Climate and groundwater effects on the establishment, growth and death of *Prosopis caldenia* trees in the Pampas (Argentina)

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ABSTRACT

Semiarid woodlands dominated by *Prosopis caldenia* thrive at the dry edge of the Argentinean Pampas. Deforestation and increased precipitation have driven sustained water table level rise in the region that are likely to affect the dynamics of remnant woody vegetation patches. Here we analyze the effect of climate and groundwater level on the establishment, growth and death of *P. caldenia* located on lowland (current water table <0.5 m deep) and upland (current water table 8 m deep) positions within rolling sandy landscape. Standard dendrochronological techniques were applied on 98 cross sections and cores of *P. caldenia* trees. Results allowed us to estimated that trees in the lowland established a few years earlier than in the upland (1929 vs. 1936) and died between 1991 and 2002, while trees in higher positions are still alive. As a result of a faster growth in the lowland, maximum mean basal area increment took place earlier (1950s vs. 1990s) and achieved a higher mean value than in the upland (41.63 vs. 37.41 mm^2). While mean annual chronologies were not associated across stands, an opposite highly significant association was found for the mean growth trends suggesting long-term effects of water table depths on growth. We found a different association between mean annual growth and climate, with lowland trees showing a negative response to precipitation before and during the growing season, and upland trees displaying a positive response to summer rainfall inputs. Temperature at the end of the growing season had a positive effect in the lowland whereas temperature during the growing season had a positive effect in the upland. These results show how groundwater can induce diverging sensitivity of forest growth and survival to climate variability, enhancing growth at optimum depths (2–8 m in our study) but depressing it or even killing trees when it approaches the surface (<2 m in our study). Groundwater dynamic should be considered in forest management and conservation strategies in semiarid woodlands in Central Argentina.

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1. Introduction

Dry temperate woodlands dominated by caldén (*Prosopis caldenia* Burkart), thrive across the drier edge of the Pampas grasslands of Argentina. After the European colonization in the early 1900s, the ecotone area between dry temperate forests and grasslands was dedicated to sheep and cattle breeding, yet in the last four decades it has experienced a fast agricultural expansion. Current deforestation rate in caldén woodlands is 0.86% year^{-1} and only 18% of their original area is left (PINBN, 2007). While the area of original woodlands shrinks, the relicts of adjacent grasslands that have not been occupied by crops experience woody encroachment by caldén, likely favored by sheep and cattle grazing (Archer, 1994; Distel et al., 1996; Dussart et al., 1998).

Land use changes interacting with a long-term rising precipitation trend between the 1950s and the 1990s have likely caused sustained water table level rises observed in many areas of this flat sedimentary region (Viglizzo et al., 2009; Santoni et al., 2010). In some areas originally covered by woodlands, ecohydrological changes involved the appearance of new surface water networks during the last four decades in landscapes that lacked them throughout their whole geologic history (Galván and Collado, 2009; Santoni et al., 2010). Rising groundwater levels can have variable effects on vegetation growth as they approach the surface, shifting from positive water supply effects to the negative influence of waterlogging (Jobbágy and Jackson, 2004; Nosetto et al., 2009).

In the study region water table level rise has been linked to localized die-off patches of caldén trees, likely resulting from waterlogging. In drier areas with less than 150 mm year^{-1} of rainfall, the presence of well developed individuals of another *Prosopis* species (*P. flexuosa*) has been linked to the positive effects of water

supply by phreatic aquifer located 6–10 m below the surface (Jobbágy et al., 2011). Water table level rise in the semiarid plains of Central Argentina over the last decades may have simultaneously propitiated tree establishment and growth in higher landscape positions through better groundwater access, while growth decline and tree death occurred in lower landscape positions.

Tree rings of woody species as proxy for reconstructing past environmental events has been widely applied, but their use to detect water table fluctuations (Ferguson and St. George, 2003; Perez-Valdivia and Sauchyn, 2011) and the effect of flooding on wood anatomy is limited to a few cases (Eckstein, 2004; Sass-Klaassen and Hanraets, 2006). A gap exists regarding the study of hydraulic adjustments in response to environmental changes over the lifetime of plants (Fonti et al., 2010).

The study of tree rings of woody species (i.e., Dendrochronology) can provide information about past and present ecological controls of tree establishment, growth and death, including those related to climate and water availability, particularly under semiarid conditions (Fritts, 1976). Besides being the dominant tree species of temperate woodlands and the most common encroacher in the grassland ecotone, *P. caldenia* is a valuable species for dendrochronological studies (Villalba et al., 2000) as shown earlier fire reconstructions (Medina, 2007), encroachment studies (Dussart et al., 1998) and growth assessments (Bogino and Villalba, 2008).

