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Response of hardwood tree regeneration to surface fires, western Chaco region, Argentina

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ABSTRACT

We assessed the response of seedlings and pole-sized individuals of *Aspidosperma quebracho-blanco* Schlecht., *Schinopsis lorentzii* (Griseb.) Engler and *Ziziphus mistol* Griseb. to surface fires. We assessed traits of fire resistance (bark thickness and bark density) and fire tolerance (mortality and sprouting type, basal or epicormic) in each species. Burns were carried out using two fine fuel loads (high, 8000 kg ha^{-1}; and low 4000 kg ha^{-1}, respectively) and two dates of fire application (early and late fire season). Field work was performed during 2008 and 2009. Using a randomized design, 120 2 m × 2 m plots were burnt each year. Using ANOVA, we tested the effect of species, fuel load and date of fire on the bark char height of the bole. The resprouting pattern (basal or epicormic) and post-fire mortality (complete or top-kill) were analysed using a logistic regression approach. There were a significant effect of species ($p < 0.0001$), fuel load ($p < 0.0001$) and of the interaction year of burning *date of fire ($p < 0.0001$) on the mean char height. *A. quebracho-blanco* had greater char height than *S. lorentzii* and *Z. mistol* ($p < 0.05$), but differences between the latter two species were no significant. Diameter to breast height (DBH) was significant and positively correlated to char height for *A. quebracho-blanco* and *Z. mistol*. High fuel load produced higher char height than the low fuel load fires. *A. quebracho-blanco* had the greatest total, inner and outer bark thickness, and the lowest bark density among the studied species. It was followed by *S. lorentzii*, while *Z. mistol* had the lowest total bark thickness, the highest inner bark proportion and the highest bark density ($p < 0.05$). The likelihood of complete mortality was significantly larger in *Z. mistol* than in A. *quebracho-blanco and S. lorentzii.* Mortality and top-kill were lower in the late season burns ($p < 0.05$). Sprouting type was significantly affected by species ($p < 0.05$), DBH, date of fire and by the interactions species × DBH and season of fire × DBH ($p < 0.0001$). *A. quebracho-blanco* presented only basal resprouts, while the other two species showed both epicormic and basal resprouts. The two species with greater bark thickness had lower mortality than *Z. mistol*. Epicormic resprouts were not observed at the more severe late burns. The three species studied showed high resistance and tolerance to medium to high severity fires.

1. Introduction

The native vegetation of the Chaco region of Argentina is composed by forests, woodlands, savannas and shrublands (Morello and Adámoli, 1974; Bucher, 1982). Fire is a main ecological disturbance in the region and it is widely used as a tool for vegetation management (Morello and Saravia Toledo, 1959; Bravo et al., 2001a; Tálamo and Caziani, 2003). The most common fires in the Chaco are surface fires occurring in the savannas of *Elionurus muticus* (Spreng) Kuntze, a grass species whose foliage is terpene-rich, making it highly flammable. In some extreme weather circumstances, savanna fires may propagate to the surrounding hardwood forests, dominated by trees of the genera *Schinopsis*, *Aspidosperma*, *Prosopis* and *Ziziphus*, in the form of crown fires, creating grasslands of *Trichloris crinita* Lag. Parodi, *T. pluriflora* E. Fourn, and *Setaria* sp. (Morello and Saravia Toledo, 1959; Bravo et al., 2001a).

In recent decades, fire recurrence in the Chaco region has increased, promoted by deep modifications in land use and climate change, affecting both fuel availability and ignition probabilities (Tálamo and Caziani, 2003; Boletta et al., 2006; Grau et al., 2005; Bravo et al., 2010). Secondary forests and brush thickets, created by timber operations exceeding regeneration rates, livestock

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overgrazing and misuse of fire are converted in grazing paddocks through roller-chopping and seeding of tropical grass species belonging to the genus *Panicum*, such as *P. maximum* cv Gatton (Kunst et al., 2014). These exotic grass species have different plant structure and potential to generate heavier fine fuel loads than native grass species, thus modifying the intensity and severity of surface fires (McDonald and McPherson, 2011). These facts convert the South American Chaco region, encompassing Argentina, Paraguay and Bolivia into one of the most threatened world ecosystems because of the conversion of native vegetation to pastures is economically more profitable (Kennard and Putz, 2005).

Currently, there is a major concern in the world as well as in the Chaco about the need to conserve the structure and dynamics of forest ecosystems due to the valuable products and services that they provide for the global and local communities (Krieger, 2001). On the other hand, fire is a natural disturbance that structures the plant communities of the Chaco region (Morello and Saravia Toledo, 1959) and prescribed fire could be a useful tool to manage the balance between woody and grass species in livestock operations (Kunst et al., 2000). Because of these issues, there is a need for more precise knowledge about the response to fire of native hardwood tree species of the Chaco region.

