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Sandra	Bravo ^{a,*} , Carlos Ku	ınst ^b , Ricardo Graı	1 ^c	
				lel Estero, Avdnida Belgrano 1912 (S),
CP4200 Sar	ntiago del Estero, Argentina acional de Tecnología Agrope			- · · · ·
	o de Investigaciones Ecológico			
Received 1	August 2006; accepted 10 M	ay 2007		
Abstract				
				as in South America and fire plays a
evaluated	their suitability for fire	dendroecological stud	ies. The selected s	native woody species of Chaco and species were "quebracho colorado
"algarrobc	blanco" (Prosopis alba	Griseb), "algarrobo neg	ro" (Prosopis nigra	osperma quebracho-blanco Schlecht), (Griseb.) Hieron), "tusca" (Acacia
different lo	ocations in the Province o	f Santiago del Estero, A	rgentina. A selection	Sampling sites were spread across n was made of individual trees with
				tree at heights of 0.3 and 1.3 m from of damaged bole perimeter and the
				was based on longevity, patterns of ire event. Two types of wound were
				<i>b-blanco, P. alba</i> and <i>P. nigra</i> are the evelopment enable them to survive in
			-	g demarcation and therefore provide otibility to fire damage of the Acacia
species, the	ey are suitable for dendro	ecological studies that re	equire analysis over	a few decades in environments with means that they can be used for
dendroeco			-	is and the phytogeography provinces
	iblished by Elsevier Gmbl	Н.		
Keywords: 2	Aspidosperma; Chaco; Dendr	oecology; Fire; Schinopsis		
			Introduction	

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55 1125-7865/\$ - see front matter © 2008 Published by Elsevier GmbH. doi:10.1016/j.dendro.2007.05.004 Fire is a major factor modelling landscape of most biomes where it affects the vegetative and animal community dynamics, and different components of

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ecosystems functioning (Hungerford et al., 1991; Dansereau and Bergeron, 1993; Taylor, 1993; Skinner et al.,

3 Q2 1996; Pausas et al., 2004). Tropical and subtropical dry forests and savannas are among the ecosystems more
5 influenced by fire (Hueck, 1978, Cutter and Guyette, 1994; Kunst et al., 2003; Boletta et al., 2006).

7 The Chaco region lies between the counties of Argentina, Paraguay, Bolivia and a small part of Brazil.
9 In Argentina, the Chaco region covers approximately

- 600,000 km² and includes the provinces of Salta, Tucumán, Jujuy, Catamarca, Santiago del Estero, Córdoba, Chaco, Santa Fe and Formosa (Hueck, 1978; de la
- 13 Q3 Balze, 2004). It is the largest continuous dry-forest biome in South America, and the largest extratropical
 15 biome reservoir in the Southern Hemisphere. Fire is assumed to play a major role in Chaco dynamics
- 17 (Martínez Carretero, 1995; Naumann and Madariaga, 2003). In the region, fire is used for brush control,
- grassland maintenance, and land clearing for agriculture expansion (Bordón, 1993; Kunst et al., 2003; Tálamo
- 21 Q4 and Caziani, 2003; Grau et al., 2005). Fire regime alterations caused by climatic or anthro23 pogenic factors have important effects on species survival (Skinner et al., 1996; Swetnam and Baisan,
 25 1996; Grau and Veblen, 2000; Pausas et al., 2004). Dendroecological techniques have contributed to study-
- 27 ing the effects of fire and other disturbances on forest dynamics (Villalba, 1995; Kitzberger et al., 2000;
 29 Medina et al., 2000; Grau et al., 2003). Owing to the importance of fire as disturbance in Chaco region there
 31 is a lack of studies to assess dendroecological potential

of woody native species.

Dendroecological techniques analyse fire scars in species with annual growth rings. Fire scars are identified as discrete marks embedded inside dendro-chronological series allowing fire dating even in dead material. Even when there are no chronologies of growth width rings, the year of the fire event can be pinpointed by counting the rings between the scars in the direction of the bark. Live material must be used for this technique and can be controlled by means of marker years or skeletons plots (Kitzberger et al., 2000).

The objectives of this work were to determine types of lesions generated by fire in the woody native species of the Chaco Region and to evaluate their suitability as material to be used for dendroecological studies of fire regimes.

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51 Materials and methods

53 Study area and species

55 Five sampling sites were established in the Province of Santiago del Estero, located in the Western sector of the



Fig. 1. Localisation of sampling sites of woody native species of the Western Chaco, province of Santiago del Estero, Argentina.