Here we analyze how climate and groundwater levels had influenced the establishment, survival and growth of *P. caldenia* in the grassland-dry forest ecotone in the semiarid Pampas of Argentina. Two hypotheses guide our observations and state that (1) as groundwater levels shift (in time or space) from deep to shallow they progressively have a neutral (no access), positive (supply) and negative (waterlogging) effects on calden trees and (2) along this groundwater depth sequence tree growth becomes increasingly decoupled from the rainfall and more responsive to other growth controls such as temperature. We explore these hypotheses based on dendrochronological and meteorological observation and the aid of old aerial photographs and present images in a sandy landscape that has experienced intense groundwater level fluctuations for, at least, the last 50 years.

2. Material and methods

A site encroached by *Prosopis caldenia* originally occupied by native grasslands was selected for the study. The study area has an annual precipitation of 639 mm (records from "El Aguila" ranch for 1908–2002) with a rising trend between 1950 and the late 1990s. Precipitation is concentrated in spring and summer (76%). Mean monthly temperature ranges between 8 °C (July) and 23 °C (January, Veneciano et al., 2000) (Fig. 1).

The wind-shaped dune landscape of Holocene origin (Tripaldi and Forman, 2007) hosts deflation basins that are presently occupied by natural lagoons connected to the water table (Fig. 2). Groundwater is at the surface in the edge of the lagoons and as deep as 15 m in the highest dune crests. Since the sixties groundwater has risen approximately 4 m increasing the level and area of the lagoons (Fig. 2) (Collado et al., 2002). Soils in this area are poorly-developed, they have little structural stability and low amounts of organic mater, consequently they are susceptible to erosive processes, particularly after the replacement of the natural vegetation (Peña Zubiate et al., 1998; Collado et al., 2002).

Two stands of caldén located in contrasting topographic positions were selected (Fig. 1). The first stand was located close to a lagoon (lowland) that experienced total tree die-off and was flooded or had the water table at less than 0.5 m of depth at the time of sampling. Located 800 m away from the previous stand we selected another one on the dune slope and crest (upland). This stand had no dead trees and water table depth is greater than 8 m at the time of sampling (Fig. 2).

We documented the expansion of the lagoon and flooding of the surrounding area combining high-resolution aerial photographs obtained in 1962 and detailed satellite imagery (quick bird scenes from Google Earth) obtained in 2002. In both scenes we were able to identify individual trees with crowns larger than ~1 m, obtaining a semi-quantitative estimate of tree growth at different elevations for the 40 year period that they encompassed (Fig. 2).

Cross sections of trees were taken from both stands, including 18 dead trees from the lowland and 25 trees that were removed for the construction of a new road in the upland. Samples in the upland were taken in 2002. Cores and samples in the lowland were taken in 2009. Cross-sections were cut at 20 cm height from dominant and co-dominant trees. In addition to the cross-sections from the upland and lowland stands we sampled 16 live trees to detect growth dynamics associated to altitudinal position. Cores were taken using an increment core along intermediate positions with groundwater depth ranging between 0.3 and 8 m of depth. Cross sections and cores were polished and then dated under a microscope Olympus SZ61 (0.9–4X) following the standard dendrochronological methodology (Stokes and Smiley, 1968).

Two radii were dated per cross section. Tree rings were measured to 0.01-mm accuracy with a measurement system Unislide TA 4020H1-S6 Velmex. The COFECHA program (Grissino-Mayer, 2001) was applied to validate sample dating and to record the year of death in lowland trees. The COFECHA program calculates correlation coefficients between individual series of dated ring widths to identify the location of absent or false rings. To compare tree-ring width to any environmental variables it is critical to date accurately the year of tree-ring formation. Two ring-width chronologies, which represent the variations in the mean radial growth of the stand through time, from the lowland and upland, were constructed.

Basal area current (BA CAI) and mean (BA MAI) increments were calculated using the formulae (Mutarelli, 1964):

$$BA\ CAI_i = \pi(r_i^2 - r_{i-1}^2),$$
$$BA\ MAI_i = \frac{\pi.r_i^2}{i}$$

where r_i is the ring width in the year i.

Low frequency variability was captured by filtering out the inter-annual fluctuations in the mean radial growth series with a cubic spline function with a nine-year periodicity. High frequency variability was captured by standardization of the original series removing low frequency variability relates to age and other long term factors (Speer, 2010).

The ARSTAN sofware (ARSTAN v6.05P, Cook and Holmes, 1984; Holmes, 2001; available at www.ltrr.arizona.edu) was used to standardize growth series and calculate chronologies. This program uses a negative exponential curve and a cubic smoothing spline to fit the growth of each tree. The program fits a curve dividing the ring width by the modeled curve, creates a tree-level index and finally averages all individual indices to develop a stand chronology. The ARSTAN chronology that was calculated by removing, modeling and reintroducing back stand-level autocorrelations (Speer, 2010) was used to obtain high frequency variability series that were compared with the climate ones.