Available information on the native tree species of the Chaco region suggests a high resistance to fire of mature individuals because of their thick bark and high crown height (Giménez et al., 1998; Tálamo and Caziani, 2003; Bravo et al., 2001a,b, 2008). These features avoid direct contact of the flames of the surface fires with the cambium tissue and the buds located in the stem and crown, thus giving fire resistance to the trees (Pausas, 1998; Gignoux et al., 1997; García Núñez and Azocar, 2004). The ability of resprouting after a fire is considered to be the main trait responsible of fire tolerance, allowing fire sensitive species to restore their aerial structure following fires (Catry et al., 2009; Clark et al., 2012).

Tree regeneration is critical for sustainable forest management (Van Mantgem and Schwartz, 2003; Esquivel et al., 2008). However, specific data about fire resistance of saplings and poles of native hardwood tree species from the Chaco region are scarce. The objectives of this research were to assess the response to surface fires of saplings and poles of three native hardwood species from the Chaco region: *Aspidosperma quebracho-blanco* Schlecht. *Apocynaceae*; *Schinopsis lorentzii* (Griseb.) Engler, *Anacardiaceae* and *Ziziphus mistol* Griseb, Rhamnaceae.

The following hypothesis were examined: (a) the response to fire severity of saplings and poles of hardwood trees vary among species, according to fire behavior and to specific traits of fire resistance such as bark thickness and density; and (b) bark features would influence fire tolerance due to the protection given to axillary buds. Therefore, species with thick bark would predominantly produce epicormic sprouts after fires, while species with thin bark would recover mainly by basal sprouts due to the high susceptibility of the aerial structure to fire damage. These hypotheses were derived from a literature review suggesting that: (i) native woody species of the Argentine Chaco region present high fire resistance (Bravo et al., 2001a,b, 2008; Tálamo and Caziani, 2003); and (ii) thickness and density of bark affect the fire tolerance of woody species because of thick barks more effectively protect the cambium and the meristematic tissues responsible of resprouting after fires (Henst and Dawson, 1994; Van Mantgem and Schwartz, 2003; Montenegro et al., 2004; Clark et al., 2012).

Studies about specific traits and their influence on the response of native hardwood tree species to fire could contribute to improve environmental decisions related to restoration of burned areas of the Chaco region, and to adjust prescribed fire protocols applied on pastures adjacent to forest areas with the goal of enhancing forest conservation.

2. Materials and methods

Research was conducted at the 'La María' Experimental Ranch, Instituto Nacional de Tecnología Agropecuaria Santiago del Estero, Santiago del Estero, Argentina (28°03′S 64°15′E). Climate is semiarid, with 574 mm of annual average rainfall (1934–2000 series, INTA Santiago del Estero Experimental Station, 2010). Winters are cold and dry, and summers hot and rainy (Boletta et al., 2006). Mean annual temperature is 19.8 °C, and the mean of the warmest (January) and coldest (July) months are 26.1 °C and 10.6 °C, respectively. Freezing temperatures can occur from May to October, reaching extreme temperatures of −10 and −12 °C (Torres Bruchmann, 1981).

Soils belong to the order Entisols, suborder Eutric Regosol (Lorenz, 1995). In the Chaco, the fire season extends from April to October in coincidence with the dry and cold weather season. During this season, the moisture content of the soil and native vegetation usually decreases generating changes in fuel conditions and ignition probability (Bravo et al., 2001b). Rainfall reported here corresponds to the amount recorded during the active growth season of plants before each experiment, October to April. Rainfall data were obtained from the Experimental Ranch INTA meteorological station.

The hardwood tree species selected for this study are dominant in the dry forests of the western Chaco region (Araujo et al., 2008; Tortorelli, 2009). *S. lorentzii* is a deciduous species that may reach a height around 20–30 m, with an average life span of 250 years (Giménez and Ríos, 1999). *A. quebracho-blanco* is a perennial species, with a height around 25–30 m and an average life span of 200 years (Moglia, 2000). *Z. mistol* is a deciduous species that could reach a height of 4–10 m. The three species have a high-density wood, ranging from 0.85 to 1.16 kg dm^{-3} (Tortorelli, 2009) and different bark thickness at their mature state (Bravo et al., 2008). Previous reports indicate that individuals with a diameter at breast height (DBH) smaller than 15 cm correspond to juvenile individuals, according to the growth curves of the species (Giménez and Ríos, 1999; Juárez de Galíndez et al., 2006).

