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Pruning effects on ring width and wood hydrosystem of *Prosopis flexuosa* DC from arid woodlands

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ABSTRACT

Pruning is a silvicultural practice that could potentially improve the productivity in arid land woodlans. However, there is not enough information about the influence of this practice on the tree-ring wood anatomy of desert *Prosopis* woodlands. We analyzed the effect of pruning trees of different diameter class (small and large, PDDC) and pruning intensity in small trees (heavy and intermediate, PDI). We evaluated tree-ring width, number of vessels, total vessel area, mean vessel size (total vessel area/number of vessels), vessel density (number of vessels/tree-ring area) and ratio of vessel area to tree-ring area in *Prosopis flexuosa*, a species widely used for firewood and poles in arid and semiarid areas of South America. For PDDC, trees were pruned during the winter of 2003, for which we focused on the period between 1995 and 2010 (8 years before and after pruning, respectively) and for PDI, trees were pruned during the winter of 2004, and we focused on the period between 1997 and 2010 (7 years before and after pruning, respectively). The data was analysed using Mixed Models. We observed that, small trees had a greater response to pruning than large individuals. In this sense, pruning increased radial growth ($F_{2,247} = 6.08$, $p \leq 0.01$) and number of vessels ($F_{2,247} = 6.36$, $p \leq 0.01$), and decreased the mean vessel size ($F_{2,247} = 6.91$, $p \leq 0.001$) and ratio of vessel area to tree-ring area ($F_{2,247} = 4.84$, $p \leq 0.01$) in small trees. Moreover, the response depended on pruning intensity, which was more evident in intermediate pruning. The increase in the vessel number and the decrease in mean vessel size observed in small trees denoted that pruning induces the generation of new, small-diameter vessels. This is considered a strategy to protect the water-conducting system in response to pruning. Studies at the anatomical level conducted in the present research revealed in detail how pruning influences wood production and anatomical modifications, indicating the importance of conducting wood anatomical analyses on tree rings in order to refine interpretations of the effect of pruning on stem growth.

1. Introduction

Pruning is one of the most used silvicultural practices for management of *Prosopis* woodlands in different parts of the world (Patch et al., 1998). Through the removal of selected stems and branches, pruning may improve tree growth, increasing both quantity and quality of wood (Elfadl and Luukkanen, 2003). The effect of pruning has been studied mostly in plantations, under controlled environmental conditions (Elfadl, 1997; Patch and Felker, 1997a,b), reflecting the orientation of these studies towards purely productive purposes. Therefore, knowledge of the pruning effect on natural forests under severe risk of water shortage, is presently scarce (Patch et al., 1998; Alvarez et al., 2013). Most studies that address the effect of pruning on the growth of woody species are based on measurements on the plant's external morphology, while the effect of pruning at the wood anatomy level has been hardly considered (DeBell et al., 2002; Sun et al., 2006; Namirembe et al., 2009). In this sense, there is not enough information on how this practice may influence changes in the wood anatomy.

Physical actions on trees induce changes in wood anatomy (Schweingruber, 2007). These changes provide information about the plasticity of trees facing changing environmental conditions

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or growth disturbances (Baas et al., 2004; Chave et al., 2009). An anatomical trait linked to these changes is the hydraulic conducting system or hydrosystem (conduction vessel elements). The importance of the wood hydrosystem in the efficiency of water transport has been recognized in pioneer studies on functional anatomy (Zimmerman, 1983). Different features related to wood porosity, such as vessel arrangement, frequency per unit area, vessel length and lumen size, cell wall thickness and other anatomical features, are relevant in establishing the degree of conducting efficiency and safety of the wood hydrosystem (Zimmermann, 1983; Carlquist, 1988). Moreover, vessel dimorphism has been recognized as a strategy to avoid cavitation processes during severe drought episodes (Carlquist, 1975; Pockman and Sperry, 2000). The partial removal of biomass in a plant, which is produced by pruning, may induce changes in the hydrosystem. This is caused by modifications to the photosynthetic capacity, stomatal conductance and competition among branches (Elfadl and Luukkanen, 2003).

The genus Prosopis is an important source of food and habitat for many organisms, playing an essential ecological role in arid and semiarid regions (Villagra et al., 2010). *Prosopis* is considered a multi-purpose tree as it provides timber, firewood and other non-timber products such as gum, tannins and food for man. In west-central Argentina, *Prosopis* woodlands are remains of extensive forests, diminished by past excessive logging and other inappropriate management practices. Most of the trees found in these woodlands are multi-stemmed, limiting their forestry potential. Therefore, pruning was considered as an alternative to improve productivity of these woodlands. Alvarez et al. (2013) found an increment in crown growth after pruning, however they observed a weaker response in basal diameter. Besides, the response varied when comparing trees of different sizes and when the intensity of pruning varied. However, there are no studies on the anatomical effect of pruning, despite its relevance in the understanding of how it might affect wood features and, the consequences it might have on the hydrological function of *Prosopis* trees. We hypothesized that changes produced by pruning in the crown-stem hydrosystem relationship, modify the anatomy of the wood. Therefore, we expect to find differences in the anatomical variables between pruned and control trees, and that these responses differ among tree size and pruning intensities. The objective of this study were to determine the effect of pruning trees of different diameter classes (small and large) and the effect of pruning intensity in small trees (heavy and intermediate) on anatomical features related to tree-ring width and wood hydrosystem in *Prosopis flexuosa* trees.

