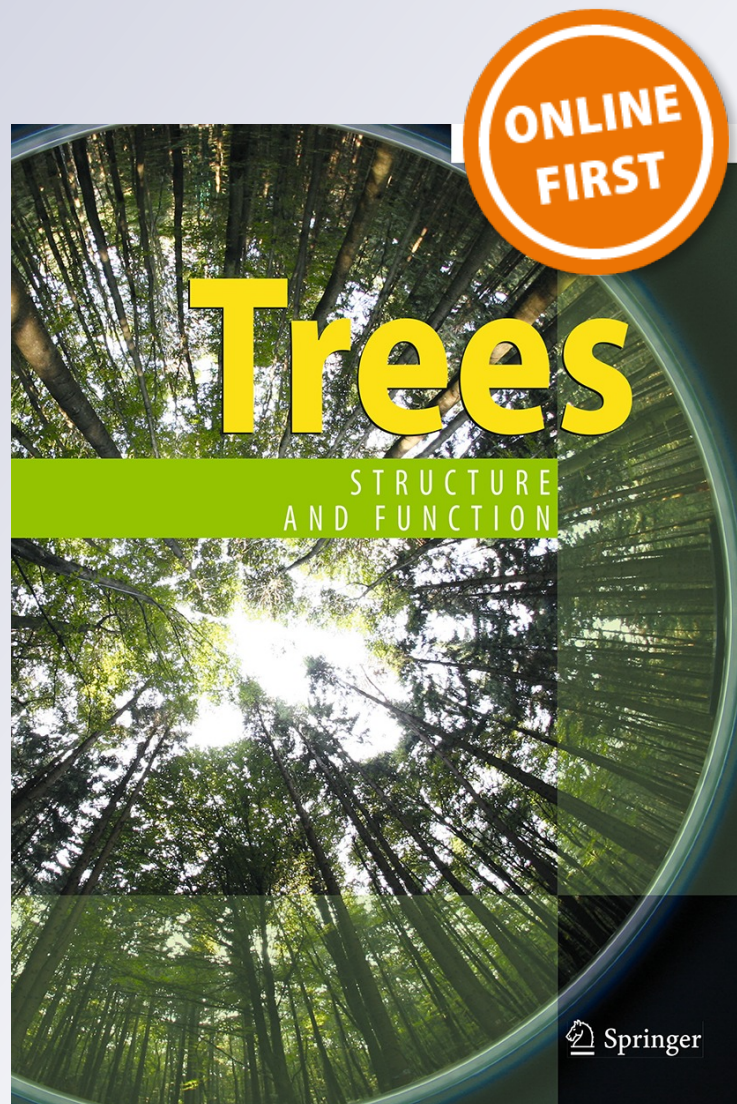# Geomorphological-related heterogeneity as reflected in tree growth and its relationships with climate of Monte Desert *Prosopis flexuosa* DC woodlands

Sergio Piraino, Elena María Abraham, Angela Diblasi & Fidel Alejandro Roig Juñent

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Geomorphological-related heterogeneity as reflected in tree growth and its relationships with climate of Monte Desert *Prosopis flexuosa* DC woodlands

Sergio Piraino · Elena María Abraham ·
Angela Diblasi · Fidel Alejandro Roig Juñent

Abstract

Key message **Across the Central Monte Desert district in Argentina, landform and soil variability drive radial growth of *Prosopis flexuosa* and its relation with precipitation.**

Abstract Desert forests grow under diverse ecological conditions, mainly resulting from the spatial heterogeneity of drylands with consequences on tree growth and its interactions with climate. In the Monte Desert, geomorphological processes generate landform and soil variability, determining the distribution and growth of plant species. *Prosopis flexuosa* DC., a dominant tree species in the Central Monte Desert, grows in territories characterized by a high variability of landform and soil. We applied classical dendrochronological and statistical analysis to disentangle the effect of spatial heterogeneity upon the species radial growth and its further relation with precipitation fluctuations. Trees from 11 plots distributed in seven *P. flexuosa* forests encompassing the most important geomorphological/landform units in the Central Monte Desert were analyzed. Tree-ring development at both high and low frequencies reflects spatial landform variability. Soil heterogeneity drives ring growth within landform. Regionally, precipitation influences radial growth at the beginning and the end of the growing season, while locally dependent mechanisms related to landform/soil variability emerged. In this sense, the negative influence of late-summer precipitation found for a riparian chronology is a function of soil permeability. Ring growth at the paleo-river environment depends on late spring and early mid-summer precipitation, with within-landform differences probably related to soil heterogeneity. In the case of inter-dune and lowland units, radial growth depends on early spring rainfall. Our findings highlight the influence of the heterogeneity of desert environments on tree growth. The information is relevant to management and conservation policies, particularly for the forests of *P. flexuosa* in Argentine Monte.

Keywords Algarrobo dulce · Dendroclimatology · Ecological gradient · Semi-arid woodland · Tree-ring variability

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Introduction

Climate, soil, topography, and disturbance are recognized as the most important natural and/or anthropogenic factors influencing the distribution, abundance and growth of tree species (Chapin and Matson 2011). Together, these factors

control the organization of plant communities and regulate various ecosystem processes, at both temporal and spatial scales (Spurr and Barnes 1980; Chapin and Matson 2011; Whitford 2002).

In climatically homogeneous areas, topographic heterogeneity is recognized as a physical component influencing forest dynamic at both population and individual levels, with consequences in growth variability, plant–climate and plant–plant interactions (Spurr and Barnes 1980; Callaway 1998; Oberhuber and Kofler 2000; Whitford 2002; Green and Hawkins 2005; Bunn et al. 2011).

In the plain deserts, geomorphological processes produce topographic heterogeneity, represented by a spatial landform mosaic composed of active and ephemeral streams placed along dune–inter-dune valley systems (Noy-Meir 1973; Aguiar and Sala 1999; Whitford 2002). This spatial heterogeneity, distinctive for arid and semi-arid areas, controls various fundamental ecosystem processes, such as plant distribution, water soil infiltration rates and storage, run-off and run-on, and nutrient availability (Noy-Meir 1973; Aguiar and Sala 1999; Whitford 2002). Thus, landform spatial variability may potentially represent a physical component influencing forest dynamics in arid environments.

The Monte Desert Biogeographical Province is a South American subtropical warm temperate desert located in western Argentina, occupying approximately 460,000 km^2 (Morello 1958; Cabrera 1976; Rundel et al. 2007; Abraham et al. 2009). The central area of these territories, known as Central Monte Desert, is characterized by great landform heterogeneity resulting from the joint action of water and wind, which in turn is constrained by a complex geomorphology defined by the presence of active high-elevation watersheds originating from Andes mountains (Jobbágy et al. 2011) and inactive (paleo) streams, dune systems and plains with fine-textured soils (Abraham and Prieto 1991; Abraham 2000; Rubio et al. 2009). Furthermore, these districts show a high degree of soil variability (e.g., texture and permeability) between and within the different landform units (Abraham et al. 2009). The combination of landform and soil heterogeneity influences water balance and therefore impacts the ecosystemic functioning (Bisigato et al. 2009).