To assess plant responses to fire we used two different approaches: (a) we characterized bark features of the selected species in the lab; and (b) we conducted fieldwork for testing the response to surface fires. The first approach gave us information about specific traits directly related to fire resistance, such as bark thickness and density and allow a better understanding and interpretation of field results. In the second approach, by manipulating fuel loads and timing of fire, we overcame limitations of research based on observations conducted after wildfires, in which intensity, rate of spread, severity and other descriptors of fire behavior that help to characterize and classify a fire event are usually unknown. This approach, by permitting changes in fire intensity and severity, is a useful tool to associate the descriptor of the disturbance to the response of plant species (Vega et al., 2000; Drewa, 2003; Quevedo Dalmau et al., 2007; Brando et al., 2012). Parameters of a disturbance, such as intensity and severity, can be used to predict possible outcomes and facilitate the transfer of knowledge (Norkko et al., 2006; Buhk et al., 2007).

2.1. Estimating bark traits

Bark description was performed using 10–14 individuals of each species (DBH $\leqslant$ 15 cm), randomly selected in a dry forest of the Experimental Ranch, near the fire testing area. The DBH of each tree was recorded, and cross sections (approximate average thickness 5 cm) of the bole were extracted with a chainsaw at the following heights from the ground: (1) 0.30 m; (2) 1.3 m and (3) 2.3 m. The diameter (cm) of each cross section was measured, and after being properly identified, they were taken to the lab and sanded until appropriate views of the bark and wood were obtained. The three species studied have easily distinguishable bark layers .Thickness of total, inner and outer bark (cm) was measured with a calliper 0.1 mm precision in each cross section (Van Mantgem and Schwartz, 2003). The mean thickness (cm) of each bark layer of an individual was calculated averaging the thickness of cross sections 1–3. The approximate age of each individual was estimated by ring counting in the 0.30 m cross section.

Bark density was estimated in 2 cm × 2 cm samples extracted from 20 additional individuals of each species using the same sampling methodology as above. Samples including inner and outer bark were oven dried at 60 °C until constant weight (g). Bark density ($kg\,dm^{-3}$) was estimated following procedures suggested by Henst and Dawson (1994). Dry bark volume was measured by the water displacement method, immediately after the samples reached constant weight (Van Mantgem and Schwartz, 2003). Despite of the short immersion times, the samples could have absorbed water, so the exact values of the bark density should be considered with some caution.

2.2. Assessing responses to surface fires

In a dry forest of the Experimental Ranch, 120 plots of 2 m × 2 m plots were randomly established in 2008 and 2009, respectively. An individual of each species, DBH ⩽ 15 cm, occurring in the center of each plot was tagged. Two times of fire were tested: early, corresponding to July–August; and late, corresponding to September–October, respectively. During these times, species are at different phenological states: during the early timing, many plant species are entering dormancy but woody species may continue growing (Robbins and Myers, 1992; Williams et al., 1998). During the late period, vegetation will be either next to restart its active growth or actively growing, facts that could influence survival of the individuals due to the potential damage to buds and new foliage by fire.

Fuel load is directly related to fire intensity (Beverly and Martell, 2003). Two fine fuel loads were tested: high, approximately 8000 $kg\,DM\,ha^{-1}$ and low, approximately 4000 $kg\,DM\,ha^{-1}$, respectively. The first load corresponds to the average above ground grass biomass observed in pastures dominated by *P. maximum* (Kunst et al., 2014), while the low fuel load represents the average biomass of pastures dominated by the native grass species of the genera *Trichloris*, *Setaria* and *Chloris* (Kunst et al., 2012a,b). In plots where the fine fuel amount did not reach the target load, we added dry grass biomass previously weighed, uniformly distributed by hand (Drewa, 2003; Wright and Clarke, 2007). In each year and date of fire application 60 plots were burnt, corresponding to 20 individuals of each species, 10 with high and 10 with low fuel loads, respectively. Herbaceous fuel moisture was around 8–10%. Burns were conducted usually in the late morning-early afternoon, and finished in two days (Table 1).

During the day of the burns, air temperature (°C), air relative humidity (%), wind speed ($km\,h^{-1}$) and wind direction were monitored every 30 min using a Kestrel 2000 hand-held electronic device at 1.5 m. These data were compared with available prescriptions in the literature (Ronde et al., 1991; Britton et al., 1987) in order to check acceptable thresholds of fire behaviour. Fire was lit using drip-torches setting a head fire. Flame length (m) was visually estimated by two independent observers, and an average was recorded for each plot (Ryan and Noste, 1985). The time (min) that took the fire front to run through a plot, and the time (min) to achieve a total consumption of the fine fuel was also recorded. Based on empirical experience, a fire was considered totally extinguished when black, fluffy ash and no smoke were observed. These data were used to estimate a rate of spread ($m\,min^{-1}$) and residence time (min) of a specific burn.