2. Materials and methods

2.1. Study site

The study site is located in the northeast of Mendoza, Argentina (Telteca Reserve, 32°–33°S, 67°–68°W; 500–550 m elevation) where climate is arid with 155 mm/year mean rainfall distributed between spring and summer. Mean annual temperature is around 18 °C, with wide daily and seasonal thermal amplitude, reaching a summer maximum of 40–42 °C (mean of 27 °C) and winter minimum of up to −10 °C (mean of 9.3 °C). Hot and dry Föhn winds produce episodes of strong evapotranspiration throughout the year. The woodlands are located on a landscape composed of fine inorganic Quaternary floodplains in which sediments are transported by rivers from the Andes (Regairaz, 2000). Large areas of aeolian sand ridges produced during the Holocene comprise a system of transverse sand dunes up to 20 m high. A major aquifer lies between 5 and 15 m below the surface and is recharged by streams from the Andes (Aranibar et al., 2011; Jobbágy et al., 2011). Biogeographically, the area comprises the central Monte desert, where vegetation consists of a shrub-steppe community intermingled with halophyte communities and open woodlands of *P. flexuosa* (Rundel et al., 2007).

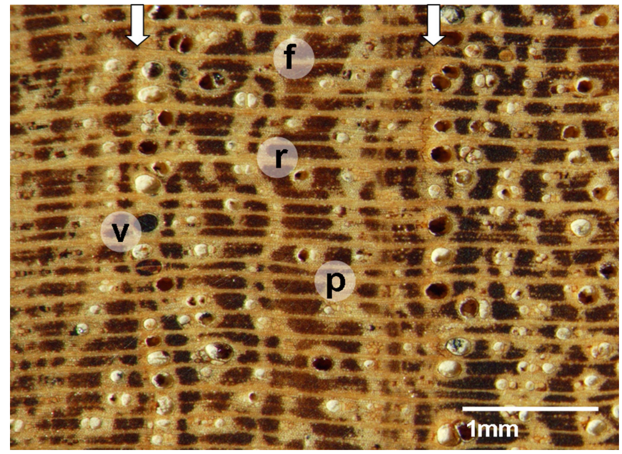

Fig. 1. Transverse section of *P. flexuosa* wood. The vertical arrows indicate the growth ring boundary due to the presence of larger diameter vessels at the beginning of earlywood and a band of terminal parenchyma. f: fiber, r: radius, v: vessels, p: parenchyma. The scale is indicated by the bar.

2.2. Wood anatomy of P. flexuosa

The *P. flexuosa* wood is semi-ring to diffuse-porous (Fig. 1). The earlywood vessels are usually solitary and larger. The axial parenchyma is abundant and almost exclusively vasicentric, occasionally confluent. The ring boundary is recognized through comparisons of vessel size between two contiguous rings and the presence of a marginal and continuous parenchyma thin layer. In some cases the ring delimitation is vague due to a very gradual transition between the anatomical characteristics of two contiguous rings (Giantomasi et al., 2009).

2.3. Experimental design

We used trees pruned during two experiments conducted by Alvarez et al. (2013). They evaluated the effect of pruning on individuals of different diameter classes (PDDC) and the effect of pruning intensity in small trees (PDI) on *P. flexuosa* trees.

For the PDDC experiment, two types of multi-stemmed *P. flexuosa* trees were selected in three different sites according to basal diameter of the main stem. Individuals with a basal diameter between 7.5 and 15 cm were called "large trees", while those with a basal diameter between 3 and 7.5 cm were called "small trees". In July 2003, individuals with similar growth habits: 24 large trees (12 control and 12 pruned trees) and 30 small trees (18 control and 12 pruned trees) were considered. In pruned trees, only one stem was left, removing approximately 50–70% of the crown (heavy pruning). Pruning was carried out during the dormancy phenophase using a chainsaw or a handsaw.

For PDI, in 2004, 30 small trees were selected in a new site different than the sites of previous experiment. Ten of these trees were pruned, leaving the main stem and lateral branches, thus removing approximately 50% of the crown (heavy pruning); the lateral branches were removed from another 10 trees, representing 25% of the crown (intermediate pruning) and the remaining 10 trees were used as control (no pruning). In the same way as for PDDC, pruning was carried out using cutting tools during dormancy. For further details, reference can be made to Alvarez et al. (2013).

Table 1
Analysis of variance table (type I) with Kenward-Roger approximation for degrees of freedom, for pruning of trees of different diameter classes (PDDC) and pruning of different intensities in small trees (PDI).

	Ring width				No.v				va				mvs				vd				ratio va			
	Ndf	Ddf	*F*	*p*	Ndf	Ddf	*F*	*p*	Ndf	Ddf	*F*	*p*	Ndf	Ddf	*F*	*p*	Ndf	Ddf	*F*	*p*	Ndf	Ddf	*F*	*p*
PDDC																								
Large trees																								
Tr.	1	121	1.32	0.25	1	124	0.12	0.72	1	121	1.08	0.30	1	118	0.01	0.93	1	121	1.39	0.23	1	118	0.92	0.33
BA	1	14	7.51	0.02*	1	14	4.37	0.06	1	14	7.28	0.02*	1	14	2.14	0.16	1	14	0.30	0.58	1	14	1.28	0.27
BA*Tr.	1	133	0.45	0.50	1	133	0.03	0.86	1	133	0.73	0.39	1	132	2.79	0.10	1	134	1.64	0.20	1	130	5.75	0.02*
Small trees																								
Tr.	1	177	0.97	0.32	1	176	1.59	0.21	1	179	0.00	0.98	1	172	0.09	0.76	1	176	0.22	0.63	1	178	4.15	0.04*
BA	1	14	1.72	0.21	1	14	0.47	0.50	1	14	0.11	0.75	1	14	0.02	0.90	1	14	2.96	0.11	1	14	4.45	0.06
BA*Tr.	1	210	2.48	0.11	1	207	8.53	0.00**	1	210	4.15	0.04*	1	212	1.06	0.30	1	211	1.06	0.30	1	210	0.01	0.91
PDI																								
Tr.	2	126	3.32	0.04*	2	127	4.75	0.01**	2	128	4.53	0.01**	2	126	1.02	0.36	2	99	1.21	0.30	2	126	1.39	0.25
BA	1	12	6.36	0.03*	1	12	2.31	0.15	1	12	1.05	0.32	1	12	6.43	0.03*	1	12	0.05	0.82	1	12	29.6	0.00***
BA*Tr.	2	247	6.08	0.00**	2	247	6.36	0.00**	2	247	1.09	0.33	2	247	6.91	0.00***	2	110	0.42	0.65	2	247	4.84	0.01**