In this context, a physiognomically characteristic woodland in the Central Monte Desert is represented by the *Prosopis flexuosa* DC. (algarrobo dulce) forests. *P. flexuosa* is a facultative phreatophyte tree species adapted to grow on different landforms and variable-texture soils (Morello 1958; Alvarez and Villagra 2009; Rubio et al. 2009). Due to its high tolerance to drought, salinity and alkalinity, it plays a key role in ecosystem organization and functioning, being able to modify the physical conditions to facilitate the establishment of shrubs and grasses (e.g., Rossi and Villagra 2003). *P. flexuosa* woodlands have been severely exploited for human consumption in the Central Monte Desert, coincident with the development of the Argentinian railroad systems at the beginning of the twentieth century and the increasing demand of timber for vineyards and furniture during the second half of the same century (Abraham and Prieto 1991; Villagra et al. 2009). Nowadays, these woodlands, now protected and managed by law, represent an important economic source for local homesteaders, particularly the Huarpe native community, since they provide wood for construction and food for cattle (Burkart 1976; Roig 1993).

The high ecological plasticity of *P. flexuosa*, expressed by its ability to grow in topo-edaphically heterogeneous areas, offers unique opportunities to analyze the landform- and soil-related growth variability of this desert tree and consequently its relations with climate. Since ring width is considered as a proxy record of the environmental variability, dendroecological approaches may be used to discern the influence of climate, topography and soil heterogeneity over tree growth (Fritts 1976; Cook 1987).

A number of studies have involved the dendrochronology and dendroclimatology of *P. flexuosa* forests in the Central Monte Desert, but always restricted to a single or small number of sites (Villalba 1985; Villalba and Boninsegna 1989; Giantomasi 2011; Giantomasi et al. 2012, 2013). Only dendrochronological networks may provide more accurate ecological descriptions of a particular tree species, contributing to improving knowledge of its ecological demands and to predicting how a species will behave in a climate change scenario (IPCC 2007).

We hypothesize that the landform and the soil heterogeneity of the Central Monte Desert is reflected in the *P. flexuosa* radial growth and this in turn may explain particular relationships between these forests and climate variability. Therefore, we analyzed several woodlands distributed along a landform transect to accomplish the following objectives: (1) develop a tree-ring network for *P. flexuosa* trees in different soil types; (2) analyze the link between ring-width variability, landform and soil heterogeneity; (3) examine the precipitation–radial growth relationship at both regional and local scales, with particular attention to possible site-dependent mechanisms. In a broader sense, this research aims to contribute to the understanding of the ecological effect of spatial environmental heterogeneity on the growth dynamic of desert woodlands.

Materials and methods

Site description

The study area is located in the Central Monte Desert district belonging to the Mendoza Province, west-central

Argentina (Fig. 1). Climate is arid to semi-arid, characterized by a mean annual precipitation of 155 mm, and by large seasonal and daily temperature variability (Morello 1958; Cabrera 1976; Rundel et al. 2007; Abraham et al. 2009) (Fig. 1).

Seven sites of *P. flexuosa* forests, between 67°38′18.1″ and 67°41′21.8″W and between 32°06′26.6″ and 32°22′23.9″S, were analyzed (Fig. 1; Table 1). Sites were selected according to the geomorphology-based classification proposed by Abraham (2000) and Rubio et al. (2009). Thus, we considered the following landform units: river, paleo-river, inter-dune valley and lowland (see Table 1 for details). To assume a common climatic influence on radial growth variability, sampled sites were selected in a relatively small area (the most distant tree populations, namely Pozo Verde and La Toma, are separated by 50 km; Fig. 1).

Prosopis woodlands grow on soils with different texture and permeability (Table 1). At both river-unit sites, soil is sandy texture, although of different permeability. At the paleo-river sites, soils exhibit variable textures (sandy, loamy and silty), which translate to different degrees of soil permeability (high, moderate and low). Finally, at the inter-dune valley site, soil is sandy with high water permeability, while at the lowland stand trees grow on sandy–loamy soil which is moderately permeable to water.
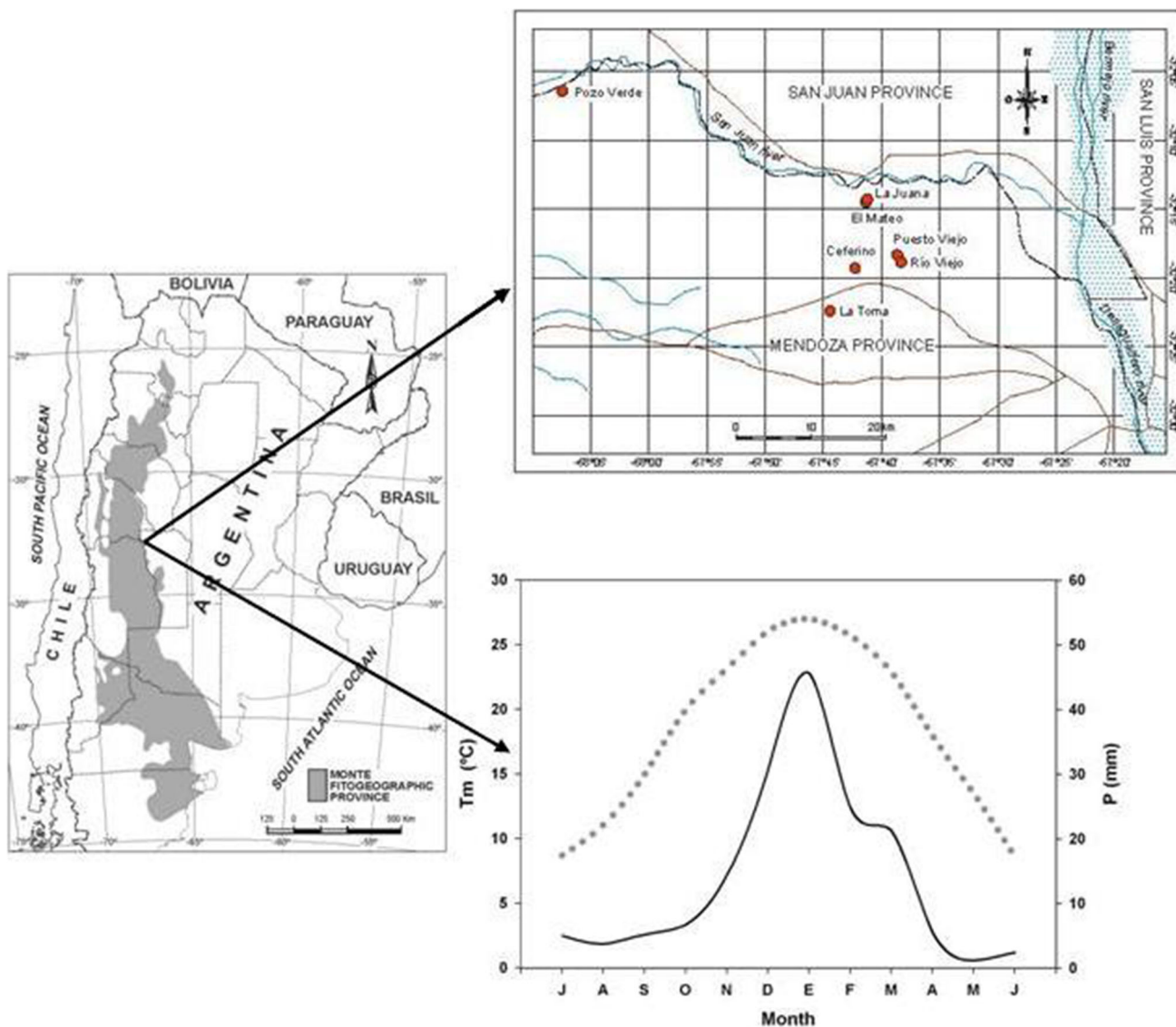