77 Chaco region of Argentina (Fig. 1). This region is characterised by a strongly seasonal climate with a mean precipitation is approximately 550 mm. Rainfall occurs 79 mainly in summer, and the dry season extends from 81 April to October. Mean temperature is 26.9 °C for the hottest month and 12.4 °C for the coldest month. Extreme temperatures range between 42 and 45 °C in 83 summer and -7 and -8 °C in winter (Boletta et al., 2006). In the sites, six species were sampled: Schinopsis 85 lorentzii, Aspidosperma quebracho blanco, Prosopis alba, 87 Prosopis nigra, Acacia aroma and Acacia furcatispina. S. lorentzii and A. quebracho blanco species are the dominant species of the upper stratum of Chaco forests 89 (>12 m height); P. nigra is well represented in the 91 intermediate canopy layer (8-10 m), P. alba is characteristic of river floodplains and moister areas, A. 93 aroma and A. furcatispina are abundant in lower canopy layer (>8 m) (Brassiolo et al., 1993; López de Casenave et al., 1995). The origin samples sites correspond to areas 95 of good conservation state with scarce signals of 97 anthropic activities. At each sampling site, we selected individuals with external fire signs as charred bark or fire scars. Because selected species produce hardwoods. 99 samples consisted on 5 cm wide wedges taken with a chainsaw from bole and branch, at 0.30 and 1.30 m 101 height. The maximum age of sampled species ranged 103 from 41 to 102 years old (Table 1). Several samples were discarded due to rotten or insect galleries that prevented their use, resulting in an uneven number of samples per 105 species.

The surfaces of samples were sanded with a band 107 sander and an orbital manual sander with 100–600 grains until a clear surface was obtained for best 109 observation of wood.

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Table 1. Number of individuals by species, the range of agesand sampling sites, located in province of Santiago del Estero,Argentina

Species	No. of individual samples	Range of ages (years)	Origin
S. lorentzii	6	60–68	1 and 4
A. quebracho-	6	55–74	1
blanco			
P. alba	4	36-102	5 and 2
P. nigra	3	41–52	3 and 2
A. aroma	8	20-41	1
А.	8	22-57	1
furcatispina			

References: 1. Experimental Ranch "La María", belonging to the
 National Institute of Agricultural Technology, Capital Department. 2.
 Coronel Rico, Alberdi Department. 3. Sachayoj, Alberdi Departmant.
 4. Copo Department. 5. Loreto Department.

21 Identification of fire wounds

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The wounds were distinguished from other types of wounds or alterations (attacks, insects or galleries) by consultation with pathologists and use of a guide to the main insect plagues of Argentina (Fiorentino and Diodato de Medina, 1991).

27 Fire marks and scars were classified qualitatively by examining the interruption of growth near the zone of 29 the wound, and quantitatively by examining the percentage of bole perimeter affected by the wound. 31 The quantitative interpretation was based on the findings of other studies on the effect of fire on the 33 survival of woody species (Ryan, 1990; Gill, 1995, Bravo et al., 2001a). The percentage of bole perimeter affected 35 was determined by measuring the angle of lesion with a protractor and projecting the bole perimeter to a 37 circumference of 360°:

³⁹ $PD = (AD/360) \times 100$

where PD is the percentage of damage and AD the angle of the damaged area expressed in degrees. This
methodology provides and estimates the wound magnitude independent of the bole diameter.

45 To maximise the record were dated fires in transverse sections taken at 0.30 and 1.30 m of height from the 47 ground. Wounds assigned to the same calendar year were assumed as originated in the same fire event since 49 fuel accumulation during one growing season is not sufficient to carry a second fire. The fire dating was 51 made by counting growth rings from the lesion towards the direction of the bark so species have annual growth 53 rings. This method was possible because were cut only living individuals (Kitzberger et al., 2000). Growth rings 55 were determined using the technical protocols (Giménez and Moglia, 1994; Bravo et al., 2006) that include

macroscopic and microscopic features of wood and the pattern of growth ring formation of native species of Chaco region.

Statistical analysis

The data of percentage of damage to bole perimeter were tested to analyse normality and homogeneity of variances. It was employed non-parametric Wilcoxon test to determine differences in percentage of damage to bole perimeter between types of wounds when the data did not show a normal distribution. In order to describe variations in percentage of damage to bole perimeter between species and types of wounds, we carried out ANOVA using following model:

 $PD = \mu + \beta_1$ type of lesion $+ \beta_2$ specie + e, j

where PD is the percentage of damage (dependent variable) and μ the general average.