The quality of the chronology was evaluated by mean sensitivity (MS), which is the measurement of the year-to-year variability (Schweingruber, 1996); signal-to-noise ratio (SNR), the proportion of the variability explained by climate or other causal factors divided by the residual or unexplained variability (Fritts and Swetnam, 1989), and expressed population signal (EPS), which describes how a finite sample estimates the hypothetical infinite
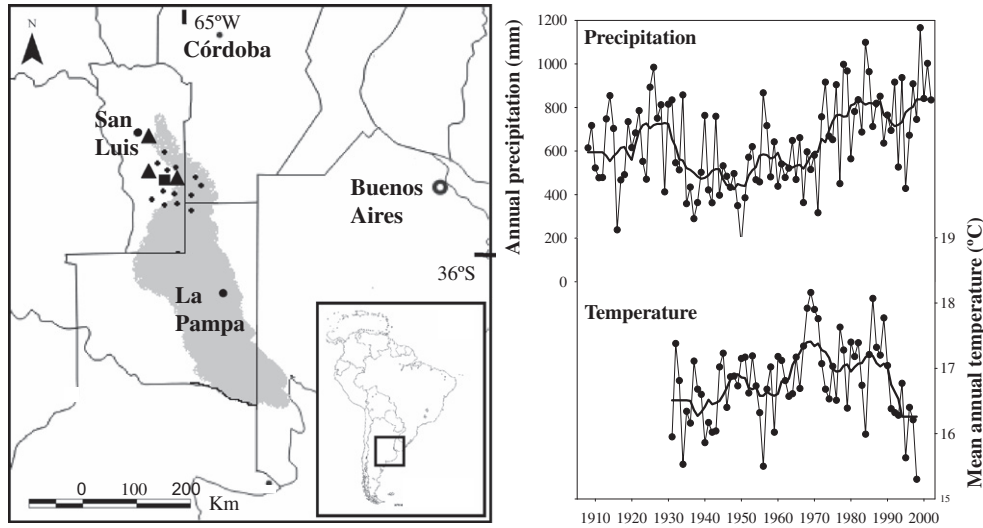
Fig. 1. *Prosopis caldenia* woodlands in Central Argentina (grey dashed), natural lagoons (black circles), the sampling site (black square) and the meteorological stations (black triangles) (Anderson et al., 1970). Annual precipitation trend from El Águila and mean annual temperature trend from San Luis are represented.
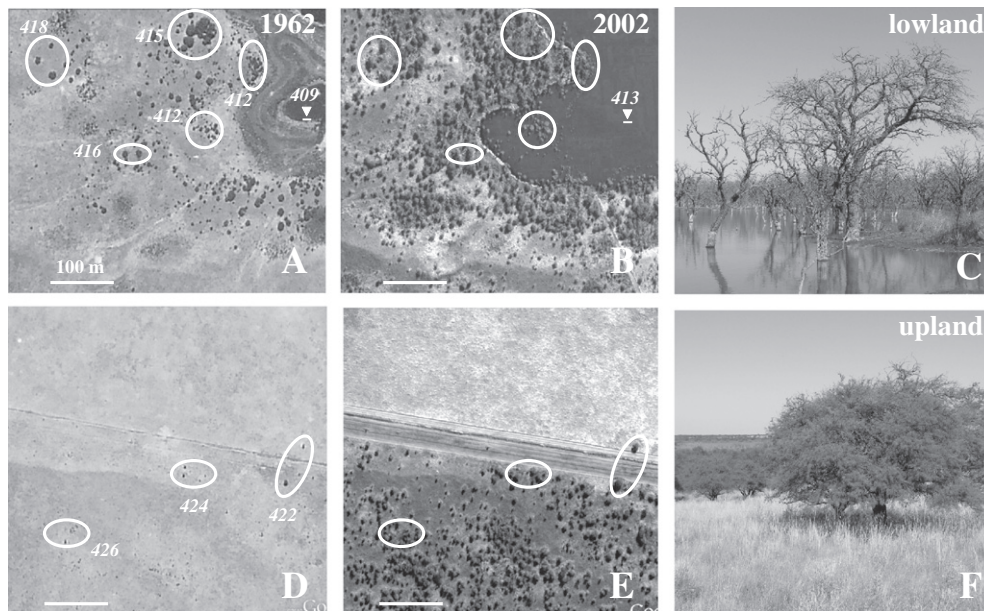

Fig. 2. Lowland and upland sampling sites at the time of our study (C and F). Aerial photographs of a lowland and upland section in 1962 (A and D) and high resolution image (from Google Earth) in 2002 (B and E). Group of trees present in both images are circled and their topographic position (elevation meters above sea level) are indicated. In this time lapse of 40 years the level of the lagoon raised approximately 4 meters.

population (Wigley et al., 1984; Briffa, 1995). Pearson's correlation coefficient between mean, spline and arstan chronologies was applied to estimate the correspondence between tree-ring growth patterns at both sampling sites.