Fig. 1 Geographical location of the sampled sites and Ombrothermic diagram drawn according to the methods of Bagnouls and Gaussen (1953). Precipitation and temperature data belong to the Encon climatic station (32°15′S, 67°47′W), covering the 1971–1987 period. *Tm* monthly air temperature, *P* monthly total rainfall. *Gray dot line* refers to monthly mean air temperature, and *black solid line* to monthly total rainfall

Table 1 Environmental and geographical characteristics of the sampled sites

Site	Landform unit	Altitude	Latitude (°S)	Longitude (°W)	Soil texture	Soil permeability
El Mateo	River	512	32°14′31.4″	67°41′21.8″	Sandy	High
Pozo Verde	River	534	32°06′26.6″	68°07′26.4″	Sandy	Moderate hydrophobic
Puesto Viejo	Paleo-river	500	32°18′20.4″	67°38′39.5″	Sandy	High
Río Viejo	Paleo-river	497	32°18′51.9″	67°38′18.1″	Loamy	Moderate
La Toma	Paleo-river	516	32°22′23.9″	67°44′24.5″	Silty	Low
Ceferino	Inter-dune valley	511	32°19′17.1″	67°42′17.0″	Sandy	High
La Juana	Lowland	512	32°14′18.3″	67°41′14.7″	Sandy–loamy	Moderate

Vegetation of the sampled populations is composed of *P. flexuosa* with shrub and low arboreal associates such as *Larrea divaricata* Cav., *Geoffroea decorticans* (Hook. and Arn.), *Capparis atamisquea* Kuntze and *Bulnesia retama* (Hook.) Griseb. Sampled sites are characterized by evidence of relatively recent human pressure (stumps), as found in most of the *P. flexuosa* woodlands distributed in the Central Monte Desert districts (Abraham and Prieto 1991; Villagra et al. 2009). Stumps are evenly distributed among the selected forests (total number of stump/site ranks between 4 and 6; data not shown). Moreover, in the La Toma population dead trees of *P. flexuosa* were observed, probably caused by root asphyxia produced by episodic natural floodings.

Tree-ring chronology development

At each site, and depending on woodland extent and landowner agreement, one or two rectangular plots of 1000 m^2 (50 m × 20 m) were established. Dendrochronological sampling was conducted on all trees within the selected plots, regardless of the one- or multi-stemmed form. Two cores per tree were extracted at about 50 cm above the ground with a gas-powered drill (TED_262R, Tanaka Kogyo Co. Ltd, Chiba, Japan). Standard dendrochronological procedures followed Stokes and Smiley (1968): wood samples were glued on wooden supports and polished with progressively finer sandpaper, then tree-ring widths were identified and dated and widths were measured from pith to bark to the nearest 0.01 mm resolution through the facilities of the IPWin4 Image Analysis software (v4.5, Media Cybernetics, USA). The obtained tree-ring series were cross-dated and their data quality validated by statistical controls (COFECHA program; Holmes 1983).

The age-related trend and the influence of exogenous disturbance (thinning) recorded in raw ring-width measurements were removed by standardization procedures through the program ARSTAN40c (Cook and Krusic 2006). Standardization removes the low-frequency ring-width variability, highlighting the effect of short-term (e.g.,

monthly) climate trends on radial growth (Cook 1985). We chose a double detrending method (Cook 1985): first, a negative exponential function was fit to each raw tree-ring series and then we applied a 32-year cubic spline function with 50 % cutoff. Tree-ring indices were computed by dividing the measured ring widths by the expected value. Finally, individual standardized series were averaged to produce a mean chronology for each site. We selected the "Residual" version standardized chronology obtained from the ARSTAN40c program, to minimize the autocorrelation present in the ring-width series and to avoid any possible overestimation of the climate–growth relation (Villalba and Veblen 1997).

The internal quality of each chronology was examined according to the following statistical indexes: EPS (expressed population signal), which is an estimation of how well a finite-sample chronology can represent the theoretical population chronology based on an infinite number of trees; RBAR, a measure of the common variance between the single series in a chronology; and the MS (mean sensitivity), a measurement of the relative year-to-year change in tree-ring width (Fritts 1976; Wigley et al. 1984). The first two indexes were calculated for a 20-year window with a 19-year overlap. EPS is generally considered satisfactory when surpassing a threshold of 0.85 (Wigley et al. 1984). However, a number of studies suggest that EPS barely reaches this value in arid woodlands (e.g., Sass-Klaassen et al. 2008; Nicolini et al. 2010; Giantomasi 2011; Giantomasi et al. 2013). On the other hand, in their original research, Wigley et al. (1984) states that "the value 0.85 for a threshold is given here only as a guide; in any particular case the chosen threshold will depend on the user's subjective evaluation of accuracy needs (Wigley et al. 1984; page 207)". Therefore, since previous successful studies performed for *P. flexuosa* woodlands distributed in the Central Monte Desert indicate EPS values ranking between 0.74 and 0.77 (Giantomasi 2011; Giantomasi et al. 2013), we decided to consider an EPS = 0.75 as a minimum threshold for the selection of a time period for analysis.

Statistical analysis

The possible influence of landform and soil variability upon raw ring-width fluctuations was investigated by means of ANOVA. When ring-width annual values lacked a normal distribution, the data were transformed by the Box–Cox methodology and ANOVA was performed on transformed data through a linear mixed model with autoregressive errors. Tree-ring fluctuations among different landform units were statistically compared by the Fisher's least significant difference test. Once the link between landform heterogeneity and radial growth fluctuations was established, ANOVA was performed on the year-to-year ring-width changes within landform units, to discern the possible influence of soil variability (soil permeability) upon tree-ring growth. Statistical analysis was computed through the "nlme" package present in the R software (R Core Development Team 2011; Pinheiro et al. 2013).

Linear relations between standardized tree-ring chronologies were explored by principal component analysis performed with the PCA software in the DPL package (Legendre and Legendre 1998; Holmes 1999).

Climate–growth relations were calculated through correlation function analysis (Blasing et al. 1984). Since precipitation is the fundamental climatic driver of plant growth in arid and semi-arid areas, we focused on the influence of this abiotic factor upon ring-width development (Noy-Meir 1973; Whitford 2002). Correlation functions were computed with the software DENDROCLIM2002 and tests for significance were determined through the bootstrap method (Guiot 1991; Biondi and Waikul 2004). A set of 12 months was selected for correlation analysis, from April of the preceding year to March of the year of growth. This period was chosen based on the physiology of *P. flexuosa*, considering that radial growth begins in October and ends in March (Giantomasi et al. 2012). Residual chronologies, as well as the first component derived from the PCA analysis (PC1), were matched against monthly total precipitation obtained from the San Juan Airport gauge station (31°34′S; 68°25′W; 598 m a.s.l.), which represents the more reliable, long and complete climatic dataset near our analyzed forest stands. In all the above-mentioned analyses, the common period 1979–2008 (30 years) was taken into account. Finally, the possible influence of landform/soil heterogeneity upon the growing season precipitation–growth relationship, between and within landform units, was analyzed by means of ANOVA computed on the r/s coefficients (r being the Pearson correlation moment and s its standard deviation).