Temperature profiles (°C) during the fires were monitored in 2 plots for each species and timing of fire by 3 type K thermocouples connected to a Campbell Scientific datalogger. One thermocouple was located horizontally on the soil surface, and the other two standing near to bole at the leeward and windward sides, respectively. Thermocouple temperatures were registered each second (s) and plotted versus time.

Char height (m) was defined as the vertical extent of the bole carbonization. It was measured in each individual with a ruler 1 mm of precision, 2 days after the burns, in the leeward side of the bole of each tree, from the ground to the top of the carbonization mark. This side of the tree is most susceptible to cambium injury because of increased residence times, flame lengths and temperatures (Gutsell and Johnson, 1996). Char height is considered an indicator of fire severity, because it is strongly associated to tree mortality (Barlow et al., 2003; Moreira et al., 2009; Catry et al., 2009; Brando et al., 2012) and was used to assess first order fire effects on trees (Reinhardt et al., 2001). We assumed that the higher the mean char height, the higher the likelihood of tree mortality (Brando et al., 2012).

Post-fire mortality and resprouting were considered secondary responses to fire, and assessed in the first growth season after the burns. Individuals of species studied were classified visually either as dead or alive. Absence of sprouts and a complete loss of foliage were considered as an indication of a dead plant, otherwise the plant was considered alive. In a second step, individuals in the live category were sorted in two sub-categories: (a) top-killed with dead woody structure; but alive, or (b) not top-killed. Sprouts were categorized either as *basal* (produced from roots or/and the plant collar); or *epicormic* (produced on the bole and main branches).

3. Statistical analysis

Flame length was used as an estimator of fire intensity (Alexander, 1982). Average flame length was analysed using ANOVA with fuel load, timing of burning and year of burning and their interactions as independent variables. We compared these results with the available literature in order to characterize the fire intensity.

Data of bark char height were rank-transformed previous to the statistical analysis in order to satisfy assumptions of linearity and homogeneity of variance (Conover, 1980). An ANOVA was

Table 1
Weather features registered during the experimental burns. La Maria Experimental Ranch, Santiago del Estero, Argentina, 2008–2009.

Fire season	Date of fire	Date	Hour	Air temperature[a] (°C)	Air relative humidity[a] (%)	Wind speed[a] ($km\,h^{-1}$)	Wind direction[a]
2008	Early	17/07/2008	9:50–12:50	24–27	48–38	0–4	N
	Late	28/10/2008	9:50–13:20	24–35	64–25	2–8 (13)	N-NE
2009	Early	05/08/2009	9:30–14:30	17–29	43–21	3.8–5.2	E-SE
		06/08/2009	8:55–13:00	7–22.3	76–13	0–2.8	E
	Late	21/10/2009	9:20–17:10	26–32	52–32	1.4–4	E-NE

[a] Measured at midflame height, 1.3–1.5 m from the ground.

performed with bark char height as the dependent variable; and species, fuel load, timing of burning, year of burning and their interactions as independent variables. DBH (cm) and flame length (m) were used as covariables. Non-significant interactions were removed from the analysis. Fuel load and date of fire were considered as treatments while year of burning and species as classification factors in a statistical sense, respectively. Two statistical models were tested: an overall model, that included all the factors listed above; and a specific model, in which the same factors were tested by species, a procedure suggested by the high significance of the interaction year of burning × timing of fire × species.

Differences in the proportions of live versus dead individuals of each species; top-killed and individuals no top-killed and sprouting type categories were analysed using a χ^2 test. In a second stage, a binary logistic model was fitted to the mortality data, with species, date of fire and fuel load as independent variables. Pattern of sprouting was analyzed using a nominal logistic model with sprouting type as dependent variable and species, date of fire and fuel load as independent variables. DBH, flame length and bark char height were introduced in the models as covariables in order to test their significance. *A. quebracho-blanco* and the late timing of fire were used as reference for the analysis of likelihood estimates. This species was selected as reference due to its great fire resistance at mature state (Bravo et al., 2008). The interpretation of the β of logistic models used to model mortality and top-kill should consider that the code = 0 was used to represent either dead or top-killed individual, respectively.

Bark features were analyzed using ANOVA with total, inner and outer bark thickness (cm) as the dependent variables; species, height of cross sections as independent variables; and DBH and/or age as covariables. Data for age, DBH, bark thickness and the proportion of inner/total bark thickness (%) were used to estimate the time and tree size needed to reach the threshold of fire protection, for each species. Linear and polynomic least squares regression models were used to summarize these results (Vanderweide and Hartnett, 2011).