Results

Types of fire damage

Two types of wounds were identified in cross-sections83of the studied species: fire scars and fire marks. The
formation of both types of wounds coincided between85six species. The data regarding damage to bole perimeter
showed a distribution with a positive bias, so most of the
lesions affected less than 20% of bole perimeter. In fire
scars the average percentage of damage was 13.17%
(n = 91, SD = 17.06%), while in fire marks this value
was 4.6% (n = 32, SD = 4.9%; Table 2).83

Fire scars

95 Fire scars were the more severe wounds and caused interruption of wood growth due to the death of cambial 97 cells likely due to carbonisation or high temperatures. The surviving cambium generated compensatory tissue at the edges of the wound contributing to the wound 99 closure. In the field, fire scars showed the typical triangular shape when extending from the bole base, 101 or lenticular shape when there were elevated from the 103 ground level. Cross-sections with fire scars displayed kidney-type shapes of compensatory wood growth near the wound (Figs. 2A and B). The wood formed before 105 the fire action has improved discoloration due to heat transference during the fire event. Discoloured wood 107 was separated from normal wood by the accumulation of dark substances (Fig. 2C). The compartmentalisation 109 of discoloured wood by means of tannin and gum secretion was more notable in samples of S. lorentzii and 111 P. nigra than others species.

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Table 2. Percentage of damage associated with fire scars and fire marks, number of fire wounds at different height and average wounds per individual in the six species of the study

Specie	Damage to bole perimeter (%)							Numb lesions		Number of		Average wounds per individual	
	Scars			Marks			_				marviduar		
	X	Min	Max	SD	Х	Min	Max	SD	0.3 m	1.3 m	Scars	Marks	
Aspidospermaquebracho- blanco	28.3	7	59	21.6	3.7	0.5	10	3.3*	10	9	9	10	3.2
Schinopsis lorentzii	26.9	4	71	25.9	5.5	0.5	22	6.6*	11	14	12	13	4.2
Prosopis alba	6.7	0.5	61	10.7	2.1	0.5	5	1.7	39	15	48	6	7.6
Prosopis nigra	11.9	1	50	13.9	8.3	3	6	7.3	12	11	20	3	13.5
Acacia aroma	21.8	3	49	16.6		Absent			10	10	20	Absent	2.5
Acacia furcatispina	20.3	4	57	14.8		Absent			10	8	18	Absent	2.3

^{*}p < 0.05.

Percentage of damage to the bole perimeter was highly variable among samples of the same specie. This variability was in part due to the presence of small, intermittent lesions within growth rings and other lesions affecting bigger areas of the bole (Table 2).
More severe fire scars caused alterations in bole shape such as ribs, bark tissue surrounding woody tissue, and cracks. Smaller fire scars did not cause these alterations and were fastly closed.

Fire marks

Fire marks were minor wounds identified by dark
zones inside growth rings, which did not interrupt radial
growth (Figs. 2E and F). Fire marks affected a smaller
percentage of bole perimeters than fire scars and
generally looked as isolated dots inside a growth ring.
Structural differences between normal wood and wood
formed adjacent to fire marks produced an abnormal
behaviour of the wood during the drying process
causing separations in the woody layers.

Height of fire cross-sections

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The number of wounds on cross-sections corresponding to 0.30 m high was similar to it found at 1.3 m high (Table 2) with exception of *P. alba*, in which the most of lesions were located in basal sector. Fire marks were the less frequent type of wound in *Prosopis* species and they were absent in *Acacia* species. A low number of fires damaged both cross-sections (0.3 and 1.3 m) of same individual (Table 3).

53 Dendroecological suitability of species

55 The species studied displayed good suitability for dendroecological studies on fire regimes since they all

form annual growth rings (Giménez and Moglia, 1994) and present wounds with features that can clearly be differentiated from damages other than fire (Table 4). The longevity of *A. quebracho*, *S. lorentzii*, *P. alba* and *P. nigra* species implies that can be used for longer time spans than the two *Acacia* species. All the analysed species showed capacity to survive recurrent fires as demonstrated by the presence of more than one lesion on all the trees (Table 2). 57

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The marginal parenchyma delimiting growth rings in 85 species of *Prosopis* and *Acacia* facilitated the fire dating process, which was made by counting growth rings 87 among fire wounds to the bark. In some cross-sections, the strong eccentricity of wood and the presence of 89 lenses made dating more problematic and more measurements needed to be taken in order to increase the 91 reliability of the data. With the only exception of A. furcatispina, it was necessary to identify growth rings 93 with a good delimitation on several radii of crosssections. The compensatory wood growth closing the 95 wound zone increased the number of false rings. One other hand, the radius opposite to fire scars frequently 97 had reduced wood growth, which sometimes produced too narrow rings that were harder to identify. In 99 consequence, the most reliable radii were those perpendicular to the radius centred in fire scar. Demarcation of 101 growth rings by bands of fibres as occurring in A. quebracho blanco and S. lorentzii required more pre-103 paration of the samples (clean process).