Results

Characteristics of the tree-ring network

Seven tree-ring chronologies were built with 155 samples collected from 121 trees (Table 2). Chronologies spanned 80 (Pozo Viejo, Río Viejo, La Toma sites) to 96 years (Ceferino site). Mean annual growth rate oscillates between 1.22 (La Juana) and 2.03 mm/year (La Toma). Mean correlation values (MC) between individual chronologies rank from 0.456 (La Juana) to 0.525 (Pozo Verde), all significant at the $p < 0.05$ level (Table 2). MS oscillates between 0.374 (Ceferino) and 0.485 (Río Viejo). The aforementioned three indexes show increasing values moving from inter-dune valley/lowland to paleo-river/river environments (Table 2). Finally, mean EPS and mean RBAR (computed considering the whole temporal extension of each tree-ring chronology) show values ranking between 0.652 (La Toma) and 0.804 (Río Viejo) for the former and between 0.166 (Pozo Verde) and 0.256 (Río Viejo) for the latter index (Table 2).

The temporal stability of EPS (Fig. 2) shows values higher than the 0.75 minimum threshold established in this research for the common period 1979–2008. This is true with the exception of the latter part of the La Toma chronology, which shows relatively high RBAR values for

Table 2 Characteristics of the tree-ring chronologies

Site	N	Period	RW (mm)	MC	MS	EPS	RBAR
El Mateo	30 (37)	1922–2010	1.51	0.507	0.444	0.723	0.181
Pozo Verde	16 (21)	1932–2011	1.45	0.525	0.395	0.696	0.166
Puesto Viejo	15 (21)	1929–2010	1.39	0.507	0.436	0.704	0.217
Río Viejo	21 (25)	1932–2010	1.66	0.497	0.485	0.804	0.256
La Toma	10 (14)	1932–2011	2.03	0.470	0.418	0.652	0.246
Ceferino	12 (18)	1916–2011	1.34	0.477	0.374	0.711	0.221
La Juana	17 (19)	1925–2010	1.22	0.456	0.388	0.745	0.215

N Number of sampled trees per site (in parenthesis: total number of dendrochronological samples), *Period* time range of the sampled cores, *RW* mean ring-width value, *MC* mean correlation between series at each stand, *MS* mean sensitivity, *EPS* expressed population signal, *RBAR* average correlation between all series
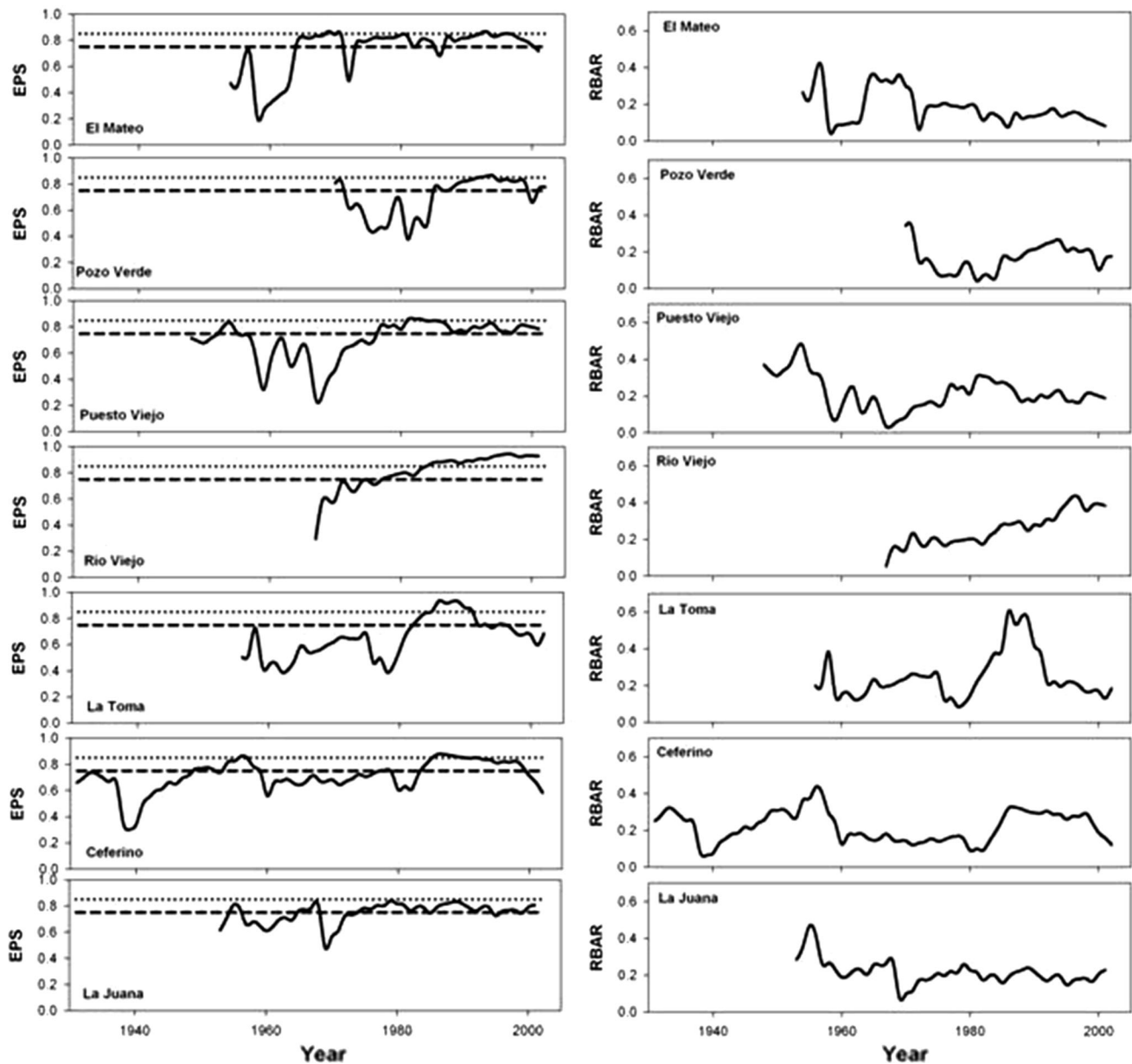
Fig. 2 Running EPS and RBAR for each chronology. *Dashed line* in the EPS graph indicates the minimum EPS threshold established in this analysis (EPS = 0.75), while *dotted line* indicates the original threshold (EPS = 0.85) established by Wigley et al. (1984)

the same time interval (Fig. 2). Therefore, we consider the selected time period for analysis to be reliable.

Influence of landform and soil heterogeneity upon tree-ring fluctuations

Multiple comparisons of means performed on transformed tree-ring series indicate that landform variability represents an important driver in radial growth fluctuations (Fig. 3). Indeed, raw dendrochronological fluctuations are statistically different at the $p < 0.05$ level between lowland and paleo-river ($p < 0.001$), paleo-river and inter-dune valley

($p = 0.00606$), and between river and lowland environments ($p = 0.00476$). Regarding the other landform units, no significant difference emerged.