No.v: number of vessels, va: vessel area, mvs: mean vessel size, vd: vessel density, ratio va: ratio vessel area. Tr.: Treatment, BA: period Before-After. Ndf: numerator degrees of freedom, Ddf: denominator degrees of freedom.

* $P \leq 0.05$.
** $P \leq 0.01$.
*** $P \leq 0.001$.

2.4. Wood sample collection and analysis

With the aim to compare the anatomical response of wood to pruning in trees of different diameter classes (PDDC) and the response of small trees to different pruning intensities (PDI), in 2011 we sampled the trees pruned by Alvarez et al. (2013). In October (austral spring), we took radial wood samples from all of the previously mentioned trees using an increment borer fitted to a mechanical drill. The use of this instrument was necessary because of the high density of the wood of *P. flexuosa* (0.73 g/cm^3, Iglesias and Barchuk, 2010). Once in the laboratory, the samples were mounted on wood holders, dried, polished and dated under a magnifying glass, following the technique proposed by Stokes and Smiley (1968). A calendar year was assigned to each growth ring taking as a dating reference the last ring formed at the time of sampling (Schulman, 1956). Samples were photographed with a digital camera (Olympus, DP12 Microscope Digital Camera System) mounted on a magnifying stereo microscope (Olympus SZX7) with 10×3.2 magnification. Photographs were taken in TIFF format and the measured window was fixed at a surface of 429 pixels high x 572 pixels wide. Tree-ring width was measured using the IPWin4 Image Analysis software (v4.5, Media Cybernetics, USA), with a precision of 0.001 mm. Measurement and analysis of the transverse area occupied by vessels in the growth ring were performed with the PC-Image program-Scion Corporation (Giantomasi et al., 2009, 2013). To determine the extent of how pruning affects the anatomical features of *P. flexuosa* wood, tree-ring width, number of vessels, total vessel area, mean vessel size (total vessel area/number of vessels), vessel density (number of vessels/tree-ring area) and ratio of total vessel area to tree-ring area were measured over the period 1995–2010 for PDDC (8 years before and 8 years after pruning done in 2003) and during the period 1997–2010 for PDI (7 years before and 7 years after pruning done in 2004).

2.5. Data analysis

Statistical analysis was conducted using Linear Mixed Models and Generalized Linear Mixed Models, implemented in the 'lme4' package (Bates et al., 2014) and by running it in the R environment (v.3.2.0, R Core Team, 2015). Models were built for each measured variable with two main factors: "Treatment" and "Period" and their interaction as fixed effects. "Treatment" varied according to PDDC (Pruned or control trees) or PDI (50–70%, 25% pruned trees or control trees) experiments, while Period (before–after pruning) was a dummy variable that distinguished the years before and after the pruning event. We were mainly interested in the interaction between these factors, since their significance is indicative of a differential response of one treatment to the pruning event. In order to estimate the significance of these interactions, likelihood ratio tests (LRT) were performed, comparing models with and without the interaction (i.e., nested models). In addition, we used the 'lmerTest' package (Kuznetsova et al., 2015) to estimate the *p* values of the main factors and their interactions in a more traditional way. Random effects, "Year", "Tree", and the interaction "Year*Tree", were used in the models. For the PDDC experiment, which was set with trees from different sites, an additional variable identifying these sites was also used as a random effect.

3. Results

3.1. Pruning effects on trees of different diameter classes (PDDC)

The ratio of vessel area to tree ring area showed a significant interaction ($F_{1,130} = 5.75$, $p = 0.02$) between treatment and period in large trees (Table 1). This variable decreased in pruned trees in the period after pruning (Figs. 2 and 3). In small trees, the number of vessel ($F_{1,207} = 8.53$, $p \leq 0.01$) and the total vessel area ($F_{1,210} = 4.15$, $p = 0.04$) showed a significant interaction between treatment and period. Both variables demonstrated an increase during the same period, especially in the number of vessels (Figs. 2 and 3). In small trees, the year 2007 presented the highest peak of these anatomical features and the maximum difference between treatments (Fig. 2). Although non-significant, the same trend was observed for tree-ring widths (Fig. 2).

With respect to random effects, the tree variable was important in the variance component in all wood anatomical variables measured, ranging from 8 to 34% (Table 2). This indicates that there is a high variability in individual response to treatments. Site, which varied according to tree type, was also important, however, only for some of the wood anatomical variables assessed (Table 2).

