of decreasing grit size. Afterward, tree rings were anatomically identified and dated using standard dendrochronological techniques (Stokes and Smiley 1968). Each growth ring was assigned to its calendar year, using as a reference the last ring formed before the sampling or cutting date. In this procedure, assignment of a calendar date to the ring follows Schulman's convention (1956), according to which the tree-ring date corresponds to the year when it began to form. Tree-ring width was measured with a Velmex-type stage with 0.001-mm precision. These measurements were recorded using the MEDIR program (International Tree-Ring Data Bank Program Library, Krusic et al. 1997) and transferred to a computer. We used cross-dating techniques (Fritts 1976) based on visual inter-series comparisons of the ring width patterns and statistical confirmation with the COFECHA program (Grissino Mayer 2001). The length of comparison segments between series was 30 years, with an overlap of 15 years because of the relatively short age of the series analyzed.

Wood hydrosystem measurement

Measurement and analysis of the area occupied by tree-ring conducting vessels were performed by taking images, captured as far as possible from the same sector where ring width was measured. Samples were photographed with a digital camera (Olympus DP12 Microscope Digital Camera System) mounted on a magnifying glass (Olympus SZX7) with 10 × 3.2 magnification. Photographs were captured in TIFF format, with a resolution of 429 pixels high 572× pixels wide, and were analyzed by use of the PC-Image program (Scion Corporation). For further details, reference can be made to Giantomasi et al. (2009). Work was done on a total of 1,666 growth rings: 401 growth rings from the Arid Chaco site, 607 from the transition site and 658 from the Monte site. Total vessel area, number of vessels, mean vessel size (total vessel area/number of vessels) and percentage of vessel area in relation to tree-ring area (total vessel area/tree-ring width) were the anatomical characters of the wood hydrosystem analyzed in this study.

Chronologies development

Tree-ring width and wood hydrosystem chronologies for all three sites were developed using the ARSTAN40c program (Cook and Krusic 2006). This program combines a standardized series of measurements with a robust estimation of mean values. The aim of standardization is to minimize the trends attributed to the age of individual trees, or biological trend, so as to be able to compare series of trees in terms of their year-to-year variability (Fritts 1976). Chronology quality was assessed by calculation of EPS (expressed population signal), *R-bar* (average of running correlations) and mean sensitivity (MS) statistics. *R-bar* corresponds to the average of all correlation coefficients calculated between segments (of a determined length) of the series from different individual trees growing at the same sampling site (Briffa 1995). The EPS statistic establishes the minimum number of samples necessary to replicate the information contained in a theoretical population of infinite size (Briffa 1995). Mean sensitivity is a measure of relative year-to-year change in tree-ring width (Fritts 1976).

Chronologies–climate relationship

The influence of climate on year-to-year variations in the anatomy of *P. flexuosa* wood was researched through the development of correlation functions between the chronologies obtained from tree-ring width and the anatomical characters of the wood hydrosystem with local monthly records of total rainfall and mean temperature. Taking into account that tree growth may be affected by climatic conditions that occurred several months prior to the formation of the growth ring (Fritts 1976), the correlation analysis included climate variables for the current and previous year of tree-ring formation. Correlations were performed using the INFOSTAT/P statistical software package (2008).

Because of the paucity of climate information for each site in particular, because most records are for short periods or incomplete, the series from climate stations nearest each sampling site were used. For this reason and to have a meteorological record as extensive and complete as possible, in the case of the Arid Chaco and transition sites, regional precipitation and temperature records were constructed, with data from the meteorological stations considered for each site, because of the significant correlation found between the stations. The regional record was obtained by using the MET routine from the DPL program library (Holmes 1999). The mean and standard deviation are estimated for each month at each station. The departure for each month and year is then calculated and averaged across stations to produce regional average departures for each month and year. In the case of the Monte site, the heterogeneity found between climate variables prevented the construction of a regional climate record. Figure 1 and Table 1 show the details and location of the climate stations considered in this study. Meteorological data were obtained from the National Meteorological Service (NMS), the National Institute of Agriculture and Range Management Technology (INTA), Provincial Department of Hydraulics of Córdoba (DPHC) and the Center for Water Research in the Semiarid Region (CIHRSA). Local records from nature reserves and private fields were also used.

Results

Tree-ring width and anatomical chronologies

Figures 2, 3 and 4 show the chronologies obtained for the Arid Chaco, transition and Monte sites, respectively. The chronologies derived from measurement of the conducting vessels were developed on the basis of 11 of the 20 samples originally included in the tree-ring width chronology for the Arid Chaco site, 18 of the 21 samples from the transition site and 12 of the 15 samples from the Monte site. The chronologies of tree-ring width, vessel area and number of vessels at the transition site were previously published in Giantomasi et al. (2009).

Although other studies of the wood structure of *P. flexuosa* have established that growth rings are defined by wider diameter vessels in the earlywood combined with a marginal parenchyma band, this anatomical pattern is not always constant throughout the life of the tree. For this reason, identification of growth rings in this species is rather difficult. Furthermore, tree-ring dating is more difficult when samples are obtained with a mechanical increment borer, because it limits the wood surface area necessary to corroborate the circularity of the growth ring. This resulted in 20/55 sampled trees cross-dated for the Arid Chaco site, while 21/78 samples were cross-correlated at the transition site and 15/61 at the Monte site (Table 2). Even though the number of individuals forming the chronologies is relatively low, inter-tree correlations were sufficiently high for tree-ring chronology construction. The significant correlation values between tree-ring series would indicate an important percentage of common variability among the trees at each site or, in other words, that the same environmental factor would be predominantly affecting their radial growth (Table 2).

In general, at all three sampling sites, the chronologies of tree-ring width showed the highest dendrochronological statistical values, indicating a higher percentage of common signal or variability pattern among their series than the chronologies of wood hydrosystem (Table 2). These results indicate the need to count a larger number of samples than that necessary for tree-ring width chronologies to enhance the quality of chronologies derived from anatomical characters of the wood hydrosystem (Villalba et al. 2006).