The Dendroclim2002 software (Biondi and Waikul, 2004) was used to analyze the association between mean and arstan tree-ring width chronologies in the lowland and upland with climate variables, mean monthly temperature and monthly precipitation, from April previous to the growing season to May after the growing season. This program applied correlation analysis using bootstrapping techniques to determine significance levels. This program was also applied to calculate moving correlations for 28-year long windows, as a way to detect long-term shifts in the climate-growth association. We used temperature records from San Luis meteorological

station (1930–1999, 33°16′ S; 66°20′ W) and precipitation records from Las Taguas (1969–2002, 34°22′ S, 65°32′ W) and El Águila (1907–2002, 34°43′ S, 65°37′ W), two ranch-homesteads located 4 and 40 km away from our study site (Fig. 1).

Statistical analyses were performed using the package Infostat V.9 (Di Rienzo et al., 2009). The climate variables that significantly correlated with mean radial growth were selected using multiple linear regression models,

$$C_t = b_0 + b_1(x_1) + b_2(x_2) + \cdots + b_k(x_k) + \varepsilon$$

where C_t is the mean radial growth at the year t, $x_1, x_2 \ldots x_k$ are the climatic variables, $b_0, b_1, b_2 \ldots b_k$ are unknown parameters of the model and ε is a normal random error.

3. Results

Consistent growth variability among successive tree rings across individuals allowed us to identify the dates of tree establishment and death. The pool of all upland and lowland series (n = 98) had an intercorrelation of 0.55 and mean sensitivity coefficients of 0.40 for the 1929–2008 period. Trees in the lowland established on average seven years earlier than in the upland, died between 1991 and 2002, and had lower and less variable annual radial increments than those in the upland. Lower mean sensitivity and intercorrelation between trees were found in the lowland trees, compared to those in the upland (Table 1).

Both chronologies displayed similar statistics after standardization except for SNR and EPS values that were lower in the lowland than in the upland (Table 2). Lowland and upland mean annual growth series displayed a stronger correlation with their derived low frequency component (spline chronologies) than with their high frequency one (arstan chronologies). This contrast was higher

in the lowland stand, suggesting that long term growth trends, such as those that decadal groundwater level changes may have introduced, were important at both sites, but particularly at the lowland position. While mean annual chronologies were not associated across stands, an opposite highly significant association existed for the spline chronologies (Table 3).

Aerial images showed large crowns in the lowland but small ones in the uplands in 1962 (Fig. 2). By 2002 most of the individuals that were large 40 years before were dead and in many cases flooded whereas those individuals that were small and isolated in the first image where alive, and appeared larger and surrounded by new visible individuals (Fig. 2). Long-term growth patterns showed strong differences between the lowland and the upland as well. Lowland tree growth was higher between 1938 and 1969 (4.28 mm year^{-1}) than afterwards displaying restricted increments between 1970 and 2002 (Fig. 3A). Upland trees had a slow growth in that initial period (2.99 mm year^{-1}), that increased afterwards, between 1970 and 1999, (4.52 mm year^{-1}; Fig. 3C), reaching levels similar to the highest ones displayed by lowland trees. As a result of a faster growth in the lowland, maximum mean basal area increment took place earlier (1951) and was highest in that date (41.63 mm^2) compared to the upland (1995, 37.41 mm^2). Arstan chronologies for both sampling sites are included (Fig. 3B and D).

Recent radial growth reflects the negative effects of shallow groundwater when examined across the whole topographic gradients (Fig. 4). Maximum growth rates in the 1990–1999 period took place in the highest topographic positions and showed a sustained decline where water tables were shallower than 4 m, likely as a result of waterlogging of deep rooted trees. Notably, in 1962, when the trees in the lowland grew still at high rates, water tables were 4 m deeper, as indicated by the lagoon position in the aerial photograph (Fig. 2). At that time trees in the lowland stand had water table levels similar to those currently experienced by intermediate transect trees with high growth rates that do not differ with those of the upland ones (Fig. 4).

We found a different association between mean annual growth and climate in the lowland and upland stands. While lowland trees showed a negative effect of precipitation before and during the growing season, upland trees displayed a positive association with summer rainfall inputs (Fig. 5A and B). Temperature at the end of the growing season had a positive effect on mean radial growth in the lowland, whereas temperature during the growing season had a positive effect in the upland (Fig. 5A and B). The high frequency component of growth (arstan chronology) showed that rainfall in the previous fall and current growing season had a negative effect in lowland trees. No effect of rainfall was detected in this high frequency component in upland except for a positive one in July. A positive effect of temperature during the early growing season was detected at both sampling sites (Fig. 5C and D).

As a result of the climate-growth analysis, annual precipitation from January of the year t to July of the year t + 1 (PPT year t + Jan.–Jul. year t + 1) was related to the mean radial growth of caldén of the year t in the lowland. The sum of temperature of

Table 1
Site and tree radial growth characteristics of populations of *Prosopis caldenia* growing in a lowland and upland position in Central Argentina.