The type III sum of squares was used for *F* tests in all ANOVAs, logistic regression and regression models. The LS Means procedure was employed for mean separation. Species represent intrinsic characteristics, date of fire the phenological and weather status, fuel load the amount of heat and associated fire intensity and severity; and year of burning the long term weather pattern. DBH was used as an indicator of the age/maturity of the individual sampled. Flame length was used as an estimator of fire intensity (Alexander, 1982).

The PROC FREQ, REG, GLM; LOGISTIC of the SAS package were used for mathematical calculations (SAS, 2002). An $\alpha = 0.05$ was used in all statistical analysis.

4. Results

4.1. Fire environment

Rainfall recorded during the growth period before the 2008 fire season (October 2007–April 2008) was approximately 514 mm, and for the 2009 growth period (October 2008–April 2009) was 357 mm. The mean rate of speed of the headfires was 3.93 (±4.14) m min^{-1}. Average flame length varied between 1.2 and 3.8 m (Fig. 1). Flame lengths were larger in the 2009 than in the 2008 fire season ($p \leqslant 0.0001$). Late burns with high fuel load produced greater flame lengths than early burns with low fuel loads in both fire seasons ($p \leqslant 0.0001$) (Fig. 1).

The average burning time of the plots was 42.05 s (±9.35). Maximum temperatures recorded by thermocouples located at the soil surface were in the range of 400–500 °C, while standing thermocouples in the windward and leeward positions registered

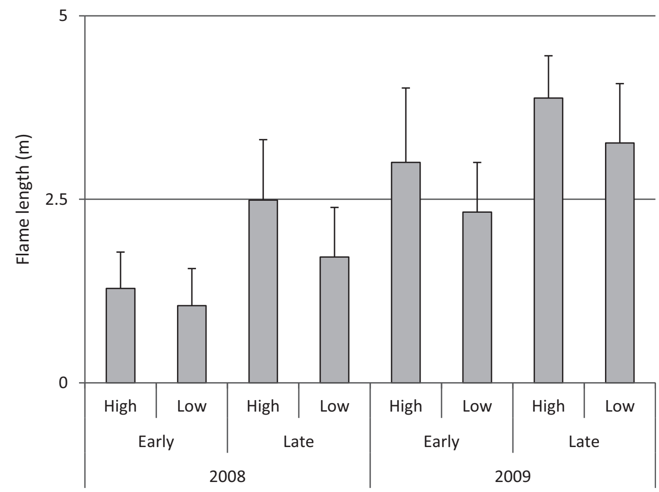

Fig. 1. Mean flame length (m) of experimental fire observed in the 2008 and 2009 fire seasons at two times of fire (early and late) and two fine fuel loads (high and low), 'La María' Experimental Ranch, Santiago del Estero, Argentina. Lines represent standard deviations. Within a date of fire, means followed by different letters are significantly different, Duncan test, α = 0.05.

temperatures between 55 and 100 °C. Thermocouple temperatures located on the leeward side of the stem were higher in the high fuel plots than in the low fuel plots, respectively.

4.2. First order fire effects

Mean bark char height was 0.82 m (±0.44 m), considering all data. In the high fuel plots, mean height of bark char was larger than in the low fuel plots (Fig. 2). The overall ANOVA explained a significant proportion of the total variation (56%, $p \leqslant 0.0001$) and indicated significant differences among species ($p \leqslant 0.0001$). *A. quebracho-blanco* had a greater mean bark char height than *S. lorentzii* and *Z. mistol*, while the means of the latter two species were not significantly different (Table 2). Immediately after the burns, individuals of *A. quebracho-blanco* and *S. lorentzii* showed a typical bark charring, but bark exfoliation occurred a few months after. *Z. mistol* individuals presented longitudinal cracks following the bark grain and the bark exfoliation occurred in several small pieces a few months after burns.

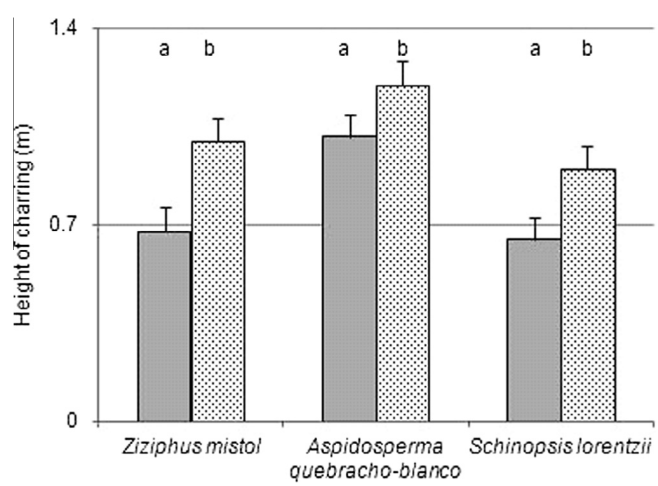

Fig. 2. Mean bark char height (m) in saplings and poles of three tree native species of the Chaco region, observed in fires with two fine fuel loads: low (4000 kg ha^{-1}, dark bars) and high (8000 kg ha^{-1}, stippled bars). 'La María' Experimental Ranch, Santiago del Estero, Argentina. Different letters represent significant differences between means of bark char height, LS Means, *t*-test, α = 0.05.