Table 1 Meteorological stations used at each study site

Site	Station	Location	Variable	Period
Arid Chaco	Villa Dolores[a,b]	31 56′S, 65 11′O, 529masl	Precipitation	1937–2005
(El Álamo)			Temperature	1961–2005
	Chancaní[c,d,e]	31 24′S, 65 27′O, 372 masl	Precipitation	1951–2003
	Chepes[a]	31 20′S, 66 35′O, 660 masl	Precipitation	1937–2002
			Temperature	1937–1960
			Temperature	1971–2004
Transition	Villa Dolores[a,b]	31 56′S, 65 11′O, 529 masl	Precipitation	1938–2004
(Luján)			Temperature	1961–2004
	Chepes[a]	31 20′S, 66 35′O, 660 masl	Precipitation	1938–2002
			Temperature	1938–1960
			Temperature	1971–2004
	San Luis[a]	33 17′S, 66 21′O, 934 masl	Precipitation	1938–2002
			Temperature	1938–2004
Monte	Mendoza[a]	32 51′S, 68 53′O, 959 masl	Precipitation	1908–2003
(Santa Luisa)			Temperature	1908–2005
	San Juan[a]	31 29′S, 68 41′O, 770 masl	Precipitation	1908–2003
			Temperature	1931–2005
	Pocito[b]	31 40′S, 68 35′O, 611 masl	Precipitation	1968–2004
			Temperature	1968–2004
	Encón[f]	32 11′S, 67 47′O, 521 masl	Precipitation	1971–1994
			Temperature	1971–1987
	El Retamo[f]	32 27′S, 67 24′O, 491 masl	Precipitation	1971–1987
			Temperature	1971–1987

Data from: [a] SMN, [b] INTA, [c] DPHC, [d] CIHRSA, [e] reserves, and [f] private fields

Climate–growth relationship

Arid Chaco site

No significant relationships were found at the Arid Chaco site among regional-scale climate variables and *P. flexuosa*'s chronologies. However, we found some relationships, although limited, between chronologies and climate variables of one meteorological station of the study site.

No relationships were found among the tree-ring width, vessel area and number of vessels chronologies, and rainfall records of available meteorological stations. Nevertheless, the chronologies of mean vessel size and percentage of vessel area per growth ring proved to have a stronger signal with Chepes climate records (1975–2002 period). The chronology obtained from mean vessel size showed a significant correlation with October and February rainfall records ($r = 0.49$ and $r = 0.42$ respectively, $P < 0.05$, Fig. 5d). The chronology of percentage of vessel area per growth ring was significantly correlated with October precipitation ($r = 0.54$, $P < 0.05$, Fig. 5e).

Regarding temperature, November values recorded by the meteorological station at Chepes were significantly and inversely related during the 1971–1990 period to chronologies of tree-ring width, vessel area and number of vessels ($r = -0.62$, $r = -0.56$ and $r = -0.58$, respectively, $P < 0.05$, Fig. 5a–c).

Transition site

Consistent relationships were found between *P. flexuosa*'s growth and climate variables from regional records obtained for this study site. According to the model estimated for the 1940–2004 period for the tree-ring width and the 1949–2004 period for anatomical parameters, the correlation coefficient indicated that the radial growth of *P. flexuosa* was positively influenced by regional precipitation for the months

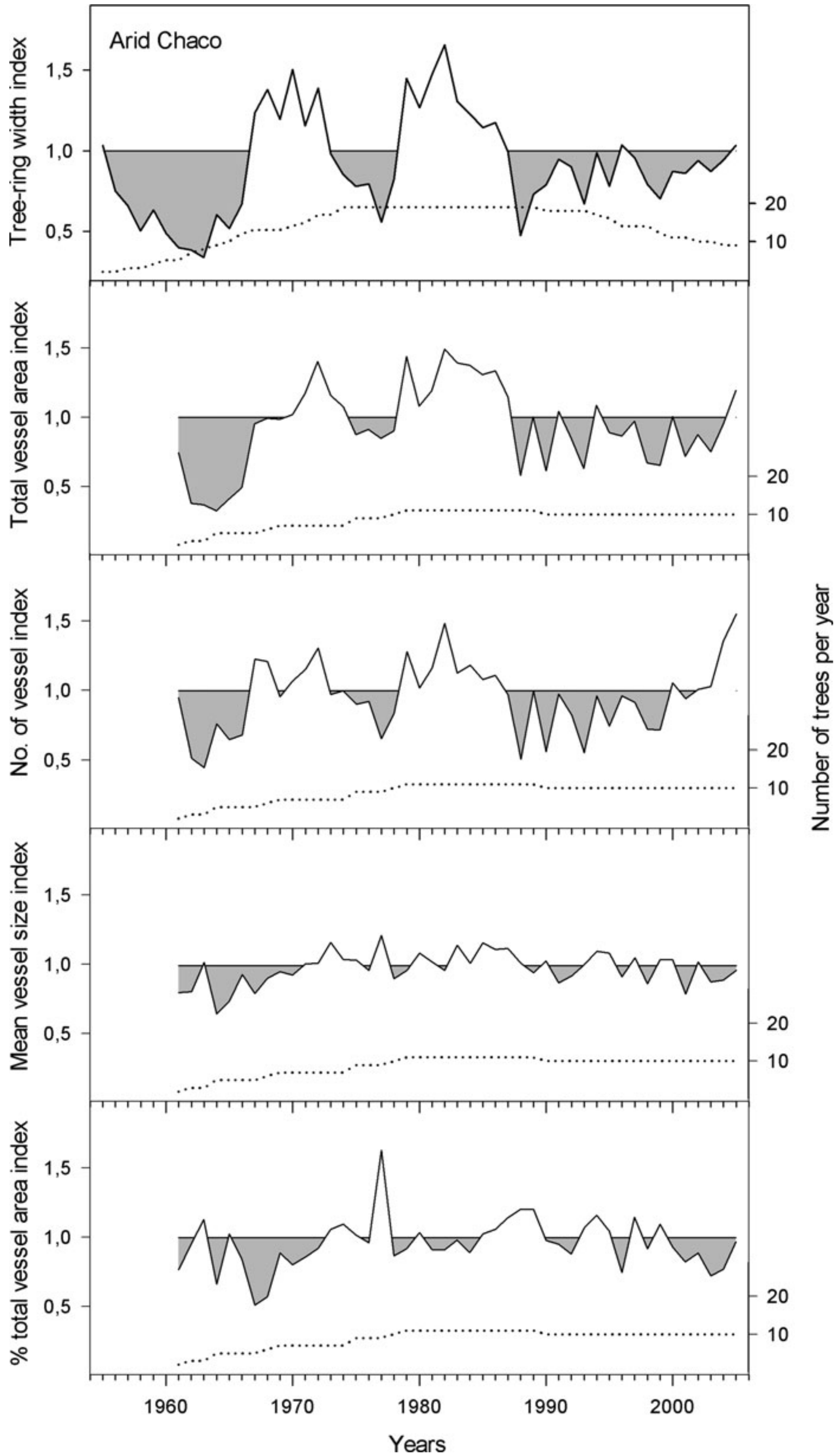

Fig. 2 Chronologies of *P. flexuosa* for the Arid Chaco site. At the *bottom* of each figure is the number of trees per year that form each chronology