	Lowland	Upland
Number of trees	18	25
Number of series	32	50
Mean current water table depth (m)	0	8
Year of establishment	1929–1978	1936–1961
Year of death	1991–2002	
Mean annual radial increment ą SD (mm)	2.91 (0.63)	3.41 (0.94)
Minimum and maximum values (mm)	0.43 – 5.28	1.57 – 6.54
Mean annual basal area increment ą SD (mm^2)	29.7 (25.1)	36.8 (29.0)
Minimum and maximum values (mm^2)	0.6 – 87.8	7.7 – 134.5
Mean sensitivity across series	0.385	0.408
Mean correlation across series	0.555	0.647

Table 2
Statistics of standardized chronologies (Arstan chronologies) of *Prosopis caldenia* growing in lowland and upland stands.

	Lowland	Upland
Time span	1929–2002	1936–1999
Number of cores	32	50
Number of rings	1733	2466
Age range (years)	16–68	39–64
SD	0.31	0.35
MS	0.20	0.25
SNR	2.82	17.56
EPS	0.74	0.95
Var	45.96	47.57
Mean Corr	0.42	0.45

SD, standard deviation; MS, mean sensitivity; SNR, signal to noise ratio; EPS, expressed population signal; Var., variance in first eigenvector; Mean Corr., mean correlation among trees.

Table 3
Pearson's correlation coefficient among mean annual radial growth series (MEAN) and their low (SPL) and high frequency (ARS) components in the lowland and upland stands.

	MEAN lowland	MEAN upland	SPL lowland	SPL upland	ARS lowland
MEAN upland	−0.24				
SPL lowland	0.87[***]	−0.46[***]			
SPL upland	−0.61[***]	0.73[***]	−0.71[***]		
ARS lowland	0.80[***]	0.31[**]	0.5[***]	−0.05	
ARS upland	−0.07	0.56[***]	−0.23	0.26[*]	0.1

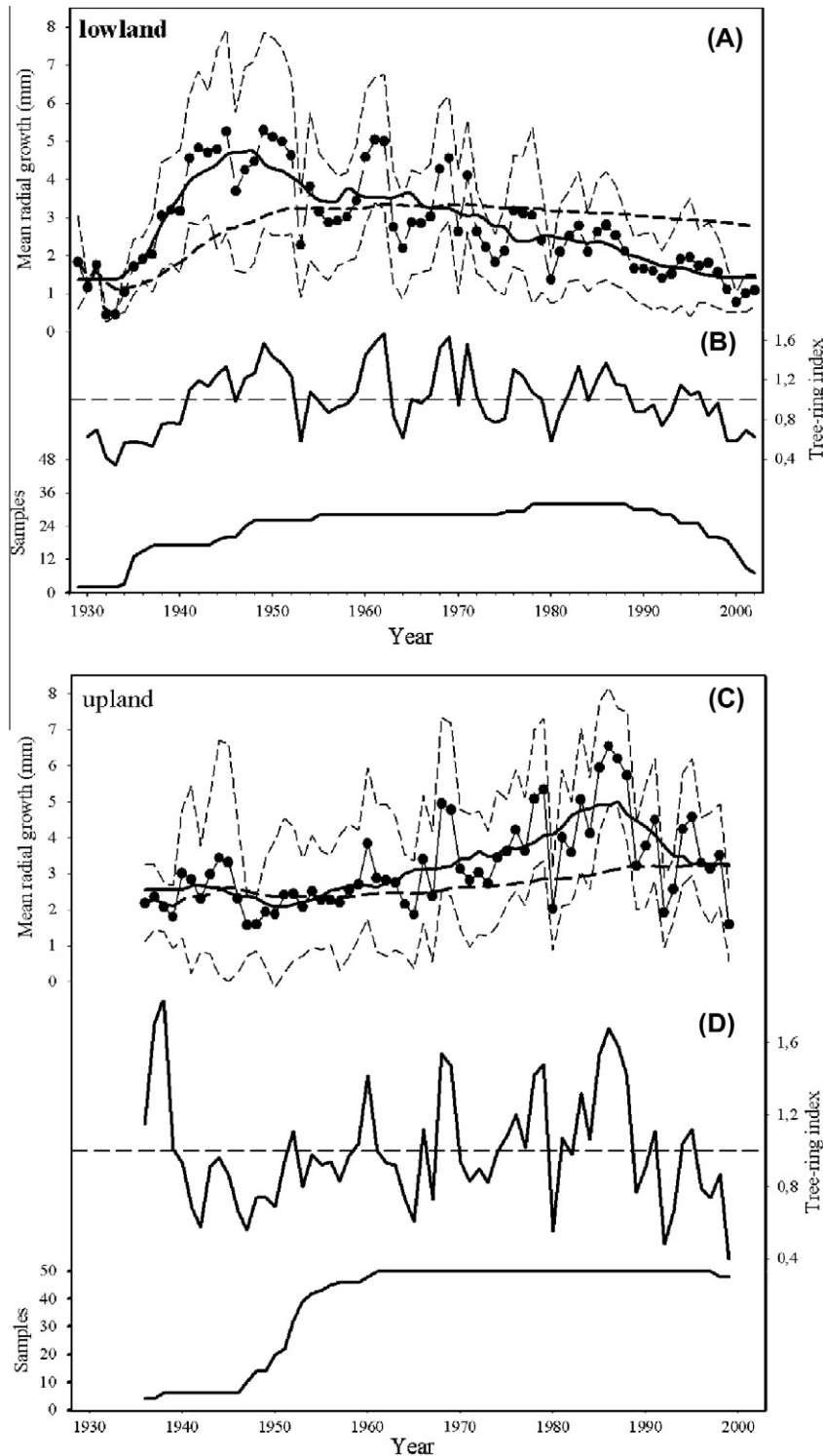[*] $p < 0.05$.
[**] $p < 0.01$.
[***] $p < 0.001$.