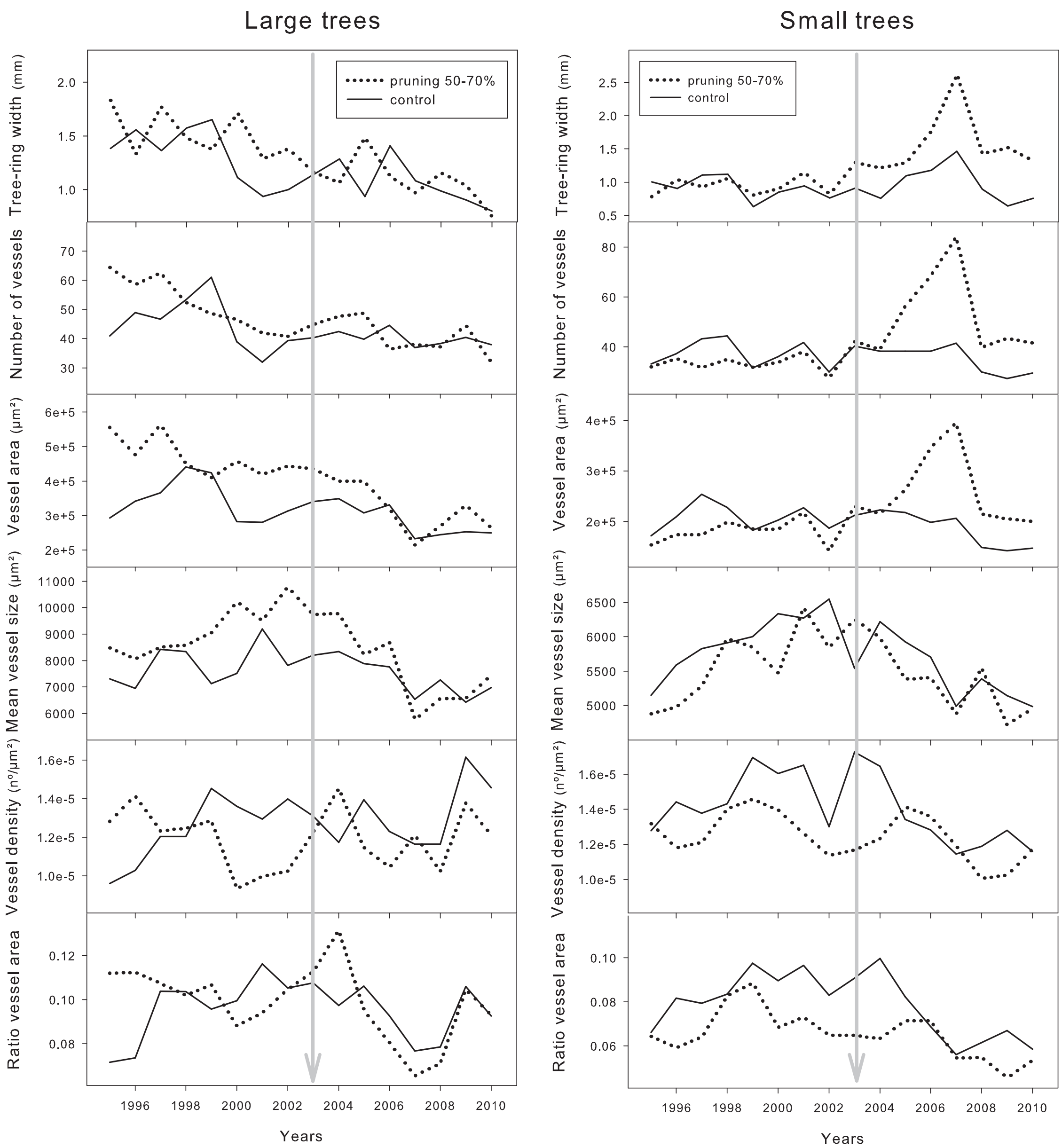

Fig. 2. Inter-annual variability in tree-ring width, number of vessels, vessel area, mean vessel size, vessel density and ratio of vessel area to tree-ring area over the period 1995–2010, for large and small trees (PDDC). Dotted lines represent the average pruned individuals and solid lines represent control trees. The gray arrow indicates year of pruning, i.e. 2003.

3.2. *Effects of pruning intensity on small trees (PDI)*

Tree-ring width ($F_{2,247}=6.08$, $p\leq0.01$), number of vessels ($F_{2,247}=6.36$, $p\leq0.01$), mean vessel size ($F_{2,247}=6.91$, $p\leq0.001$) and ratio of vessel area to tree-ring area ($F_{2,247}=4.84$, $p\leq0.01$) showed a significant interaction between Treatment and Period (Table 1). Individuals subjected to both pruning intensities exhibited higher tree-ring width and number of vessels than control trees (Figs. 4 and 5), which was more evident in trees under intermediate pruning (25%, Fig. 5). Heavily pruned individuals showed the highest increase in tree-ring width and number of vessels in 2007 (Fig. 4). In contrast, pruned individuals had a lower mean vessel size and ratio of vessel area to tree-ring area than control trees (Figs. 4 and 5), which was more evident under intermediate pruning (25%, Fig. 5).

With respect to random effects, the tree variable was important in the variance component in all wood anatomical variables measured (Table 2). However, the interaction between tree and year in vessel density accounted for 91% of the random effects variance (Table 2).

4. Discussion

Studies at the anatomical level conducted in the present research revealed in detail how pruning influences wood production and anatomical modifications, indicating the importance of conducting wood anatomical analysis on tree rings to refine interpretations of the effect of pruning on stem growth. Small trees had a greater response to pruning than large individuals. Pruning increased radial growth and number of vessels (thus, larger hydrosystem surface), and decreased the mean vessel lumen and the ratio of vessel area to tree-ring area of *P. flexuosa* trees at its young stage. Moreover, the response depends on pruning intensity, which is more evident in intermediate pruning (25%). A similar response for the effect of pruning on tree-ring width was obtained

Table 2
Model inferences for wood anatomy variables measured for *P. flexuosa*, for pruning of trees of different diameter classes (PDDC) and pruning of different intensities in small trees (PDI).