S. lorentzii, A. quebracho blanco, P. alba and P. nigra
had medium to very thick barks (0.5–1.5 cm), displayed105fire scars or fire marks, and formed healing tissue to
allow recovery and close the wounds. The shrubby
Acacia species had thin to very thin barks (0.1–0.5 cm),
displayed only fire scars, and showed a reduced capacity
to close them. The wood discoloured by heat during a
fire event showed high susceptibility to pathogen attacks105

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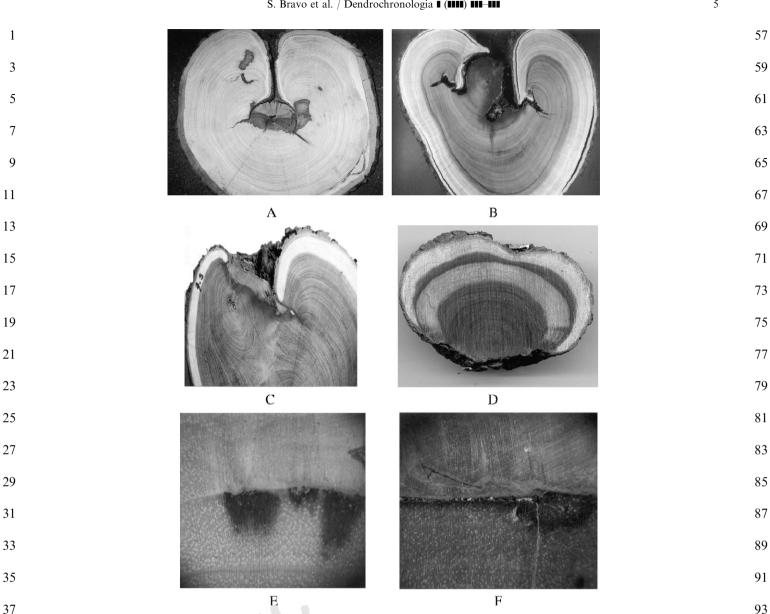


Fig. 2. Wood with fire wounds: (A, B) Fire scars A. A. quebracho-blanco. (B) S. lorentzii. (C, D) Discoloured wood C. P. nigra. D. A. furcatispina. (E, F) Fire marks E. A. quebracho blanco. F. S. lorentzii.

such as fungi or insects and notably reduced the quality of the wood samples (Table 4).

Discussion

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The pattern of scar formation in six studied species 49 agrees with that described for gymnosperms and Q5 angiosperms in response to fire damage (Barret and 51 Arno, 1988; Agge, 1993; Giménez et al., 1997; Kitzberger et al., 2000, Smith and Sutherland, 2001; Giménez, 53 2003). Fire marks have not described in others papers on this subject. Kitzberger et al. (2000) mentioned the 55 importance of both fire scars and fire marks and considered them to be effective tools for dating disturbances in dendrochronological series, nevertheless 97 the differences existing between them were not determined. Gutsell and Johnson (1996), and Smith and 99 Sutherland (2001) described the process of formation of scar without differentiating different types of wounds. 101 The most fire dendroecology research is based exclu-103 sively on fire scars (Guyette and Cutter, 1991; Taylor, 1993; Arno et al., 1995; Swetnam and Baisan, 1996; Medina et al., 2000; Grau et al., 2003). 105

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Since fire marks do not interrupt wood growth, it is possible that they were not included in fire records 107 obtained by dendroecological techniques thus leading to underestimation of fire frequency. Inside environments 109 of the Chaco region fire marks seem to be an important 111 tool to get a complete record of fire.