Table 2
ANOVA analyses of bark char height (rank transformed) of saplings and pole individuals (DBH ⩽ 15 cm) of three native Chaco species.

Source of variation	Species		
	Ziziphus mistol	*Aspidosperma quebracho-blanco*	*Schinopsis lorentzii*
Model r^b	0.59	0.57	0.49
Mean charring height (m)[a]	0.77 (0.05)[b]a[c]	1.09 (0.05)b	0.84 (0.05)a
Effects		$p > F =$	
Year of study (2008–2009)	0.65	0.09	0.48
Date of fire (early–late)	0.29	0.77	0.48
Fine fuel load (high–low)	0.10	0.04	0.03
Year × date of fire	<.0001	<.0001	<.0001
Covariables			
Flame length (m)	0.007	0.0003	0.03
DBH (cm)	0.04	0.003	0.56

[a] LS Means.
[b] LS Means standard deviation of mean charring height between brackets.
[c] Means followed by the same letter are not significantly different, *t*-test, α = 0.05.

Analysis by species indicated that bark char height was affected by year and date of fire (Table 2). Mean bark char height of *A. quebracho-blanco* and *S. lorentzii* were significantly affected by the fuel load, while the interaction year of burning *x* date of fire was significant for the three species ($p \leqslant 0.0001$, Table 2). DBH and flame length were both significant and positively related to bark char height in *A. quebracho-blanco* and *Z. mistol*, but DBH was non-significant for *S. lorentzii* (Table 2).

High fuel loads produced a higher bark char height than the low fuel loads in the three species studied ($p \leqslant 0.0001$, Table 2 and Fig. 2). Burns conducted in 2009 produced a higher mean bark char height than the 2008 burns (1.29 m versus 0.71 m, respectively), the difference was significant ($p < 0.05$). Early burns in 2009 produced a greater bark char height than those carried out in late date in the same year, and that those carried out on July and October of 2008 (Table 2 and Fig. 3).

4.3. Second order fire effects

Considering all data, only 5%, 8% and 10% of the individuals of *A. quebracho-blanco*, *S. lorentzii* and *Z. mistol* individuals were

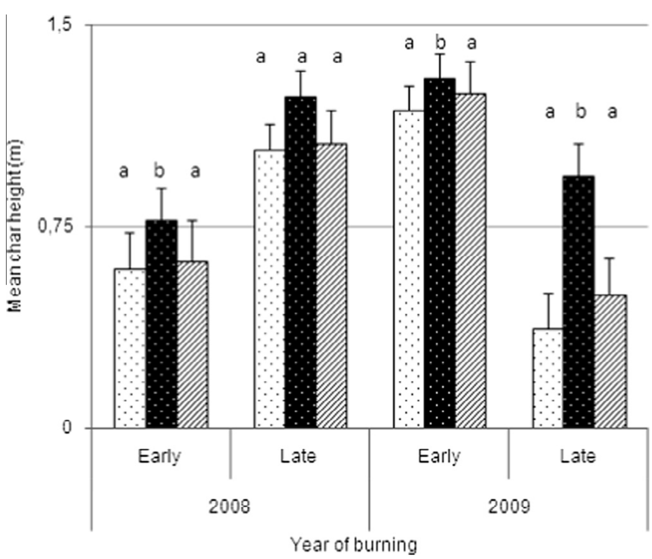

Fig. 3. Mean char height of three native tree species of the Chaco region at two dates of burning during the fire season: early (July–August) and late (September–October), 2008–09. References: *Ziziphus mistol* (dotted bars), *Aspidosperma quebracho-blanco* (full bars) and *Schinopsis lorentzii* (diagonal lines bars). La María' Experimental Ranch, Santiago del Estero, Argentina. Means with the same letter are not significantly different, *t*-test, α = 0.05; data rank transformed, means calculated by the LS Means procedure.

declared dead, respectively. Differences in mortality were significant ($p \geqslant \chi^2 < 0.0001$). The logistic model for mortality showed a low R^2, although species was a significant factor (Table 3). The probability of mortality was significantly larger in *Z. mistol* compared to *A. quebracho-blanco* (Table 3). There was no difference in mortality between *A. quebracho-blanco* and *S. lorentzii*. Likelihood of mortality was lower at the late timing of fire than early timing of fire. DBH had no significant effect on mortality (Table 3).