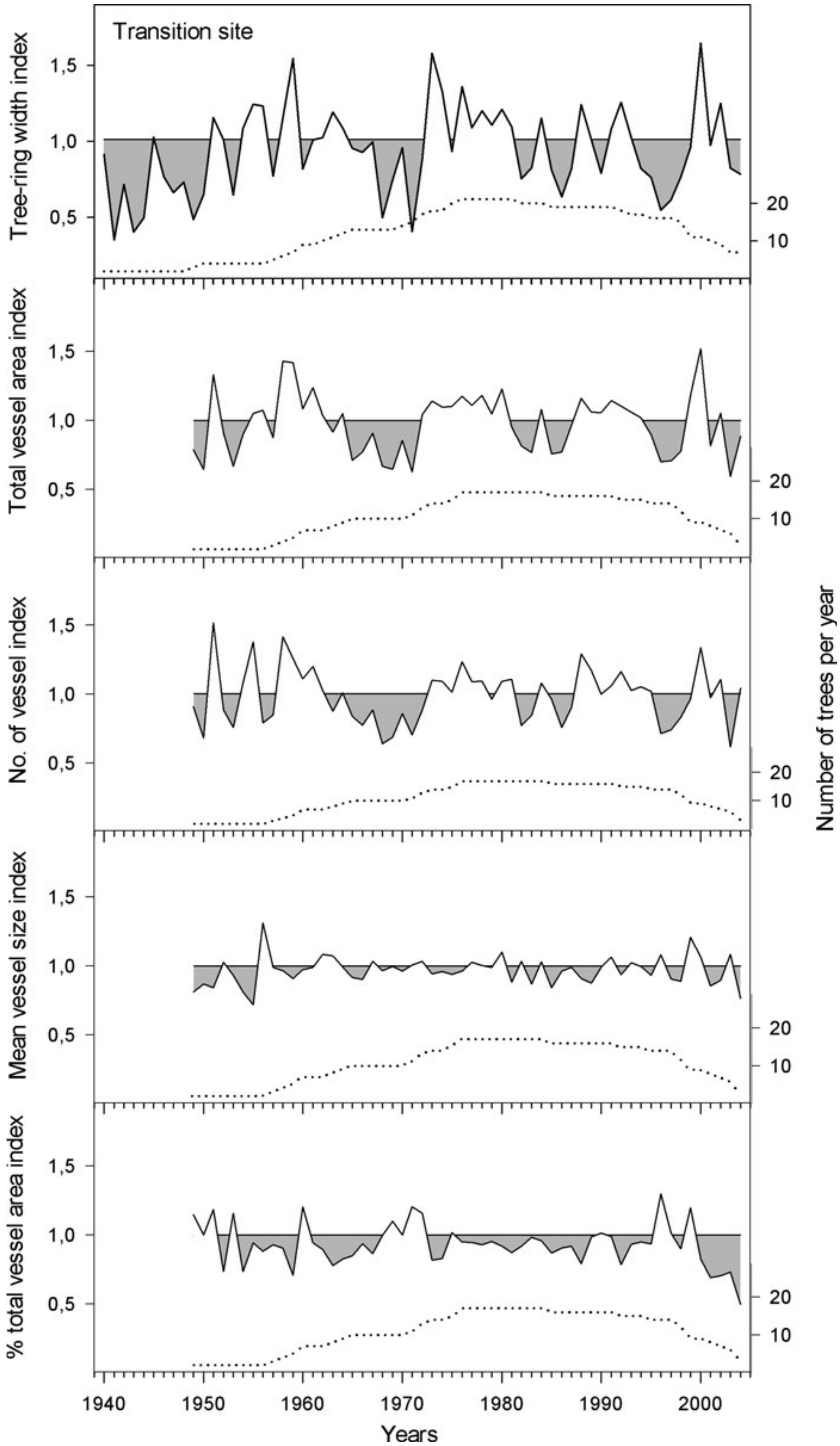

Fig. 3 Chronologies of *P. flexuosa* for the transition site. At the *bottom* of each figure is the number of trees per year that form each chronology

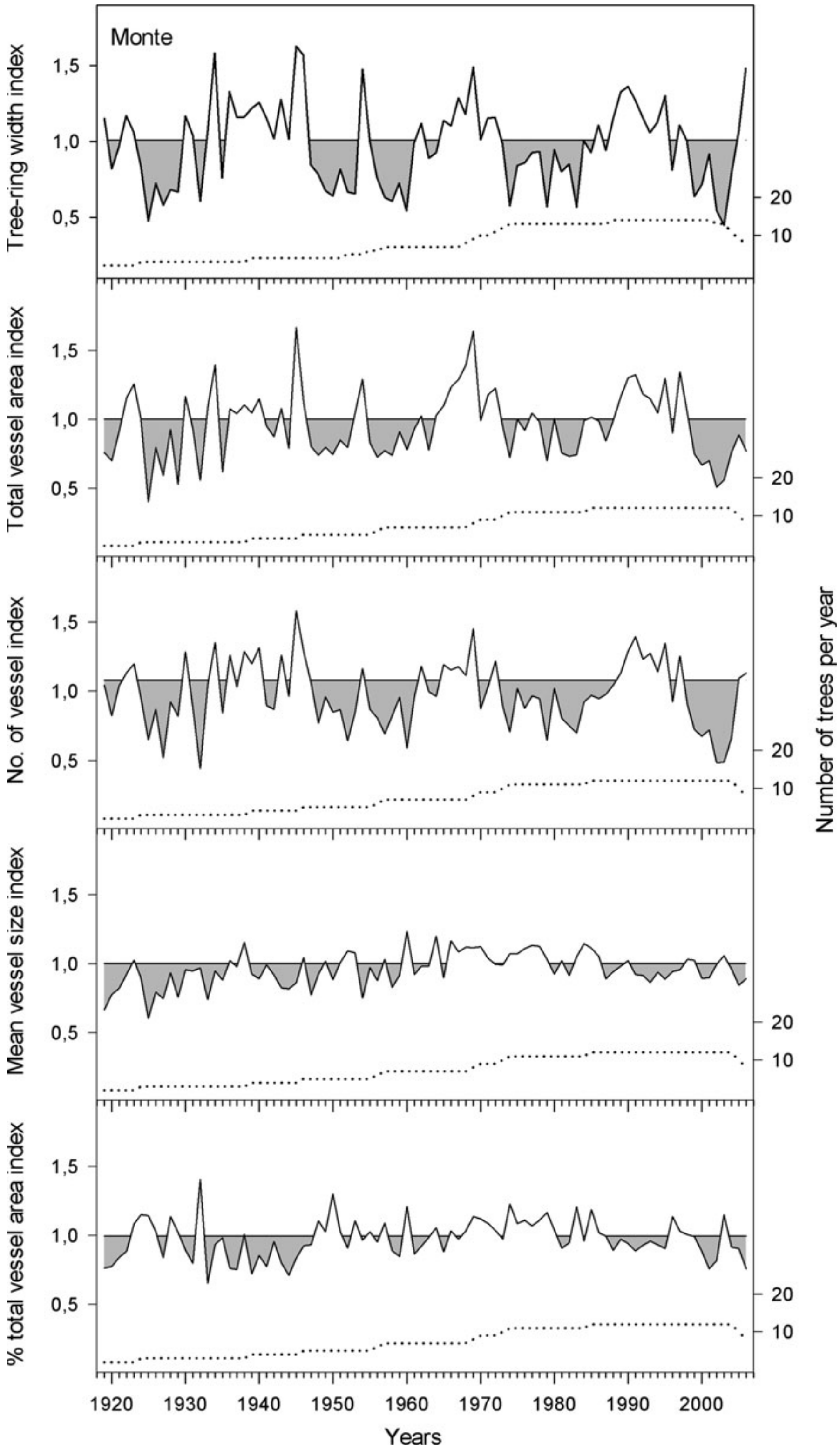

Fig. 4 Chronologies of *P. flexuosa* for the Monte site. At the *bottom* of each figure is the number of trees per year that form each chronology