	PDDC – Large trees							PDDC – Small trees					PDI						
	Fixed effects	df	AIC	LRT	BM[1]	Random effects	Var.%	AIC	LRT	BM[1]	Random effects	Var.%	Fixed effects	df	AIC	LRT	BM[1]	Random effects	Var. %
Ring width	T + P + T*P	9	607.7	$\chi^2=0.45$ df = 1 $p=0.49$		Tr	18	804.6	$\chi^2=2.48$ df = 1 $p=0.11$		Tr	15.1	T + P + T*P	10	950.4	$\chi^2=12.1$ df = 2 $p=0.002$	3.4	Tr	34
	T + P	8	606.2			Y	2	805.1			Y	7.2	T+P	8	958.6			Y	11
	T	7	610.7			Tr*Y	0	804.8			Tr*Y	0	T	7	962.3			Tr*Y	0
	P	7	605.5		1	S	3	804.1			S	6.3	P	6	960.3			Res.	55
						Res.	77	803.8		X	Res.	71.3							
No.v	T + P + T*P	8	2987.1	$\chi^2=0.06$ df = 1 $p=0.80$		Tr	22	3834.8	$\chi^2=81.07$ df = 1 $p<0.001$	2.3	Tr	8.2	T + P + T*P	9	3589.2	$\chi^2=163.6$ df = 2 $p<0.001$	5.8	Tr	51
	T + P	7	2985.2			Y	20	3913.9			Y	9.6	T + P	7	3748.8			Y	9
	T	6	2986.5			Tr*Y	58	3912.4			Tr*Y	65.5	T	6	3748.3			Tr*Y	40
	P	6	2983.6			S	0	3925.4			S	16.5	P	6	3912.3			Res.	–
	~1	5	2984.9		X	Res.	–				Res.	–							
va	T + P + T*P	9	6915.7	$\chi^2=0.73$ df = 1 $p=0.39$		Tr	29	9836.5	$\chi^2=4.15$ df = 1 $p=0.04$	2.4	Tr	22	T + P + T*P	9	3589.2	$\chi^2=2.21$ df = 2 $p=0.32$		Tr	39
	T + P	8	6914.4			Y	10	9838.6			Y	17	T + P	7	3748.8			Y	7
	T	7	6918.8			Tr*Y	0	9836.7			Tr*Y	0	T	6	3748.3		X	Tr*Y	0
	P	7	6913.5		1	S	4	9836.6			S	0	P	6	3912.3			Res.	54
						Res.	57				Res.	61							
mvs	T + P + T*P	9	4717.6	$\chi^2=2.81$ df = 1 $p=0.09$		Tr	34	11397	$\chi^2=1.09$ df = 1 $p=0.29$		Tr	8	T + P + T*P	10	5766.3	$\chi^2=13.7$ df = 2 $p=0.001$	3.4	Tr	35
	T+P	8	4718.4			Y	12	11396			Y	0	T+P	8	5776.1			Y	3
	T	7	4718.5			Tr*Y	10	11394			Tr*Y	0	T	7	5779.9			Tr*Y	0
	P	7	4716.4			S	0	11394			S	0	P	6	5773.8			Res.	62
	~1	6	4716.5		X	Res.	43	11392		X	Res.	92							
vd	T + P + T*P	9	−5618	$\chi^2=1.66$ df = 1 $p=0.19$		Tr	23	−8132	$\chi^2=1.06$ df = 1 $p=0.30$		Tr	33	T + P + T*P	10	−3445	$\chi^2=0.89$ df = 2 $p=0.64$		Tr	0
	T+P	8	−5618			Y	0	−8132			Y	11	T + P	8	−3448			Y	0
	T	7	−5620			Tr*Y	0	−8132			Tr*Y	0	T	7	−3450			Tr*Y	91
	P	7	−5618			S	27	−8134			S	0	P	6	−3449			Res.	9
	~1	6	−5620		X	Res.	50	−8133		X	Res.	56	~1	5	−3451		X		
Ratio va	T + P + T*P	9	−972.1	$\chi^2=5.71$ df = 1 $p=0.01$	2.6	Tr	19	−1486	$\chi^2=0.01$ df = 1 $p=0.90$		Tr	25	T + P + T*P	10	−1186	$\chi^2=9.73$ df = 2 $p=0.007$	3.4	Tr	37
	T + P	8	−968.3			Y	6	−1488		1	Y	15	T+P	8	−1178			Y	1
	T	7	−969.1			Tr*Y	15	−1485			Tr*Y	0	T	7	−1160			Tr*Y	0
	P	7	−969.4			S	26	−1485			S	0	P	6	−1178			Res.	62
						Res.	34				Res.	60							

No.v: number of vessels, va: vessel area, mvs: mean vessel size, vd: vessel density, ratio va: ratio vessel area. Fixed effects: (T) Treatment, (P) Period, (T*P) interaction between treatment and period; df: degree of freedom; AIC: Akaike information criterion; LRT: Likelyhood ratio test between nested models with and withoutinteraction term. [1] Best model selected according to AIC are indicated by an X (when there is only one or none variables in the fixed factor part of the model) or by a VIF (variance inflation factor) value; Random effects: (Tr) Tree, (Y) Year, (Tr*Y) interaction between Tree and Year, (S) Site, (Res.) Residual variance.