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 Table 3.
 Dated fires in Prosopis alba, Chaco region,

 Argentina

	_	Tree 1	Tree 2	Tree 3	Tree 4			
	1913				0.3-1.3			
	1917				0.3			
	1947		0.3					
	1948	0.3						
	1952	0.3						
	1956		1.3					
	1961				0.3			
	1963				0.3			
	1965	1.3						
	1968				0.3			
	1969	0.3-1.3						
	1972				0.3			
	1975				0.3-1.3			
	1976	0.3						
	1977				0.3			
	1978	0.3						
	1980		0.3					
	1981	1.3	0.3	0.3	1.3			
	1983				1.3			
;	1985				0.3			
	1987	0.3						
	1990		0.3		1.3			
	1993		0.3	0.3	0.3-1.3			
	1993							
	1994				0.3			
	1995				0.3			
	1996				0.3			

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33 Although the average percentage of damage to bole perimeter was higher in fire scars than in fire marks, the 35 interruption of wood growth was necessary to differentiate the scars from the marks in wounds of smaller 37 magnitude. The formation of scars or marks in tree species characterised by a greater bark thickness would 39 indicate its importance on the type of wound forming during the fire. Considering that bark thickness is 41 thought to be an important influence on the resistance of trees to fire (Ryan, 1990; Cutter and Guyette, 1994; 43 Gill, 1995; Sutherland and Smith, 2000) it is possible that tree scars are caused by severe fires and marks are 45 caused by more minor burns.

A significant difference in the percentage of damage
to bole perimeter between scars and marks in *A. quebracho-blanco* and *S. lorentzii* (Table 2) seems to
support this hypothesis. The absence of fire marks in *Acacia*'s species suggests that thin barks constitute
insufficient protection even for light fires, and therefore all fires are reflected as fire scars. The absence of
significant differences in percentage damage caused fire scars and fire marks in *P. alba* and *P. nigra* can be attributed to the high frequency of small lesions, which

could indicate lower survival rates to more intense fires (Bravo et al., 2001b).

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59 In areas characterised by medium to elevated fire intensity such as the Chaco savannas (Bravo et al., 2001a) using only species with thick bark would likely 61 miss recording low intensity fires, and therefore lead to an underestimation of fire frequency. This problem was 63 observed in other fire chronology in savanna ecosystems (Cutter and Guyette, 1994). On the other hand, shrub 65 species with thin barks are usually very susceptible and die during very intense fires (Gill, 1995; Kunst et al., 67 2000) without leaving signs of disturbance. Our results indicate Chaco forests have a variety of potential 69 recorder species due to the differences in bark thickness allow to capture the diversity of fire occurring in the 71 region.

The similar number of wounds on cross-sections taken at the 0.3 and 1.3 m eight indicate that within this range, sampling is similarly efficient. The fact that wedges at different height capture different fires indicate that the extraction of more than one sample at different heights is recommended to a complete fire record.

The underestimation of fire frequency for a reduced sampling may be accentuated in species with thick barks as observed in *A. quebracho blanco* and *P. alba*. Bravo et al. (2001b) recorded in *P. alba* and *P. nigra* that most fire wounds were located until 2.30 m height and they affected the bole without continuity or orientation. Bravo et al. (2001a) mentioned the presence of fire scars up to 4.3 m in height in *A. quebracho blanco* and *S. lorentzii* in a savanna of Chaco region. In this study, *P. alba* was the only species in which most fires were recorded as wounds at 0.30 m of the ground.

A. quebracho blanco, S. lorentzii, P. alba and P. nigra were found to be the most useful species for fire dendroecological due to their longevity, capacity to survive recurrent fires and the formation of both fire scars or fire marks according to the differing fire intensities (Tables 3 and 4). Longevity is considered an important factor in the study of disturbance regimes (Villalba, 1995; Kitzberger et al., 2000; Grau et al., 2003). Species of *Prosopis* showed the greater number of wounds per individual and the oldest individual among studied species.

The growth ring demarcation by marginal parenchy-
ma bands is a common feature in the *Prosopis* species
(Castro, 1994; Giménez et al., 1998; Morales et al., 2001;
Villagra et al., 2002) and *Acacia* species (Giménez, 1993)
and is more reliable for establishing fire dates. The
growth ring demarcation by fibre bands requires careful
observation and growth rings must be counted along
several bole radii to obtain accurate results.101

The lack of growth ring curves (master chronologies)109for studied species in the Chaco region have prevented111cross-dating fire years up to now. Fire dating by111counting growth rings from the lesions to the bark is111

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Table 4. Characteristics of woody species of Chaco region for fire dendroecology