Table 2 Descriptive and statistical parameters of chronologies developed at all three sampling sites. Tree-ring width, vessel area and no. of vessel chronologies at transition site were published in Giantomasi et al. (2009)

Site	Chronology	No. trees[a]	Period	Years	Corr.	s.m.	*R-bar*	EPS
Arid Chaco								
	Tree-ring width	20 (2–9)	1955–2005	51	0.506	0.427	0.329	0.941
	Vessel area	11 (2–10)	1961–2005	45	0.293	0.444	0.287	0.806
	No. vessel				0.317	0.439	0.407	0.876
	Vessel size				0.137	0.239	0.126	0.598
	% vessel area				0.279	0.279	0.061	0.368
Transition								
	Tree-ring width	21 (2–9)	1940–2004	65	0.567	0.426	0.243	0.913
	Vessel area	18 (2–3)	1949–2004	56	0.337	0.337	0.218	0.760
	No. vessel				0.246	0.370	0.093	0.570
	Vessel size				0.038	0.272	0.170	0.693
	% vessel area				0.201	0.290	0.064	0.450
Monte								
	Tree-ring width	15 (2–9)	1919–2006	88	0.524	0.399	0.231	0.774
	Vessel area	12 (2–8)			0.346	0.377	0.112	0.502
	No. vessel				0.370	0.371	0.127	0.537
	Vessel size				−0.054	0.240	0.074	0.170
	% vessel area				0.112	0.274	0.002	0.039

[a] In *parentheses*, trees covering the period of the chronology

of November and December ($r = 0.34$ and $r = 0.41$, respectively, $P < 0.05$, Fig. 6a). In the same direction, the mean regional precipitation for November and December was positively correlated with the chronologies of total vessel area ($r = 0.34$ and $r = 0.37$, respectively, $P < 0.05$) and number of vessels ($r = 0.26$ and $r = 0.41$, respectively, $P < 0.05$). Significant relationships were found between chronology of mean vessel size and the precipitation occurred in the month of March during the current growth period ($r = 0.29$, $P < 0.05$, Fig. 6d).

The mean regional temperatures for November and December were negatively correlated with the chronologies of tree-ring width ($r = -0.28$ and $r = -0.45$, respectively, $P < 0.05$) and vessel area ($r = -0.33$ and $r = -0.36$, respectively, $P < 0.05$). In the case of the chronology of number of vessels, the month of December showed a significant and inverse correlation ($r = -0.27$, $P < 0.05$, Fig. 6c).

Finally, the chronology obtained from the percentage of vessel area per growth ring presented somewhat different relationships with climate variables compared with previous results. The relationship with temperature tended to be positive, with temperature for December of the previous growth period being significant ($r = 0.48$, $P < 0.05$). Conversely, precipitation tended to show a negative effect, yielding significant values for the month of December of the previous growth period ($r = -0.33$, $P < 0.05$, Fig. 6e).

Monte site

Overall, this site showed a pattern of direct correlations between chronologies and temperature, and one of indirect correlations between chronologies and precipitation, contrary to what was observed at the previous sites (Fig. 7). For instance, the chronologies of tree-ring width, vessel area and vessel number were negatively correlated with October precipitation of the current growth period, when compared with the Encón meteorological station ($r = -0.48$, $r = -0.51$ and $r = -0.51$, respectively, $P < 0.05$). In turn, the vessel area chronology was negatively correlated with precipitation for December ($r = -0.46$, $P < 0.05$, Fig. 7b). Unlike what was observed previously, the chronology of percentage of vessel area per growth ring was positively correlated with October precipitation ($r = 0.41$, $P < 0.05$, Fig. 7e).