The probability of top-kill was significantly affected by season of fire (Table 3).Top-kill was lower at the late-season than at early season burns, and there was no significant effect of species, DBH and the interactions. The logistic model for sprouting type had the greatest R^2 of the three variables modelled (Table 3). Sprouting type was significantly affected by species, timing of fire and DBH, and by the interactions species × DBH and timing of fire × DBH (Table 3). *A. quebracho-blanco* and *Z. mistol* showed a lower percentage of resprouting individuals (30% and 40%, respectively) than *S. lorentzii* (90%). *A. quebracho-blanco* produced only basal resprouts, while the other two species developed both epicormic and basal resprouts (Fig. 4). Epicormic resprouts were observed only in early burns, and were absent in late burns. Resprouting individuals had a lower average DBH (5.17 ± 6.5 cm) than non resprouting individuals (9.20 ± 14.1 cm). Likelihood of occurrence of not sprouting increased in *S. lorentzii* in late burns ($p \leqslant 0.0001$; Table 3).

4.4. Bark features

The age and DBH of the individuals sampled ranged from 4 to 40 years and from 1 to 14 cm, respectively (Fig. 5). Total bark thickness, age and DBH were positively and significantly associated in the three species studied ($r^2 = 0.80$, $p \leqslant 0.001$). Mean thickness of total, inner and outer bark differed significantly among species ($p \leqslant 0.001$, Table 4). Cross section height was not a significant factor. *A. quebracho-blanco* had the highest mean of total, outer and inner bark mean thickness among the three species (Table 4). Total bark thickness increased with the age of the individual in the three species (Fig. 5A–C). Slopes of total bark thickness *vs.* tree age at DBH, an indicator of the rate of bark growth, was significantly different for *A. quebracho-blanco* versus *Z. mistol* ($p > F = 0.08$) and *S. lorenzii* ($p > F = 0.04$), respectively; but the slopes of the latter two species were not significantly different. *A. quebracho-blanco* had the highest increasing rate of bark thickness with age (Fig. 5, Table 4).

Bark density varied significantly among the species ($p \leqslant 0.05$) and had an inverse relationship with the total bark thickness. *A. quebracho-blanco* had the lowest mean bark density while *Z. mistol*

Table 3
Analysis of mortality, top-kill and sprout type in saplings and pole-sized individuals of three native hardwood species of the Chaco. 'La María' Experimental Ranch, Santiago del Estero, Argentina.

Variables		Wald test $P > \chi^2$	Maximum rescaled R^2	Test for global Ho: $\beta = 0$
Dependent	Independent			
Mortality	Species	0.0495	0.27	0.015
	Date of fire	0.246		
	DBH	0.2		
	DBH * species	0.126		
	DBH * date of fire	0.4		
Top-kill	Species	0.14	0.49	<0.0001
	Date of fire	0.0149		
	DBH	0.13		
	DBH * species	0.16		
	DBH * date of fire	0.12		
Sprouting type	Species	<.0338	0.67	<.0001
	Date of fire	<.0001		
	DBH	<.0001		
	DBH * species	0.0311		
	DBH * date of fire	<.0001		

the highest (Table 4). The proportion of inner bark decreased with age in the three species. In *A. quebracho-blanco* and *Z. mistol* the proportion of inner bark was always above 50% of the total bark thickness within the age range of 5–40 years (Fig. 5). In *S. lorentzii* this proportion decreased below 50% at 26 years (Fig. 5C).

5. Discussion

5.1. Fire environment

Mean flame length was within the range reported for *E. muticus* savannas and other open pastures of the Chaco by Kunst et al. (2000) and Bravo et al. (2001a), but surpassed the thresholds suggested for prescribed under burning in pine plantations (Ronde et al., 1991) and reached magnitudes reported in rangeland fires around the world (Britton et al., 1987, Trollope et al., 2002; Cochrane, 2009). The mean rate of fire speed was lower than that observed in open native pastures (Kunst et al., 2001; Kunst et al., 2012b) which could be related to lower wind speed within the forest canopy. Significant differences in mean flames length between study years suggest the influence of fine fuel desiccation since rainfall recorded in the 2009 growth season was approximately 31% less than the rainfall in the 2008 grow season.