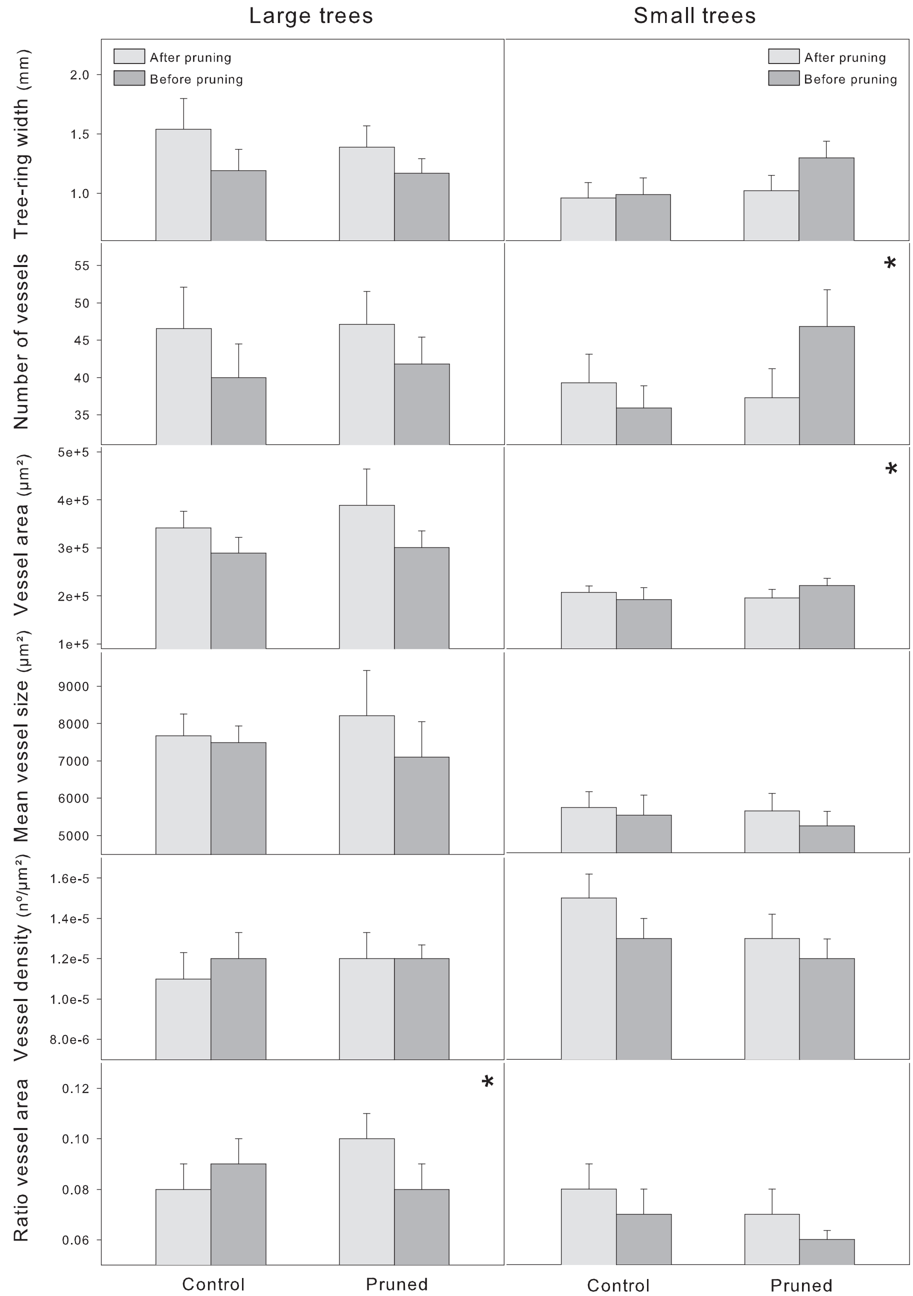

Fig. 3. Pruning effects on trees of different diameter classes (large and small) on wood anatomical variables measured. The bars represent de mean values for control trees and pruned trees before pruning (period 1995–2002) and after pruning (period 2003–2010). Lines indicate the standard error. Asterisks indicated significant interactions between Period (BA) and Treatment (Tr.), see Table 1.

by DeBell et al. (2002), who reported no effect on the ring width of heavily pruned young *Populus* clones growing in an intensively cultured plantation.

There are very few studies dealing with the effect of pruning on tree-ring width. Studies on the pruning effect on wood radial growth are largely based on basal diameter measurements. Elfadl and Luukkanen (2003) studied the effects of pruning on biomass growth in *Prosopis juliflora* seedlings, observing a linear increase in their growth when increasing pruning intensity, unlike in young control trees, after 1, 2 and 3 years of pruning. In a previous study on the same trees considered in this research, Alvarez et al. (2013) recorded no initial response to pruning, neither in the increase of the stem diameter nor in the plant height. It was only after the fifth year following the pruning that these authors found a tendency toward diameter increments in large plants, in contrast with the increase in tree-ring widths of small individuals observed in the present study (anatomical analysis). In addition, large trees showed a higher crown response, indicating that the photosynthetic area could limit stem growth. Therefore, these authors suggest that, at this first stage, pruning could improve the shape of *P. flexuosa* trees, although it would not largely affect an increase in wood production. The differences found between the previous study and the results of this new analysis could be explained by the fact that Alvarez et al. (2013) considered the equivalent diameter instead of the diameter of the main stem. Equivalent diameter integrates in a single value the growth of all stems of a plant. Therefore the integration of the growth of several stems in control trees might have equalized the higher initial growth of the main stem of pruned small trees. Field measurements are useful for the direct quantification and study of growth variables (e.g. the basal diameter), however there are not