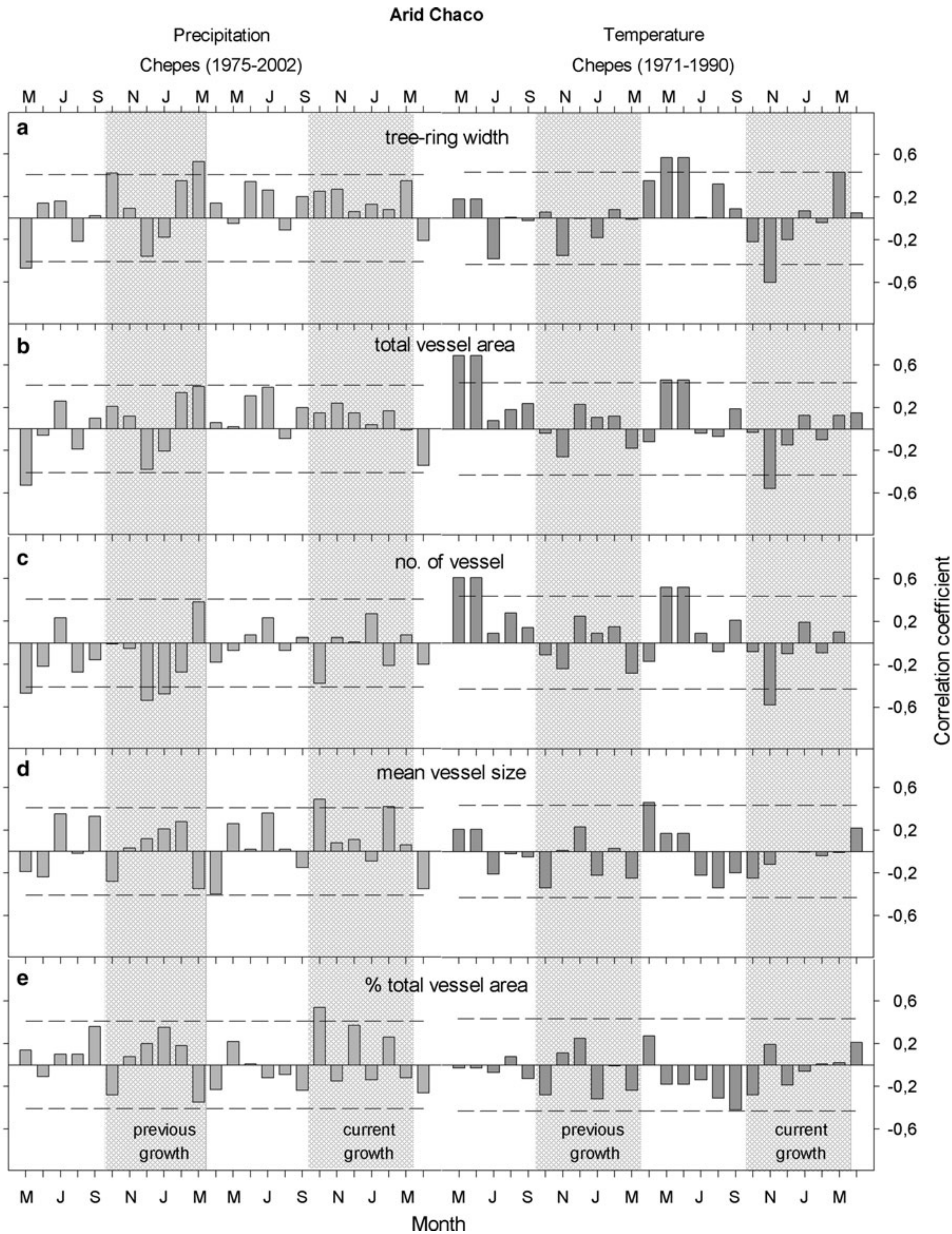

Fig. 5 Correlation function between chronologies and local precipitation and temperature records for Arid Chaco. The *shaded area* represents the period of growth. *Horizontal dashed lines* represent 95 % of reliability for correlation coefficients

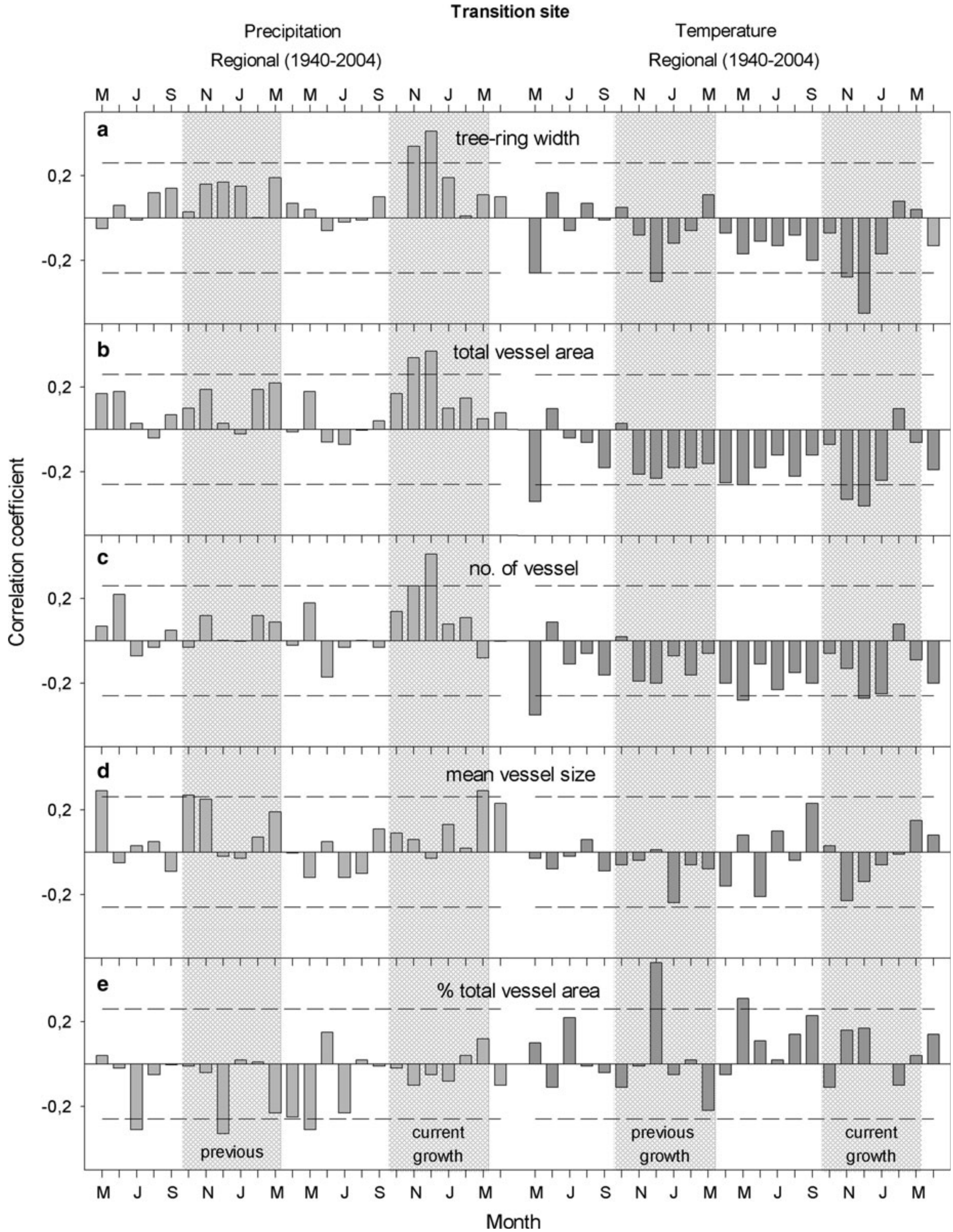

Fig. 6 Correlation function between chronologies and regional precipitation and temperature records for transition site. The *shaded area* represents the period of growth. *Horizontal dashed lines* represent 95 % of reliability for correlation coefficients