Focusing on the within-landform growth variability, a significant statistical difference (one-way ANOVA, $F = 5.31$; $p = 0.0067$, $df = 2$; Fig. 3) emerged between raw ring-width fluctuations at the La Toma and the Puesto Viejo chronologies, both belonging to the paleo-river unit. This is not the case for the river-unit sites, where differences in soil permeability do not seem to represent a source of radial growth variability (one-way ANOVA, $F = 0.24$; $p = 0.6293$, $df = 1$; Fig. 3).

Multidimensional analysis performed on the standardized site chronologies indicates that the first PCA eigenvalue explains 31.8 % of the total inertia, while the second contributes up to 54.2 % (Fig. 4). All chronologies, except Pozo Verde and La Toma, contribute in a positive way to PCA1. Regarding PCA2, this axis separates Ceferino, La Juana and La Toma chronologies from the remaining ones, all negatively correlated to the second axis of the PCA (Fig. 4).

Precipitation, landform, soil permeability and growth interactions

The correlation function analysis performed between the PC1 and monthly total precipitation values indicates that at regional scale, tree-ring development is favored by abundant precipitation during October of the year preceding growth, and February and March of the year of growth (Fig. 5). However, at local scale, correlation function analysis indicates the existence of dendroclimatological differences among the *P. flexuosa* populations, when related to among- and within-landform spatial heterogeneity (Fig. 6).

Regarding the river environment, the El Mateo and Pozo Verde chronologies do not show any significant positive relation with precipitation values, while Pozo Verde is negatively correlated to current-year March rainfall amount (Fig. 6). Correlation functions for the paleo-river environment indicate that tree-ring development is positively related to abundant precipitation in the months of November and December of the preceding year (respectively, La Toma and Puesto Viejo) and February of the year of growth (Río Viejo) (Fig. 6). Furthermore, there are negative correlations between Puesto Viejo and Río Viejo chronologies and winter precipitation (corresponding to June and August of the year preceding growth), and a positive correlation for the La Toma chronology (June of the year of growth) (Fig. 6). The inter-dune valley chronology (Ceferino) is positively related to the precipitation amount of preceding-year October and current-year March (Fig. 6). Finally, at the lowland environment (La Juana), tree-ring growth is positively related to rainfall during October of the year preceding growth (Fig. 6).

Landform heterogeneity does not translate into significant differences of the climate–growth relationship (expressed by the *r/s* coefficient) among the selected stands (one-way ANOVA, $F = 1.09$; $p = 0.3632$, $df = 3$; Fig. 7). On the other hand, at the within-landform level (Fig. 7), soil permeability heterogeneity represents a source of dendroclimatological variability at the river sites (one-way ANOVA, $F = 10.41$; $p = 0.0091$, $df = 1$), but not at the paleo-river environment (one-way ANOVA, $F = 1.91$; $p = 0.1819$, $df = 2$).

Discussion

This is a first attempt to describe the radial growth variability of *P. flexuosa* in the Monte Desert territories with respect to landform and soil heterogeneity as potential influencing factors in tree-ring growth fluctuations and their consequent relationships with climate.

Considering the MC and MS values, we distinguished a positive trend for both statistics moving from inter-dune valley/lowland to paleo-river/river environment. These results can reflect hydrological differences among the selected stands and their effects on common growth signal at the population level (MC), and possibly on the common growth sensitivity to the environment (MS) (Fritts et al. 1965). Regarding MC, a stable water supply, likely due to water infiltration resulting from the presence of active/inactive streams, can probably translate to a reduction of the "noise" factor recorded in the ring widths, minimizing the individualistic response to water table fluctuations in facultative phreatophytic species such as *P. flexuosa* (Morello 1958; Cook 1987; Jobbágy et al. 2011). The MS index is strictly related to MC (Fritts et al. 1965). In our analysis, indeed, with the exception of Pozo Verde, the lowest values of MS emerged for the ring-width chronologies characterized by the lowest values of MC.

Through the joint analysis of EPS and RBAR we were able to select a relatively lengthy common time period for analysis ($n = 30$). Regarding EPS, we face the same difficulties of relatively low values reported by recent dendrochronological studies performed for a desert tree species (Sass-Klaassen et al. 2008; Nicolini et al. 2010; Giantomasi 2011; Giantomasi et al. 2013). Since Wigley et al. (1984) clearly suggest the utility of adjusting the EPS threshold depending on the ecological characteristics of the analyzed species, we consider an adjustment of the assumed 0.85 value useful, particularly for semi-arid areas where woodlands often show a patchy spatial distribution that strongly limits the possibility to obtain a large dendrochronological dataset (Aguiar and Sala 1999).

Landform heterogeneity represents a source of variability for *P. flexuosa* ring widths at both low (raw) and high (standardized) frequencies. The multiple comparison analysis indicates the presence of significant differences in raw tree-ring fluctuations according to landform differences. Multidimensional analysis suggests that PC1 separates residual chronologies along a W–E gradient. The PC2 suggests how the spatial arrangement of ring-width chronologies seems to follow another pattern of separation. Indeed, PC2 divided forest units growing in river/paleo-river and inter-dune valley/lowland environments (sites El Mateo, Puesto Viejo and Río Viejo from Ceferino and La Juana sites), respectively. In the same way, PC2 separates
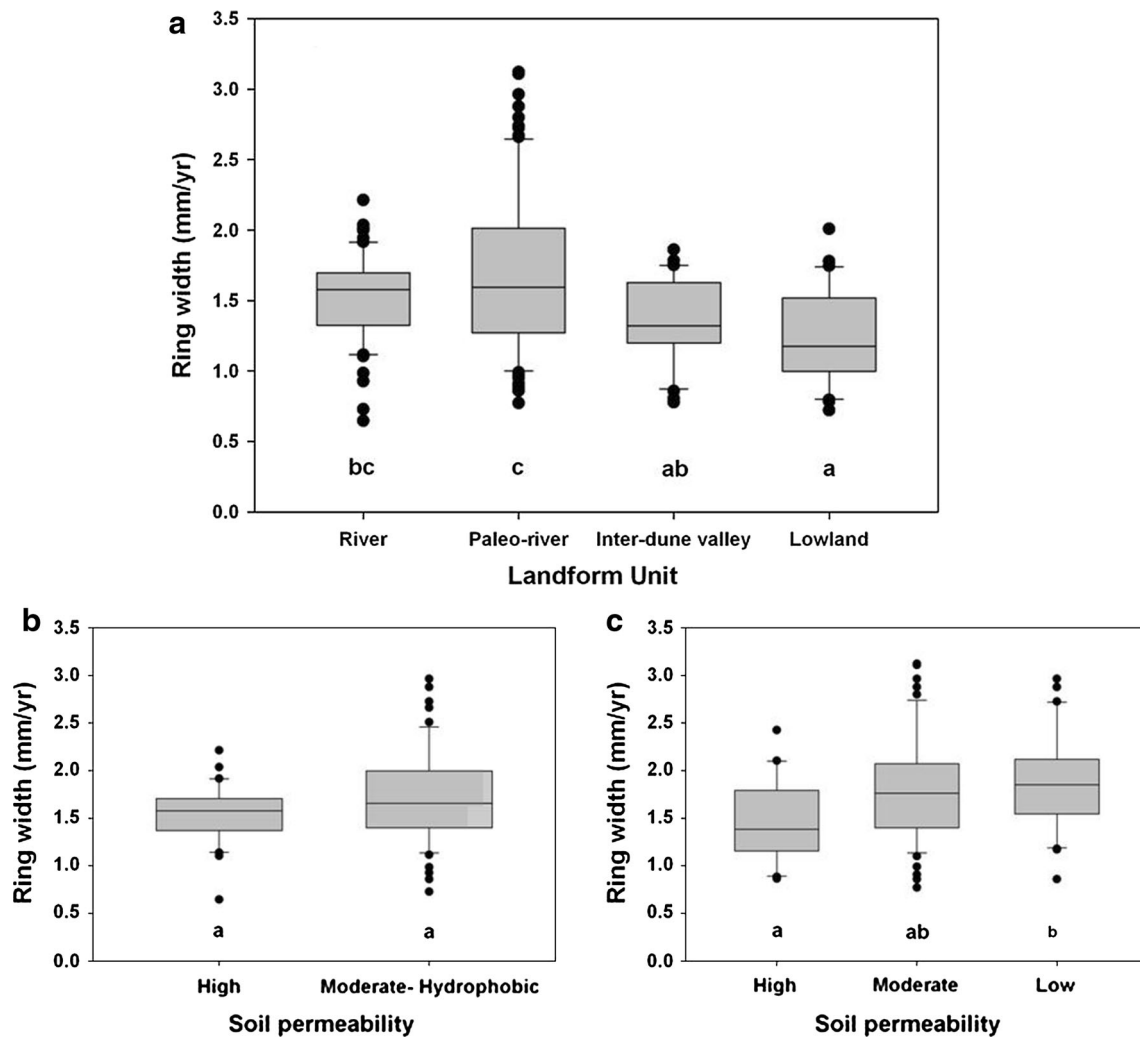
Fig. 3 *Box plot* for ring growth fluctuations of the 1979–2008 period: **a** between different landform units; **b** within-river environment; **c** within paleo-river environment. Each *box* shows the values within one interquartile distance (ID 25 % above and below the median).