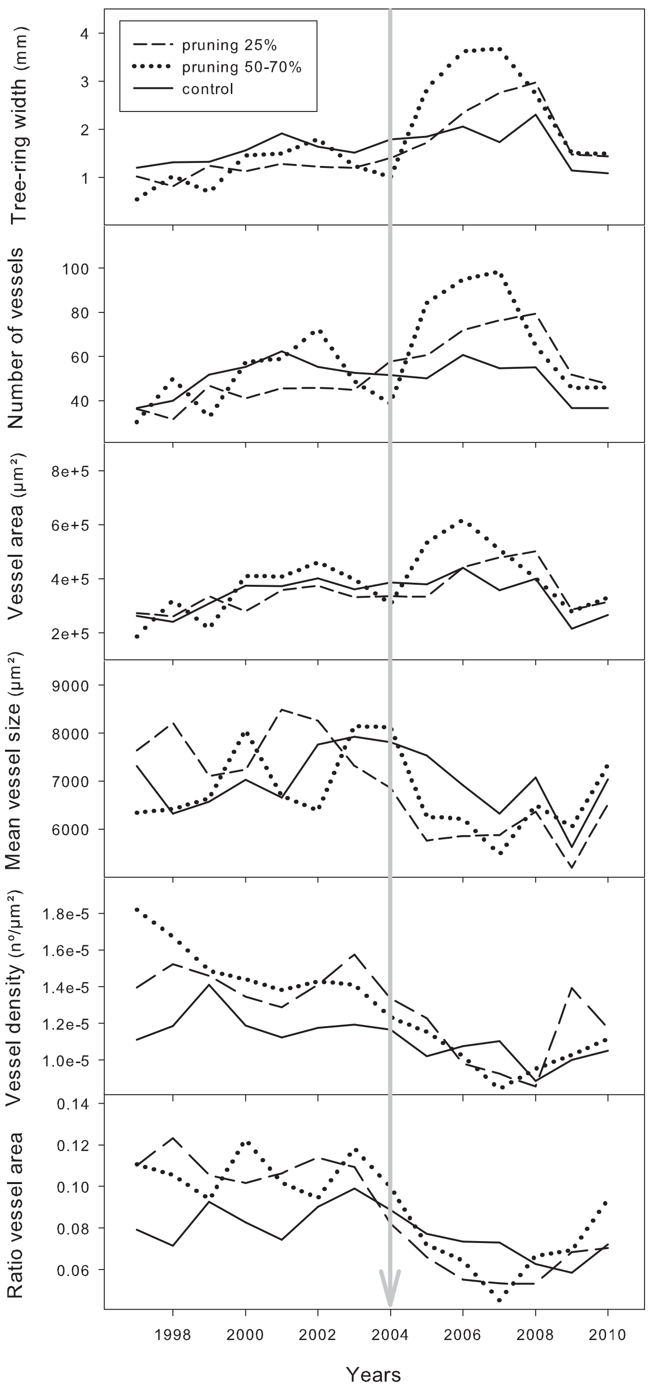

Fig. 4. Inter-annual variability in tree-ring width, number of vessels, vessel area, mean vessel size, vessel density and ratio of vessel area to tree-ring area over the period 1997–2010, for small trees (PDI). Dotted lines indicate average individuals under heavy pruning (50–70%), dashed lines indicate intermediate pruning (25%), and solid lines represent control trees. The gray arrow indicates year of pruning, i.e. 2004.