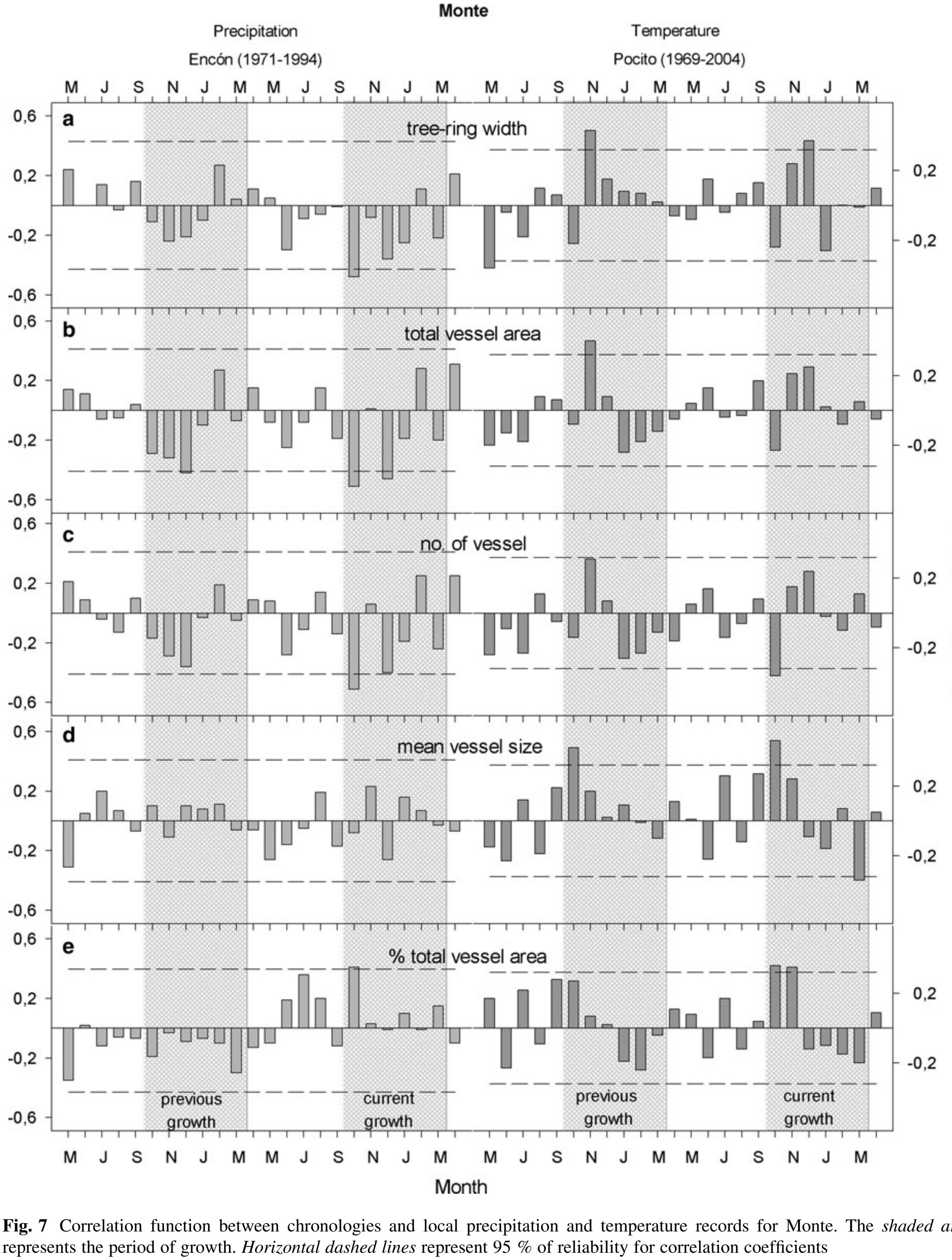

Fig. 7 Correlation function between chronologies and local precipitation and temperature records for Monte. The *shaded area* represents the period of growth. *Horizontal dashed lines* represent 95 % of reliability for correlation coefficients

Related to October temperature records of the Pocito meteorological station, there was a tendency to negatively affect the chronologies of tree-ring width, vessel area and vessel number, which was significant in the latter ($r = -0.36$, Fig. 7c). Conversely, the month of October was positively correlated with the chronologies of mean vessel size ($r = 0.46$, $P < 0.05$, Fig. 7d) and percentage of vessel area per growth ring ($r = 0.36$, $P < 0.05$, Fig. 7e).

Discussion

Research including development of dendrochronological records for arid and semiarid regions of Argentina are still scarce, perhaps because of the difficulties in recognizing growth rings and, consequently, in chronologically dating their wood. Specifically, *P. flexuosa* has been particularly indicated as a species with tree-ring boundaries hard to identify, therefore, making cross-dating difficult (Villalba and Boninsegna 1989; Catalán 2000).

This study explores new frontiers in the dendrochronological study of woodlands of *P. flexuosa*, the primary tree species in the arid and semiarid regions of the central-west of Argentina, through the analysis of the relationship between climate variables and anatomical characteristics of growth rings. Our results present evidence of how climate influences the tree-ring width and hydrosystem of *P. flexuosa* wood across the environmental gradient between the Arid Chaco and Monte ecosystems. This study indicates that in the case of Arid Chaco in transition to the Monte (transition site), in terms of the relationship between growth index and climate variables, both precipitation and temperature for early spring of the current year had a significant influence on the radial growth of *P. flexuosa*. Precipitation coincides with the beginning of the growth period of this species, which is relevant to wood formation. On the other hand, the high temperatures in spring would increase soil evapotranspiration, resulting in a negative effect on growth. This same response to meteorological variables was found, to a lesser extent, in the chronologies of vessel area and vessel number. In the case of chronologies of mean vessel size and percentage of vessel area per growth ring, the climate signal was not so clear. At the Arid Chaco site, the chronologies of mean vessel size and percentage of vessel area per growth ring proved to have a stronger signal with precipitation than found for the other chronologies. Therefore, the effort to develop chronologies for this species based on anatomical characters is justified here because, at this particular study site, they provided climate information additional to that given by tree-ring width. A different chronology–climate relationship was observed at the Monte site, where precipitation tended to be negatively correlated at the beginning of the growth period, whereas temperature was in general positively correlated.

According to the preceding remarks, the response of the chronologies to climate variables was different for the three sampling sites. At the transition site, growth was strongly controlled by climate variables, because perhaps of the little influence that the groundwater resource might exert on growth because, at this particular site, the water table level would lie at the limit of access for *P. flexuosa* roots. At Arid Chaco and Monte, where the water table is accessible, there was not such a clear pattern in the relationship between growth and climate variables. Hence, we could say that, at those two sites, the presence of accessible water tables would be masking the species' response to climate variability. On the other hand, more significant relationships between growth and meteorological variables might be obtained if we would have extensive, complete and reliable climate records from the same sampling site. This is fundamental in the case of precipitation, which is locally highly variable because of its convective nature (short and localized rains). The study area has no complete long-time series of climate information, which compels use of records from distant sites that do not necessarily reflect climate variability at each particular sampling site.

In concurrence with the relationship found between climate variables and ring width chronology at the transition site, Morales et al. (2001) observed that variations in ring width among individuals of *Prosopis ferox* from Quebrada de Humahuaca are strongly controlled by water balance during the growing season. A dendroclimatic study conducted in San Luis province, but on ecologically different sites and with *Prosopis caldenia*, reflected high variability in the growth response of this species to climate (Bogino 2005), because only a few of the chronologies developed were positively and significantly correlated with the climate variables: precipitation and temperature. The author points out that this variability is likely because of differences in soil type, water table depth and extended growth cycle and silvopastoral management of these woodlands. The only dendroclimatic study so far addressing *P. flexuosa* was conducted in the Arid Chaco (Villalba and Boninsegna 1989). These authors found that radial growth was favored by rainy springs with temperatures less than the mean. However, the percentage of growth variance accounted for by climate variations was low, reaching only 29 %. Authors conclude that, owing to the phreatophytic nature of *P. flexuosa*, its radial growth could be more influenced by water table than by year-to-year rainfall variations, in keeping with our results.