Fig. 3. Time series of radial growth for the lowland (A) and the upland (C) populations of *Prosopis caldenia*. Annual growth (dotted lines) and a 9-year spline (solid line) are presented. Thin dashed lines in the upper plots correspond to one standard deviation of annual radial growth across sampled individuals. The thick dashed line is the mean annual increment of radial growth. Arstan chronologies for the lowland (B) and the upland (D) are represented. The number of available samples is presented at the bottom of the plots.

October and November (T Oct. + Nov.) and rainfall from December to March (PPT Dec.–Mar.) in the growing season were selected for a linear regression model for the mean radial growth in the upland (Table 4).

Mean radial growth-climate association has changed through time at both sampling places. In lowland, temperature in the grow-

ing season became positively significant from the 60s decade (December) and in the beginning of the 80s decade (November) (Fig. 6). In upland, temperature changed from no significant to positively significant from 1968 to 1981 in July and April. The negative effect of rainfall in the lowland started in the 60s decade (December and April). May rainfall started to be negatively significant
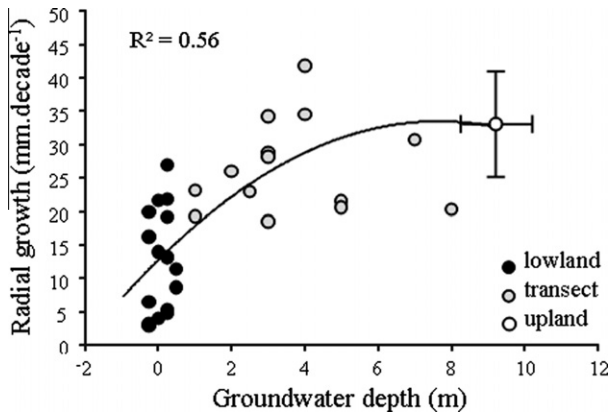
Fig. 4. Recent tree growth (1990–1999) patterns along a groundwater depth gradient. Depth to the water table varies as a result of topography with values below zero indicating flooded conditions. Growth values for lowland and upland individuals come from tree slices whereas those for transect individuals, located in intermediate topographic positions between the other two stands, come from increment cores. Groundwater depth values where inferred based on the topographic position of trees and the level of the lagoon and the water table in two monitoring wells along the transect, as measured in 2010. The lagoon levels at this time where only 0.6 meters below the record level, as indicated by flood marks in the tree stems, and represented the average levels observed throughout the 1990–1999 period as pointed out by local ranchers.

from the 90s. In the highland, rainfall changed from no significant to positively significant in winter (July) and summer (December and January) from the middle of the 80s decade onwards.

4. Discussion

Tree growth synchrony across stands allowed crossing date individuals and obtaining establishment dates, which took place a few years earlier in the lowland. Growth correspondence across landscape positions, however, was dominated by high frequency variability, indicative of a common broad control by climate. Low frequency variability, instead, showed opposite trends in both stands indicating contrasting local environmental influences at this temporal scale.

In agreement with our first hypothesis, a switch of maximum growth from lowland to upland was observed. We can hypothesize that before 1960 deep water table levels, like those shown by the aerial photograph and described by local settlers for earlier decades, made the lowland the most favorable environment, not only enhancing growth but perhaps also propitiating the observed earlier tree establishment in that landscape position. In this period, trees in the upland were growing at very low rates as confirmed by their minimal crown size in the aerial photograph. Similarly low growth rates for caldén have been found in areas with deep water tables (Bogino and Villalba, 2008).

Water level rise after the 1960s was accompanied by a long-term growth decline in the lowland and an increase in the upland. While aging of the already large lowland trees may have played a role creating these differences, the sustained raise of upland tree growth and eventual death of lowland trees suggest increasingly positive and negative groundwater effect at each position, respectively. Spatial patterns support this view, with the topographic transect indicating that maximum growth takes place in the upland and declines gradually towards die-off as groundwater levels become shallower towards the lagoon. Studies on related algarrobo dulce (*Prosopis flexuosa*) populations, west of our study area, have demonstrated groundwater consumption with water table levels of 6–10 m (Jobbágy et al., 2011) and shown massive tree death episodes following waterlogging events (Morello, 1958).