The median is shown as a *black bar*. *Whiskers* represent values of 1.5 times the IDs and are shown as *black lines*. *Circles* represent outliers. *Different letters* indicate significant differences at $p < 0.05$

river from paleo-river environments (Pozo Verde from La Toma sites).

At the within-landform level, differences in soil permeability to water seem to represent an additional source of radial growth variability. Indeed, at the paleo-river environment ring-width fluctuations significantly differ between Puesto Viejo, characterized by coarse-textured and high permeable soils, and La Toma, where trees grow on fine-textured soils with low permeability.

In summary, raw and standardized tree-ring series fluctuations seem to reflect the presence of a water availability gradient, as an expression of the landform (and to a lesser extent the soil) heterogeneity in the study area. The environmental gradient analyzed in this research can reflect plausible differences in the hydrological balance and therefore help to explain these results. In river and paleo-

river environments, *P. flexuosa* radial growth can rely on possible recharge of superficial soil layers due to the presence of active and inactive streams, while at inter-dune valley and lowland landforms the trees are distributed far away from any additional source of water (Roig et al. 1992). Furthermore, soil heterogeneity within the paleo-river environment can influence fundamental abiotic processes, such as water infiltration and storage following run-off events (Noy-Meir 1973; Whitford 2002). Therefore, our results seem to confirm the species dendrochronological plasticity to the presence of hydrological gradients (Villagra et al. 2005; Giantomasi 2011). Nevertheless, while the aforementioned researches were performed for *P. flexuosa* woodlands distributed in territories characterized by important differences in the precipitation regime, our findings concern a homogeneous area in terms of precipitation
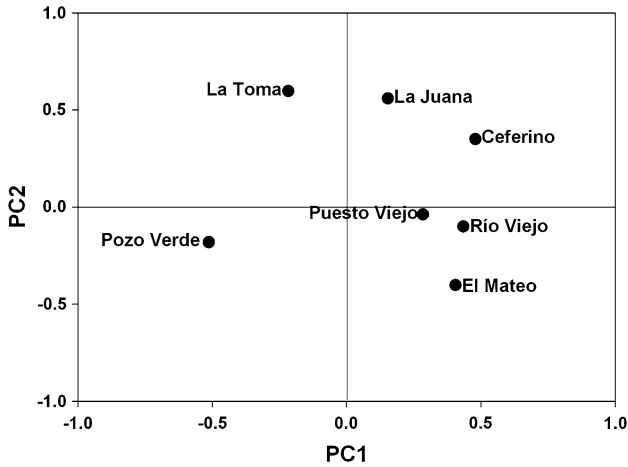
Fig. 4 Pattern of the first principal components of PCA performed for residual tree-ring-width chronologies for the common period 1979–2008
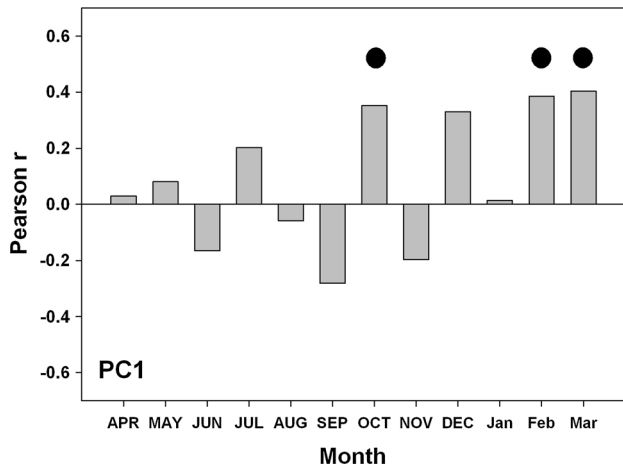

Fig. 5 Correlation functions between PC1 and monthly total precipitation for the common period 1979–2008. *Uppercase* months of the preceding year. *Lowercase* months of the current year. *Dots* significance at $p < 0.05$

variability. Thus, our analyses highlight the fundamental influence of landform and soil heterogeneity upon the ring-width development of *P. flexuosa*.

From correlation function analyses, *P. flexuosa* tree-ring growth at regional scale is favored by abundant rainfall at the beginning (October of preceding year) and the end (February–March of the year of growth) of the growing season, while at local scale there emerged differences among the selected stands, likely related to the landform and soil variability.