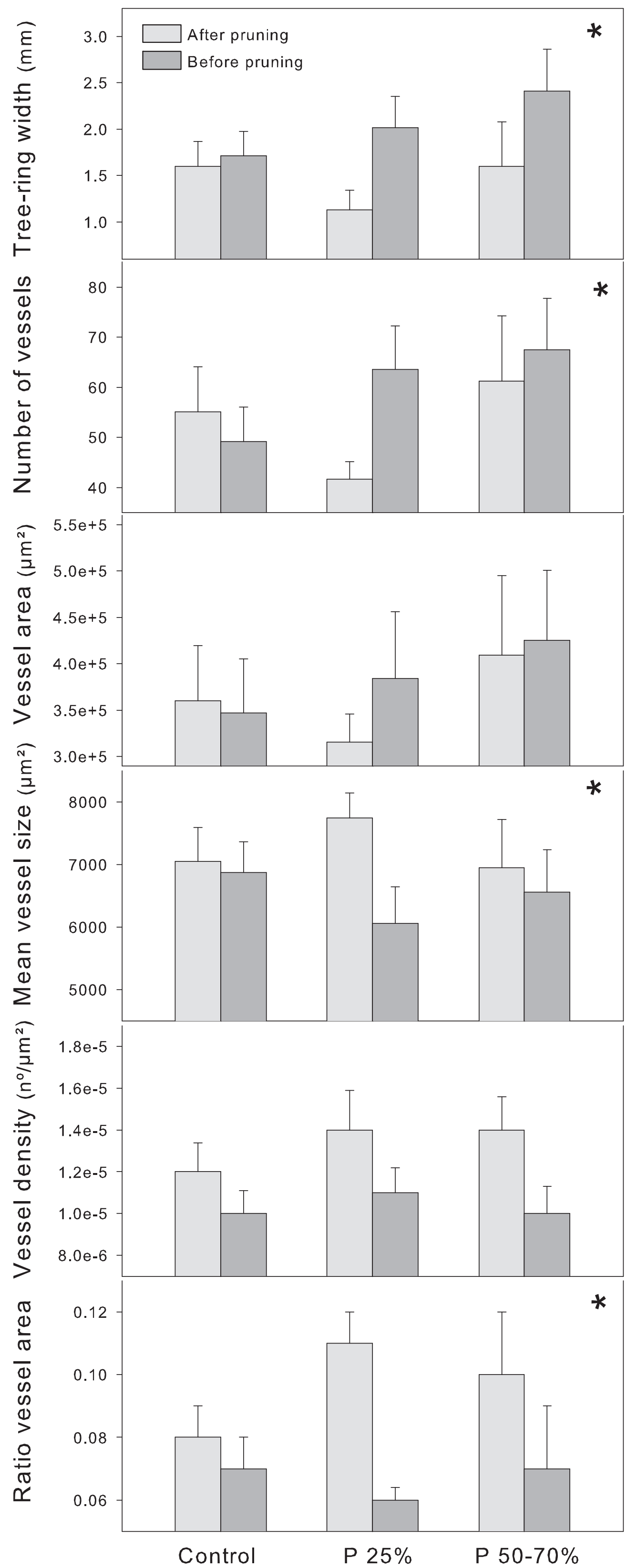

Fig. 5. Effects of different pruning intensities on the growth of small trees. The bars represent the mean values of control trees, trees under intermediate pruning (P 25%) and trees under heavy pruning (P 50–70%) before pruning (period 1997–2003) and after pruning (period 2004–2010). Lines indicate the standard error. Asterisks indicated significant interactions between Period (BA) and Treatment (Tr.), see Table 1.

enough ways to measure small growth increments; demonstrating that an anatomical study such as the one conducted here is quite important. Our results provide a better understanding of the response of the different kinds of trees to pruning, suggesting the initial response in small trees would result from a concentration of assimilates in the remaining stem, whereas large trees would show a longer-term response after recovery of their photosynthetic capacity.

Shoot pruning can potentially reduce the volume of transpired water (Schulze et al., 1985), through manipulation of timing of the maximum leaf area and crown architecture, which in turn affect water conductivity of the wood in stems (Namirembe et al., 2009). Both efficiency and safety in water transport are strongly related to the size and number of wood vessels. Increased vessel diameter enhances efficient water conduction, but may reduce the safety of the wood hydrosystem, since narrow vessels are less likely affected by cavitation processes due to closer surface area-volume relationship (Carlquist, 1988). Arid-climate tree species show strategies in the wood to safe the water-conducting systems by developing numerous vessels with smaller lumen size (Zimmermann and Brown, 1977; Baas, 1986; Fahn et al., 1986; Carlquist, 1988 Fahn et al., 1986). The increase in the vessel number and the decrease in mean vessel size observed in small trees denote that pruning induces the generation of new, small-diameter vessels. This would be a strategy for a safer water-conducting system in response to pruning. In agreement with our results, Namirembe et al. (2009) found that pruning induced the production of narrow xylem vessels with low water conductivity and a tendency toward a larger number of vessels on 4-year-old *Senna spectabilis* trees.

From the results obtained in the present study, we observed that the year 2007 exhibited the maximum amount of peaks and the maximum difference between treatments in terms of tree-ring width, vessel number and area in pruned small trees, with respect to control and large trees. It is worth noting that 280 mm of rain fell during 2007, 4 times the average rainfall for the 5 previous years (average rainfall for the period 2002–2006 was 61.5 mm, data from El Pichón weather station, 32° 23′S, 68° 03′W, 556 m elevation). This fact suggests that the effect of pruning would be even more evident in years when water availability is higher. The response found in small trees, alternatively, might be related to the root architecture of *P. flexuosa*, which presents a structure modulated by the geomorphology, nutrient availability and water supply (Guevara et al., 2010). *P. flexuosa* has a deep root system that allows trees to access the water table, thereby regulating the water supply; this provides some relative independence from the sporadic precipitation pulses that are typical in these arid regions (Noy Meir, 1973; Jobbágy et al., 2011). Therefore, adult trees with more developed root system in depth would be uncoupled from rainfall events. On the other hand, younger trees with a much shallower root system would depend more on precipitation events and show a greater response to them.

Aforementioned, Alvarez et al. (2013) found an increment in crown growth after pruning but a weaker response in basal diameter. Furthermore, a different response was observed among the size of trees and among the intensity of pruning. However, there are no studies on the anatomical effect of pruning, despite its relevance in understanding the effect on the wood features and, its consequences on the hydrological function of the *Prosopis* trees. We know that in arid lands, and particularly in the Central Monte, most of the trees of these woodlands are multi-stemmed and with low woody growth. These features account for the low value of forest product and, consequently, a low potential for wood production (Alvarez et al., 2011). The importance of these woodlands lies in the direct benefit to desert families through a variety of wood and non-wood products. The main woody product in the Monte desert is firewood, with a low prize in the market (U$S 0.31 kg^{-1}). Pruning appears to be a tool to improve the productivity of these woodlands and the price of the obtained products. For example, if pruning improved the quality of wood from multi-stemmed trees, transforming firewood into poles, the price of the products would increase to U$S 0.48 kg^{-1}. In the first stage after pruning, several studies observed that pruning reduces stem growth (Takiya et al., 2010; Chandrashekara, 2007). However, in this work we confirmed that, at least in small trees, pruning increase the growth of the main stem. Besides, we did not find any evidence of a considerable change in the quality of the wood. We found a reduction in proportion of vessel area in the wood, suggesting no reduction on wood density. We suggest further studies on the effects of pruning on wood quality to gain a better understanding.

In conclusion, the measurement of wood anatomical features allowed us to determine the extent to which pruning improves the growth of *P. flexuosa* at early stages of growth. This silvicultural tool increased the radial growth in small trees and the wood hydrosystem safety in this multi-purpose tree widely used for firewood and poles in arid and semiarid regions of South America.

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