Chronologies suggest that climate-growth association depends on groundwater depth. Growth becomes increasingly decoupled by rainfall and more responsive to other growth controls such as temperature in the lowland. Lower growth coherence across lowland trees, compared to the upland ones, as suggested by the mean sensitivity and the principal component analysis suggested a more diverse response and/or environment in the lowland. In the lowland, groundwater effects were consistent with the negative impact of rainfall on growth, which would have risen water table levels causing waterlogging. Positive groundwater effects on growth would prevail before 1960 in the lowland and are likely to be important contemporarily in the upland, as suggested by other dendrochronological studies in Canada that illustrate favorable effects for 7.6–19.8 m depth range for *Pseudotsuga menziesii* (Mirbel) Franco and *Pinus banksiana* Lamb. throughout a 300 year-long record (Perez-Valdivia and Sauchyn, 2011).

Temperature effect was more significant when standardization was applied avoiding the effect of low frequency variability associated to water table fluctuation. These results are not coincident with those that suggested that applying age-related detrending methods ensure a more accurate reconstruction of temperature variability (Esper and Schweingruber, 2004). The negative effect of rainfall was more evident in the low-frequency domain of radial growth, while the positive effect of temperature has been evidenced in the high frequency variation, when standardization was applied.

In the upland, growth was favored by extended growing periods and adequate wet conditions as it was previously stated for trees growing in semiarid environments (Speer, 2010), and both temperature and rainfall were essential for modelling tree ring growth. High temperatures at the beginning (October and November) and the end of the growing season (April) may move forward and extend the growing season of the caldén. The accuracy of the regression models suggested that caldén may be used for reconstructing climate conditions in the Argentine Pampas using tree rings, particularly at dry sites without shallow groundwater were sensitive to December–March rainfall is the highest (Fritts, 1976).

While great attention has been dedicated to tree mortality under drought conditions, particularly in the context of global climate change (Allen et al., 2010); our results highlight the fact that even under dry climates, increasing rainfall can be a driver of tree mortality as well as shown for more humid systems (Laurance et al., 2009).

Dendrochronology allowed us to gain new insight on establishment, growth, and death of one of the most important tree species of Central Argentina. Results suggest that shallow water table depths can favour growth, but introduce at the same time the risk of waterlogging and massive tree die-off. Managing forest relicts in a context of fluctuating and in the long-term rising water table levels (Barros et al., 2006; Viglizzo et al., 2009) poses a difficult challenge that requires careful hydrological monitoring and flexible land use planning. *P. caldenia* proved to be an accurate tool for climate reconstructing on the edge of Argentinean Pampas as long shifts in climate-growth patterns in response to topography/hydrology are acknowledged.
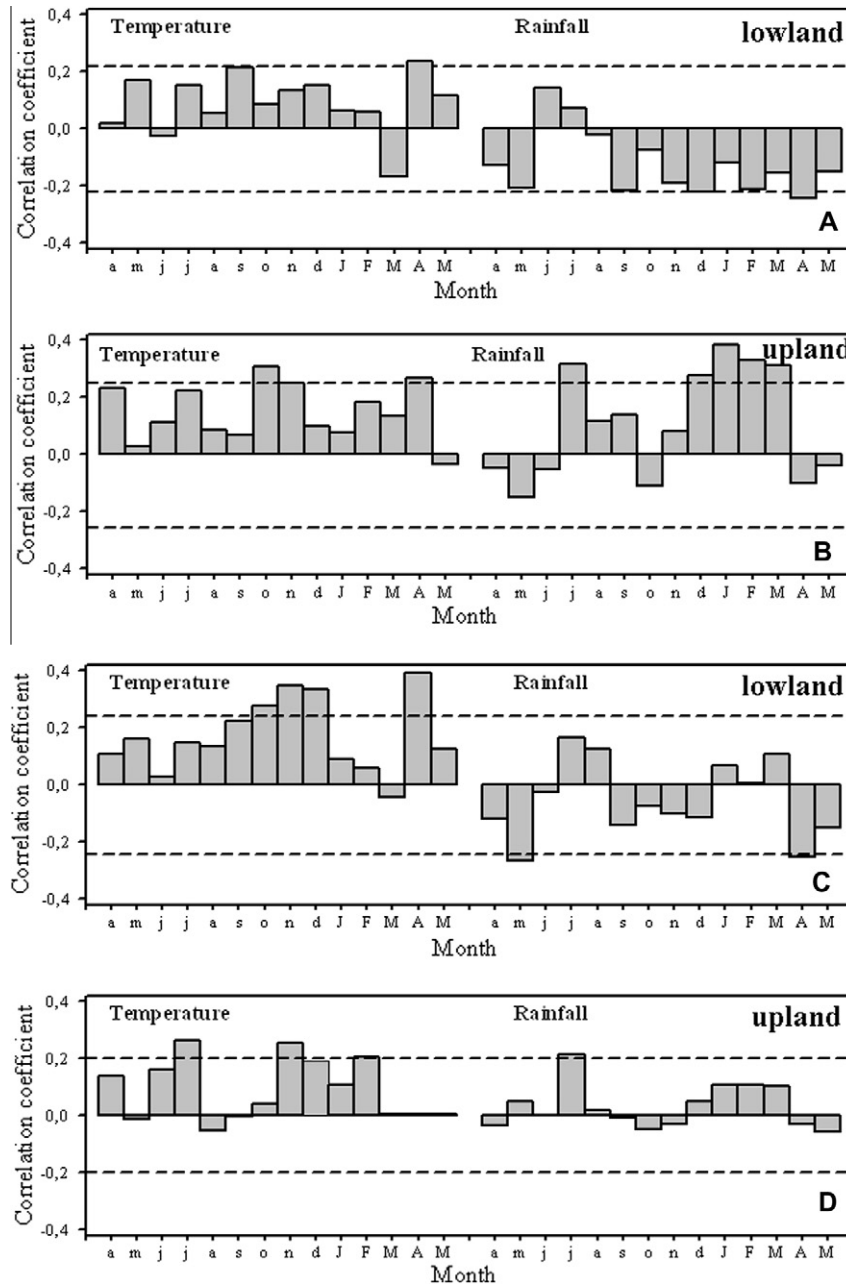
Acknowledgments