Previous analysis demonstrated that tree-ring growth of *P. flexuosa* in Central Monte Desert begins in October synchronized with leaf flush (Giantomasi et al. 2012). Even though earlywood begins to develop during November,
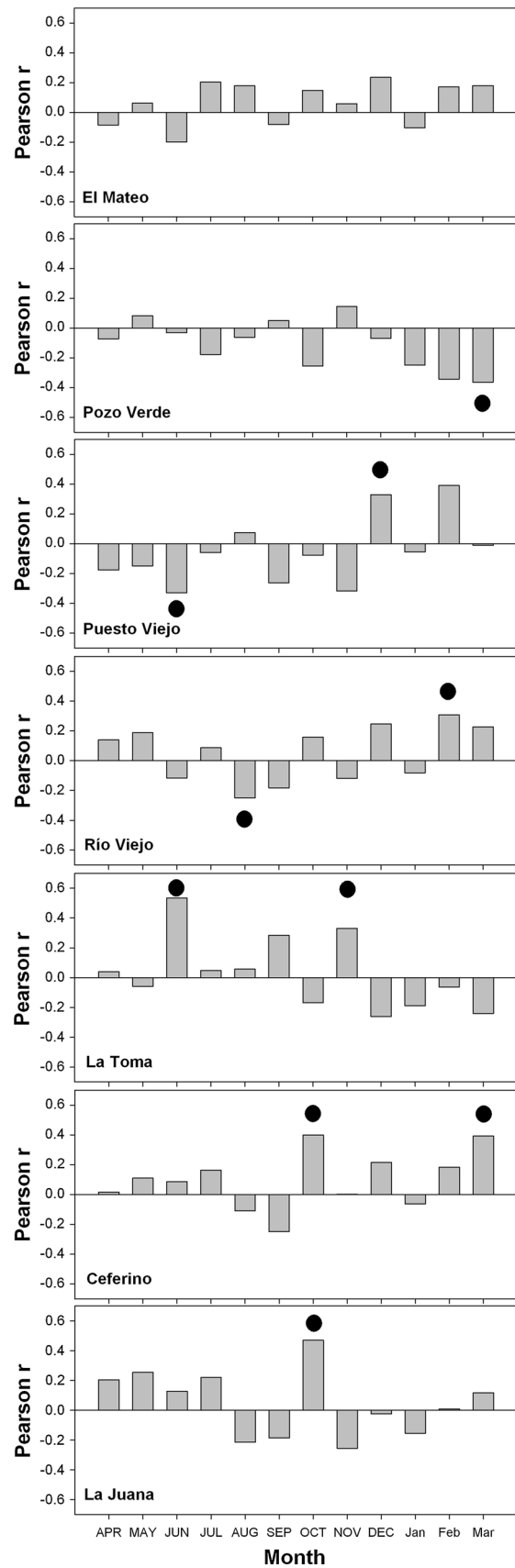
◄**Fig. 6** Correlation functions between each residual chronology and monthly total precipitation for the common period 1979–2008. *Uppercase* months of the preceding year. *Lowercase* months of the current year. *Dots* significance at $p < 0.05$

there is an apparent dormancy of the cambium during January (Giantomasi et al. 2012). Nevertheless, cambial activity may restart and complete the ring formation between the end of January and March, coincident with a new precipitation pulse along with a reduction in temperature values at summer's end (Giantomasi et al. 2012). Therefore, we will focus our attention on the climate–growth correlations during the species̒ growing season.

River chronologies do not show any significant positive relations with precipitation. Particularly, the Pozo Verde ring series is negatively related to abundant rainfall during March of the year of growth. Tree-ring development in paleo-river environments is positively and significantly related to the precipitation amount of late spring–early summer (La Toma and Puesto Viejo sites) and mid-summer periods (Río Viejo site). From a biological point of view, these results are easily understandable considering that rainfall (along with relatively lower air temperatures according to Giantomasi et al. (2012)) may reduce evapotranspiration rates favoring cell cambial divisions during the first growth pulse (La Toma and Puesto Viejo sites), as well as the reactivation of the meristematic tissue in a
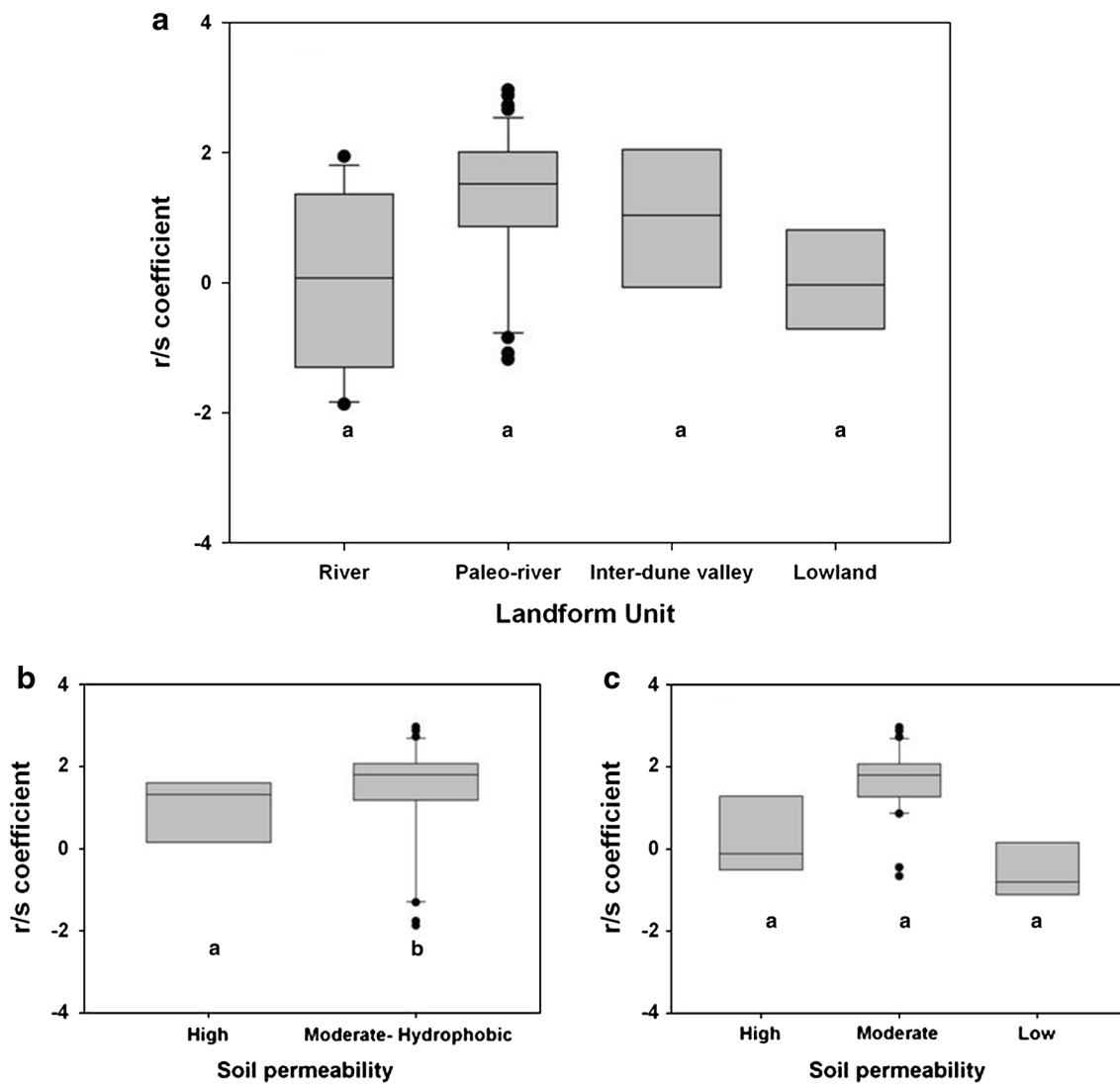

Fig. 7 *Box plot* for ring r/s coefficient of the 1979–2008 period: **a** between different landform units; **b** within-river environment; **c** within paleo-river environment. Each *box* shows the values within one interquartile distance (ID 25 % above and below the median).

The median is shown as a *black bar*. *Whiskers* represent values of 1.5 times the IDs and are shown as *black lines*. *Circles* represent outliers. *Different letters* indicate significant differences at $p < 0.05$

second pulse of ring growth (Río Viejo site) (Giantomasi et al. 2012). The *P. flexuosa* woodlands at both inter-dune valley and lowland show a positive relation of growth to October precipitation of the preceding year, when cambium activity begins (Giantomasi et al. 2012). Therefore, in these environments ring development is strongly influenced by climatic variability at the beginning of the growing season. Finally, tree-ring growth at inter-dune valley (Ceferino stand) is favored by abundant precipitation during March of the current year, probably related to a decrease in water stress and a reactivation of cambial activity (Giantomasi et al. 2012).