Species	Distribution area	Longevity	Growth rings demarcation	Thickness bark (cm)	Type of fire wounds	Suitability to cover fire wounds	Difficulties for fire dating
S. lorentzii	Bolivia, Paraguay and Argentina (Distrito Chaqueño Occidental) ^a	250 years ^b	Band of fibres compressed in tangential section ^b	Medium (0.5–1) ^f	Scars and marks	Good	The presence of tannins produces dark fibre bands that delimit ring growth
A. quebracho- blanco	Bolivia, Paraguay, Uruguay y Argentina (Distrito Chaqueño Western and Eastern, Province of Monte and Mesopotámica) ^a	200 years ^c	Band of fibres compressed in tangential section ^c	Very thick $(1-1.5)^{f}$	Scars and marks	Good	Eccentricity and formation of lens
P. alba	Peru, Bolivia, Paraguay and Argentina (Chaco Semiárido and Subhúmedo, North of Espinal and del Monte) ^a	Data not available	Band of marginal parenchyma until 3 cells of thickness ^d	Very thick $(1-1.5 \text{ cm})^{\text{f}}$	Scars and marks	Very good	Occasionally eccentricity of bole
P. nigra	Bolivia, Paraguay, Uruguay and Argentina (Chaco and Espinal) ^a	Data not available	Band of marginal parenchyma of 2 cells of thickness ^d	Very thick (0.9–1.5) ^f	Scars and marks	Very good	Insect attacks and rot of discoloured wood
4. aroma	Peru, Bolivia, Paraguay and Argentina (Western Chaco and Serrano and Provincia del Monte) ^a	50 years ^e	Band of marginal parenchyma 2–3 cells of thickness) ^d	Thin (0.3–0.5) ^f	Scars	Scarce	Heart rot and insect tunnels
4. furcatispina	Paraguay, Bolivia and Argentina (Western Chaco and Serrano and Provincia del Monte) ^a	60 years ^e	Band of marginal parenchyma of 5–8 cells of thickness ^e	Very thin (0.1–0.4) ^f	Scars	Scarce	Occasional heart rot
^e Bravo et al. (998). 1). 1 Moglia (1994).						

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S. Bravo et al. / Dendrochronologia ∎ (■■■) ■■-=■■ considered a reliable method when it is done on live trees at the time of sampling (Kitzberger et al., 2000). The

- reliability of this method allowed to built the first fire 3 chronology in a savanna ecosystem of Chaco, obtaining
- a good coincidence if fire years within a same site and between sites using a set of different woody species in the sampling (Bravo et al., 2001a). The low coincidence of fire years between individuals of P. alba showed in 9
- Table 4, could be related to the sampling of a low number of individuals living in not nearby sites.

11 The capacity of *P. alba* and *P. nigra* to regrow over the fire scar has been reported in previous observations 13 (Giménez et al., 1998; Giménez, 2003). Bravo et al. (2001a) determined that the ability to regrow over fire 15 scars in A. quebracho blanco and S. lorentzii was higher when damage did not affect more 10% of bole 17 perimeter. Therefore a selective sampling of individuals with external signs of fire scars would only register part

19 of the fire spectrum.

The species analysed in this study showed the ability 21 to compartmentalise wood altered by fire by way of secreting products such as tannins and gums and 23 limiting the expansion of wood decay (Bravo et al., 2001b, 2006). The ability to compartmentalise altered 25 wood is considered to be a genetic control factor and varies markedly between species (Rademacher et al., 27 1984; Smith and Sutherland, 2001). P. nigra and A. aroma were the species most affected by pathogen attacks (Bravo et al., 2001b, 2006). 29

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Conclusions

35 Fire causes scars or marks in boles and /or branches 37 of the woody species studied. Fire marks were present in tree species and they are clearly important signals to 39 obtain a complete fire record in Chaco region, but they have not been described in previous studies. Fire dating 41 using native woody species is reliable if live individuals at the time of sampling are used. The six studied species 43 can survive to recurrent fires. Tree species are more suitable to dendroecological studies than shrubby 45 species so they have longer life span and can form scars or marks in response to different fire intensity. The 47 sampling of near individuals within of each site and the extraction of more one sample per individual at different 49 heights is recommended to obtain a complete fire record. The distribution areas of the studied species mean that

they could be used for dendroecological studies of fire 51 regimes in Western, Eastern and Mountain Chaco, and 53 the phytogeography provinces of Monte and Espinal,

and provide a highly valuable tool to study fire regime at 55 temporal scales ranging from multidecadal to a few centuries.

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