Fig. 5. Correlation between growth and climate variability in lowland and upland stands. Pearson's correlation coefficients of monthly temperature and precipitation vs. radial growth (A and B) and arstan chronologies (high frequency growth variability) (C and D) for 1931–2002 in the lowland and 1938–1999 in the upland are presented. The analysis considered monthly climate variation starting at the end of the previous growing season (April of previous year) and ending at the end of the current growing season (May of current year). Dashed lines show significant coefficients at $p < 0.05$.

Table 4
Linear regression models that relate mean and standardized growth of *Prosopis caldenia* and grouped monthly climate variables in the lowland and upland.

Variable	N	R^2	R^2 Adj	Coef.	Est.	p-value
Mean lowland	74	0.25	0.24	constant	5.46	<0.0001
				PPT year t + Jan.–Jul. year t + 1	−0.0027	<0.0001
Mean upland	62	0.31	0.29	constant	−2.79	0.0167
				T Oct. + Nov.	0.01	0.0261
				PPT Dec.–Mar.	0.004	<0.0001

PPT year t + jan.-jul. year t + 1: precipitation from January of the year t to July of the year t + 1, T Oct. + Nov., temperature of October and November, PPT Dec.–Mar., rainfall from December to March.
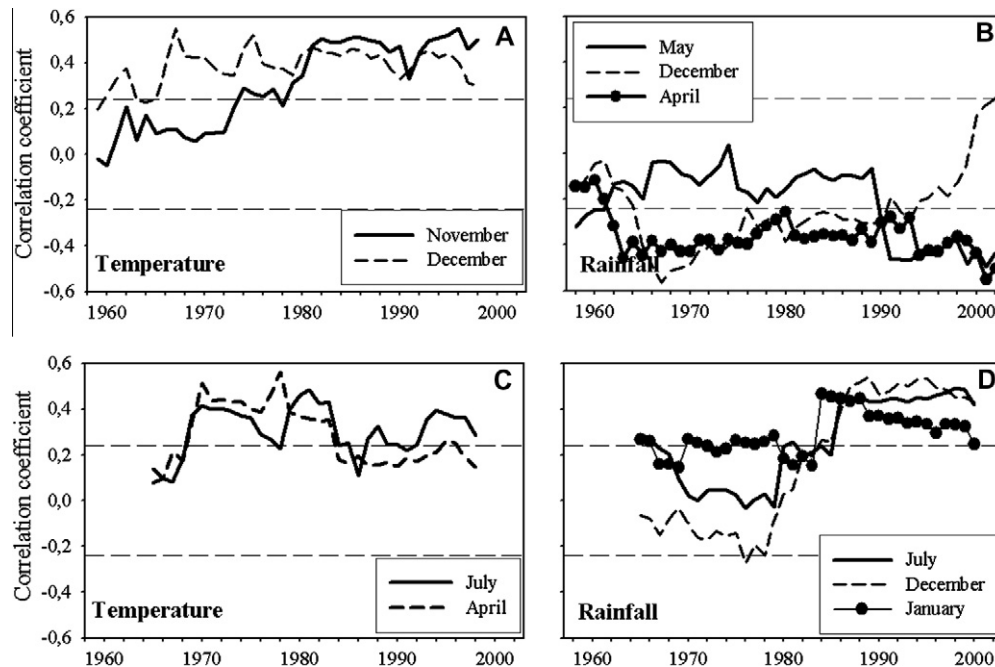
Fig. 6. Climate-growth association through time using a moving window of 28 years in the lowland (upper plots, A and B) and upland (lower plots, C and D). Only months showing significant association with radial growth ($p < 0.05$) are presented. Dashed lines show significant coefficients at $p < 0.05$.

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