Consistently with this last quote, the notion that in arid and semiarid areas, where rainfall is scanty, the presence of *P. flexuosa* is coupled with the availability of shallow groundwater accessible to its root system has long ago been indirectly suggested by various authors (Morello 1958; Roig 1985; Cavagnaro and Passera 1993). More recently, Villagra et al. (2005a, b) studied *P. flexuosa* woodland in different environmental conditions along a latitudinal gradient in the region of Monte, with different precipitation amounts and accessibility to the water table. These authors found, along this north–south transect, that differences in woodland structure, productivity and rates of growth reflect differences in environmental variables such as mean temperature and water availability. Therefore, the highest number of tall trees with larger basal areas and the fastest rates of radial growth were observed in areas where, despite having less rainfall, groundwater appears to be the most important source of water for tree growth, and may reflect a more abundant and/or stable water supply at this site. The previously cited studies demonstrate that, at regional scale, the mean growth of *P. flexuosa* populations is not related to mean precipitation in the Monte, suggesting dependence on the water table. The results from our study deepen these conclusions by showing that also at the scale of the individual plant there is no clear relationship between precipitation and inter-annual growth of the species. A study recently conducted in the Monte region by Jobbágy et al. (2011) has shown the first direct evidence of use of the water table by *P. flexuosa*, through assessment of the isotropic contrasts (H^2 and O^{18}) existing among water from the water table, soil and the free water from the xylem of different woody species, among them *P. flexuosa*.

The importance of the availability of a water table to the growth of *P. flexuosa* suggests that, facing events of climate change or changes in soil use, the water table could undergo changes in level, possibly affecting the growth of these populations. Unfortunately, there are no precise data on past fluctuations at our study sites so as to be able to analyze the preceding observations. Jobbágy et al. (2011) noted changes in the level of the water table, of up to 15 cm in the Monte area, during three years of sampling. No longer-term information is available. For the Chaco region, it is suggested that conversion of woodland into rainfed crops produces rises in the level of water tables (Jobbágy et al. 2008). These possible changes should be considered as a potential problem of our analysis, for they could have modified the growth of this species in the past and might do so in the future. The analysis of the effect of climate change and land use change on water table levels could alter the current scenario of growth in this species, emerging as a new challenge to upcoming studies.

The results obtained in this study represent a new contribution to the understanding of the relationships between growth of this species and climate, for we have been able to enhance the scope of the study along a precipitation gradient with different accessibility to the water table. In this sense, for the first time it has been possible to assess the dendroclimatic potential of the anatomical characters of *P. flexuosa*'s wood hydrosystem; thus, allowing us to expand the current range of environmental information on this species so important in arid and semiarid lands. By use of dendroecological analysis, it has been possible to interpret how water availability, expressed within a precipitation gradient with different water table accessibility, affects growth development in *P. flexuosa*.

Acknowledgments This study was funded by the Argentinean National Agency of Scientific and Technological Promotion (ANPCyT), Project PICT 2002-00200. We are grateful to Mr Carranza and Mrs Ledesma for providing most of the samples of the El Álamo site, to Mr Azaguate, Marquez and Patriti for allowing us to collect samples from their properties. We thank Juan Alvarez, Enrique Barrio, Hugo Debandi, José Hernández and Gualberto Zalazar for their field assistance, Silvia Delgado for the programming of PC-Image, Rafael Bottero for the location map, Nelly Horak for the English version and M. Eugenia Ferrero for the English assistance. We appreciate the many helpful suggestions and insightful comments from the reviewers.

References

Alvarez JA, Villagra PE, Villalba R, Cony MA, Alberto M (2011) Wood productivity of *Prosopis flexuosa* D.C.

woodlands in the central Monte: influence of population structure and tree-growth habit. J Arid Environ 75:7–13

Baas P (1986) Ecological patterns in xylem anatomy. In: Givnish TT (ed) On the economy of plant form and function. Cambridge University Press, New York, pp 327–352

Bogino SM (2005) Crecimiento radial, turno biológico de corta y potencial dendroclimático del Caldén (*Prosopis caldenia* Burkart), en la provincia de San Luis, Argentina. Master dissertation, Universidad Nacional de Córdoba, Argentina

Briffa KR (1995) Interpreting high-resolution proxy climate data—the example of dendroclimatology. In: Von Storch H, Navarra A (eds) Analysis of climate variability, applications of statistical techniques. Springer, Berlin, pp 77–94

Cabido M, González C, Acosta A, Díaz S (1993) Vegetation changes along a precipitation gradient in Central Argentina. Vegetatio 109:5–14

Capitanelli RG (1967) Climatología de Mendoza. Boletín de Estudios Geográficos. Volúmen XIV No 54-57

Capitanelli R (1979) Clima. In: Vasquez J, Miatello R, Roque M (eds) Geografía Física de la Provincia de Córdoba. Boldt, Buenos Aires, pp 45–138

Capitanelli RG, Zamorano M (1972) Geografía regional de la provincia de San Luis. Universidad Nacional de Cuyo. Fac. de Filosofía y letras, Instituto de Geografía. Boletín de estudios geográficos. Vol. XIX. No 74-77. Mendoza, Argentina

Carlquist S (1975) Ecological strategies of xylem evolution. University of California Press, Berkeley

Castro MA (1994) Maderas Argentinas de *Prosopis.* Atlas Anatómico. Secretaría General de la Presidencia de la Nación, República Argentina

Catalán LA (2000) Crecimiento leñoso de *Prosopis flexuosa* en una sucesión postagrícola en el Chaco Árido: efectos y relaciones de distintos factores de proximidad. Doctoral dissertation, Universidad Nacional de Córdoba, Argentina

Cavagnaro JB, Passera CB (1993) Relaciones hídricas de *Prosopis flexuosa* (algarrobo dulce) en el Monte, Argentina. In: IADIZA (ed) Contribuciones Mendocinas a la Quinta Reunión de Regional para América Latina y el Caribe de la Red de Forestación del CIID. Conservación y Mejoramiento de Especies del Género Prosopis, IADIZA-CRICYT-CIID, Mendoza

Coirini R (1992) Caracterización Social y Económica del Área Problema. In: FCA-UNC-GTZ (ed) Sistemas Agroforestales para Pequeños Productores de Zonas Áridas. Córdoba, Argentina, pp 54–59

Cook ER, Krusic PJ (2006) ARSTAN 41: a tree-ring standardization program based on detrending and autoregressive time series modeling, with interactive graphics. Tree-Ring Laboratory, Lamont Doherty Earth Observatory of Columbia University, New York

Eckstein D, Frisse E (1982) The influence of temperature and precipitation on vessel area and ring width of oak and beech. In: Hughes MK, Kelly MP, Pilcher JR, La Marche VC (eds) Climate from tree-rings. Cambridge University Press, Cambridge, p 12