The distribution and growth of *P. flexuosa* in the Central Monte Desert depends on phreatic water availability as well as seasonal contributions of precipitation, which is why the species is defined as a facultative phreatophyte (Morello 1958; Jobbágy et al. 2011; Giantomasi et al. 2012). Differences in precipitation–radial growth relations that emerged among the studied woodlands can be interpreted based on site characteristics and possible physiological mechanisms.

A recent dendroclimatological study has shown that when phreatic water is accessible to the *P. flexuosa* root system, precipitation–growth signal is indefinite, suggesting a possible partial decoupling of radial growth from precipitation water (Giantomasi et al. 2013). Then, we can hypothesize that the lack of positive correlations for riparian woodlands can depend on the presence of a stable subsurface water supply (possibly due to stream-water infiltration and groundwater recharge; Brunke and Gonser 1997), with resulting less dependence of the species growth on precipitation variability (Giantomasi et al. 2013). In the paleo-river environment, the radial growth may be promoted by surface runoff processes, particularly coincident with large and intense precipitation events (Roig et al. 1992; Whitford 2002). On the other hand, in the inter-dune valley/lowland, tree-ring development relies solely on precipitation and groundwater availability. Therefore, site characteristics, expression of landform heterogeneity and its resulting influence on surface and subsurface hydrological balance, can partially account for the differences in the precipitation–radial growth signals among the selected forest stands (Giantomasi et al. 2013).

On the other hand, the within-landform soil heterogeneity, expressed by differences in soil permeability, seems to represent an additional source of dendroclimatological variability only for the river-unit forests. Nevertheless, the overall negative precipitation–tree-ring trend founded at the La Toma stand (although not significant at the $p < 0.05$ level, and with the important exception of a positive significant relation between ring growth and November rainfall amount) can possibly reflect site (soil)-dependent mechanisms also at the paleo-river

environment. Differences in soil permeability within the paleo-river landform can possibly impact rainfall infiltration and therefore plant growth dynamic (Noy-Meir 1973; Whitford 2002). As previously commented, it is worth mentioning that at the La Toma stand we observed dead trees of *P. flexuosa*, likely due to root anoxia produced by long-lasting floods in sites of low-permeable soils.

From a physiological viewpoint, we can hypothesize possible intra-specific differences in water-use efficiency along the landform/hydrological gradient analyzed in this research, with resulting variability in the presence and the strength of the precipitation–growth relations (Ehleringer and Cooper 1988). Although water-use efficiency was not measured in this study, differences in this variable have been recorded along a soil moisture gradient for *P. flexuosa* and for *P. glandulosa* in manipulative experiments, where trees growing in wetter conditions express the lowest values of water-use efficiency (Vilela et al. 2003; Ansley et al. 2007).

This research shows evidence of site (landform, and to a lesser extent soil)-dependent mechanisms in the dendrochronological and dendroclimatological variability of *P. flexuosa* in the Central Monte Desert. Site-dependent effects on radial growth fluctuations and their relations with climate have been reported for forests growing under different climatic conditions (Villalba et al. 1994; Orwig and Abrams 1997; Oberhuber and Kofler 2000; Bunn et al. 2005; Liang et al. 2006; Ferrero et al. 2013). Site (topographic) dependence has been found to be more important than species dependence mechanisms in influencing radial growth variability of mountainous conifers of Northern America and China (Villalba et al. 1994; Liang et al. 2006). Orwig and Abrams (1997) indicate that the dominant species distributed in mixed forest clearly present differences in growth fluctuations depending on topographic heterogeneity. Topography represents a driver of ring growth variability for *Pinus sylvestris* woodlands distributed in the Alpine mountain belt as well as for *P. balfouriana* located at western North America tree line, where forests distributed in areas of variable slope and aspect differ in radial growth and in their relations with climate (Oberhuber and Kofler 2000; Bunn et al. 2005). Finally, topography-dependent mechanisms influence the dendroclimatological variability of a set of broadleaf species distributed in subtropical forests of northwestern Argentina (Ferrero et al. 2013).

We are not aware of studies that link topographic and soil heterogeneity to intra-specific climate–growth relation variability in the *Prosopis* genus. Miller et al. (2001) analyzed the basal area increment variability of *P. glandulosa* in a subtropical savanna, where a dendrometric observation over a 6-year interval did not show statistical differences in its radial growth along the topographic transect. Martínez and López-Portillo (2003) examined

allometric relations of *P. glandulosa* along an altitudinal and topographical gradient in the Chihuahuan desert. The authors found that topographic heterogeneity is expressed in growth variability, as exemplified by the correlation between maximum plant size and inter-year shoot pre-dawn water potentials, reflecting the water availability gradient along the selected topographic sequence (Martínez and López-Portillo 2003). Finally, topography is considered the main factor regulating the *P. glandulosa* woodland dynamics in a savanna landscape of the southwestern USA (Wu and Archer 2005).

Conclusions

In this work, we provide the first evidence of site (landform/soil)-dependent mechanisms in the radial growth variability of *P. flexuosa* in the Monte Desert territories. Landform and soil heterogeneity translated into a water availability gradient has consequences in the variability of radial growth and its relation with precipitation. Indeed, while at the regional scale the species' growth is influenced by the precipitation amount at the beginning and the end of the growing season, at local scale it seems that the climatic responses of *P. flexuosa* are influenced by a complex combination of landform and soil variability. Landform influence on the species dendroclimatology is exemplified, for instance, by the distinct radial growth–precipitation signals that emerged between woodlands distributed on sandy soils, but growing in landform units differing by their surface water balance, such as river, paleo-river and inter-dune valley. On a finer scale, i.e. at within-landform levels, the edaphic variability may act as an additional source of heterogeneity in the species' response to precipitation, probably by regulating rainfall infiltration and storage in soils. These results contribute to improve the knowledge of the autoecological characteristics of the studied species, information particularly useful for forest management and possible influences of climate change on desert woodlands (IPCC 2007).

Climatic projections for the Central Monte Desert indicate an increase in intense summer rainfall pulses and a parallel decrease in winter precipitation of approximately 5–20 % (Boulanger et al. 2006; Labraga and Villalba 2009). Both situations may modify in a different way the natural dynamics of the *P. flexuosa* woodlands of the analyzed area.

Riparian woodlands along active rivers will probably experience a negative modification of the hydrological equilibrium due to the decline in the Andes winter precipitation, producing a decrease of river water volume. On the other hand, paleo-river and particularly inter-dune valley and lowland populations will probably benefit from a trend of increasing summer precipitation. However, extreme rainfall events would be detrimental for long-term forest dynamics, as suggested by tree mortality as a consequence of episodic floodings (personal observation). Finally, the results reflect the high spatial environmental heterogeneity characteristic of semi-arid lands such as the Central Monte Desert (Aguiar and Sala 1999; Bisigato et al. 2009). Our findings suggest the need and convenience to consider landform and soil heterogeneity of arid areas as an influencing factor on tree growth and its relation with precipitation in desert regions.

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