Fonti P, von Arx G, García González I, Eilmann B, Sass Klaassen U, Gartner H, Eckstein D (2010) Studying global change through investigation of the plastic responses of xylem anatomy in tree rings. New Phytol 185:42–53

Fritts HC (1976) Tree ring and climate. Academic Press Inc, London

Giantomasi MA, Roig Juñent FA, Villagra PE, Srur AM (2009) Annual variation and influence of climate on the ring width and wood hydrosystem of *Prosopis flexuosa* DC trees using image analysis. Trees 23:117–126

Giantomasi MA, Roig Juñet FA, Patón Domínguez D, Massaccesi G (2012) Climate modulation of the seasonal cambial activity in *Prosopis flexuosa* DC trees from the Monte woodland of Argentina. J Arid Environ 76:17–22

Grissino Mayer HD (2001) Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-ring Res 57:205–221

Holmes RL (1999) Dendrochronology Progra Librery (DPL). Use manual by laboratory of tree-ring research. University of Arizona, Tucson

Iglesias MR (2010) Evaluación de la vegetación leñosa como depósito de carbono en un gradiente Árid—Semiárido Argentino. Doctoral dissertation, Universidad Nacional de Córdoba, Argentina

INFOSTAT/P (2008) Infostat profesional. UNC, FCA, Córdoba

Jobbágy EG, Nosetto MD, Santoni CS, Baldi G (2008) El desafío ecohidrológico de las transiciones entre sistemas leñosos y herbáceos en la llanura Chaco-Pampeana. Ecol Aust 18:305–322

Jobbágy EG, Nosetto MD, Villagra PE, Jackson RB (2011) Water subsidies from mountains to deserts: their role in sustaining groundwater-fed oases in a sandy landscape. Ecol Appl 21:678–694

Karlin UOT, Catalán LA, Coirini RO (1994) La Naturaleza y el Hombre en El Chaco Seco. Colección Nuestros Ecosistemas. Fac Cs Agro, UNC, Salta

Karlin U, Coirini R, Catalán L, Zapata R (1997) *Prosopis flexuosa*. In: FAO (ed) Especies arbóreas y arbustivas para las Zonas Áridas y Semiáridas de América Latina. Serie Zonas Áridas y Semiáridas. Santiago, Chile, vol 12, pp 51–61

Krusic PJ, Holmes RL, King JC (1997) The international tree-ring data bank program library version 2.1 user's manual. In: Grissino-Mayer HD, Holmes RL, Fritts HC (eds) MEDIR version 1.13 measurement program. Laboratory of Tree-Ring Research, University of Arizona, Tucson, pp 18–20

Lorenz G (1995) Ecological characterization of a Eutric Regosol soil in Argentina Semiarid Chaco forest. Quebracho 3:13–23

Luti R, Solís M, Galera F et al (1979) Vegetación. In: Vázquez JR, Miatello R, Roqué M (eds) Geografía Física de la Provincia de Córdoba. Boldt, Buenos Aires, pp 297–368

Morales MS, Villalba R, Grau HR (2001) Potencialidad de *Prosopis ferox* Griseb (Leguminosae, subfamilia: Mimosoideae) para estudios dendrocronológicos en los desiertos subtropicales de alta montaña. Revista Chilena de Historia Natural 74:865–872

Morello J (1958) La Provincia Fitogeográfica del Monte. Opera Lilloana 2:5–115

Noy Meir I (1973) Desert Ecosystems: environment and Producers. Annu Rev Ecol Syst 4:25–51

Regairaz MC (2000) Suelos de Mendoza. In: Abraham EM, Rodríguez Martínez F (eds) Argentina. Recurso y problemas ambientales de la zona árida. Provincias de Mendoza, San Juan y La Rioja. Junta de Gobierno de Andalucía—Universidades y Centros de Investigación de la Región Andina Argentina. Mendoza, Argentina pp 59–62

Roig FA (1985) Árboles y bosques de la región árida centro oeste de la Argentina (Provincias de Mendoza y San Juan) y sus posibilidades silvícolas, Forestación en zonas áridas y semiáridas. In: Segundo encuentro regional CIID. América Latina y el Caribe. CIID, Santiago, Chile, pp 145-188

Roig FA, Boninsegna JA (1990) Environmental factors affecting growth of “Adesmia” communities as determined from tree rings. Dendrochronologia 8:39–66

Schulman E (1956) Dendroclimatic changes in semiarid America. University of Arizona Press, Tucson

Srur A, Villalba R (2009) Annual growth rings of the shrub *Anarthrophyllum rigidum* across Patagonia: interannual variations and relationships with climate. J Arid Environ 73:1974–1975

Staff Soil Survey (1999) Soil taxonomy: A basic system of soil classification for making and interpreting soil surveys, 2nd edn. Natural Resources Conservation Service. U.S. Department of Agriculture Handbook 436, USA

Stokes MA, Smiley TL (1968) And introduction to tree ring dating. University of Chicago Press, Chicago

Villagra PE, Cony MA, Mantován NG et al (2004) Ecología y Manejo de los algarrobales de la Provincia Fitogeográfica del Monte. In: Arturi MF, Frangi JL, Goya JF (eds) Ecología y Manejo de Bosques Nativos de Argentina. Editorial Universidad Nacional de La Plata, Argentina

Villagra PE, Boninsegna JA, Alvarez JA, Cony M, Cesca E, Villalba R (2005a) Dendroecology of *Prosopis flexuosa* woodlands in the Monte desert: implications for their management. Dendrochronologia 22:209–213

Villagra PE, Villalba R, Boninsegna JA (2005b) Structure and growth rate of *Prosopis flexuosa* woodlands in two contrasting environments of the central Monte desert. J Arid Environ 60:187–199

Villagra PE, Vilela A, Giordano C, Alvarez JA (2010) Ecophisiology of *Prosopis* species from the arid land of Argentina: What do we know about adaptation to stressful environments? In: Ramawat KG (ed) Desert plant, biology and biotechnology. Springer, Berlin

Villalba R, Boninsegna JA (1989) Dendrochronological studies on *Prosopis flexuosa* D.C. IAWA Bull 10:155–160

Villalba R, Delgado S, De Membiela M, Mendoza D (2006) Variabilidad interanual de los caracteres anatómicos en el leño de *Cedrela lilloi* en el noroeste de Argentina. In: Pacheco S, Brown A (eds) Ecología y producción de cedro (género *Cedrela*) en las Yungas australes. LIEY ProYungas, Tucumán, pp 59–82

Villar Salvador P, Castro Díez P, Pérez Rontomé C, Montserrat Martí G (1997) Stem xylem features in three *Quercus* (Fagaceae) species along a climatic gradient in NE Spain. Trees 12:90–96

Whitford W (2002) Ecology of desert systems. Academic Press, Cornwall