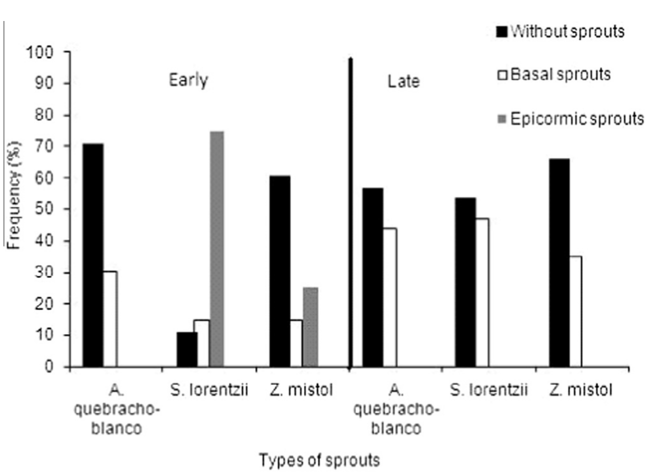

Fig. 4. Frequency of type of resprout after early (July) and late (October) burns in live individuals of three native woody species of Argentine Chaco region. 'La María' Experimental Ranch, Santiago del Estero, Argentina.

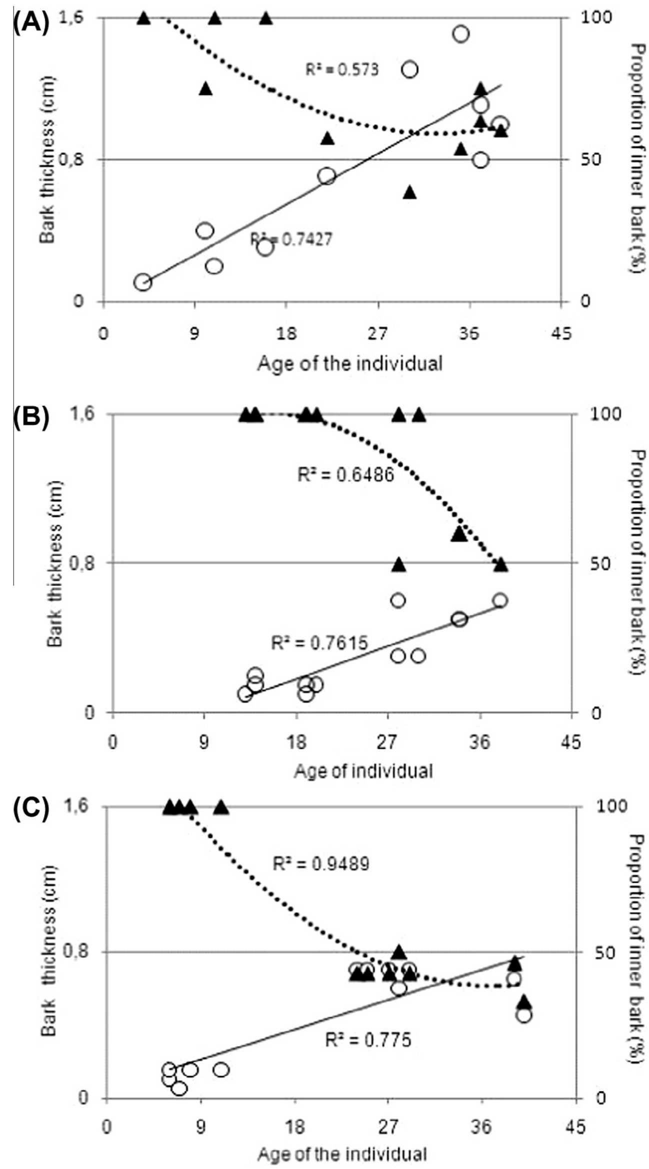

Fig. 5. Relationship between mean total bark thickness (cm, circles and solid line) and proportion of inner bark (triangles and broken line) with age (year) at DBH. A – *Aspidosperma quebracho-blanco*, B – *Ziziphus mistol* and C – *Schinopsis lorentzii*.

Temperatures recorded by soil thermocouples in our study agree with those observed by Pinard and Huffman (1997) in a dry open forest in the Bolivian Chaco. However, the mean of bark char height was greater in our study, despite of the short residence time of the fires and the low temperatures registered by standing thermocouples, on both the windward and leeward sides of the trees. This difference could be attributed to chemical components (terpenes, oils and tannins) which may increase bark flammability and therefore fire intensity and severity (Kunst et al., 2012b).

In gallery forests of North America, Vanderweide and Hartnett (2011) considered low intensity fires those with temperatures less than 400 °C. Kennard and Putz (2005), in the transition zone between the humid forests and the thorn scrub formations of the Gran Chaco, considered low intensity fires those reaching approximately 225 °C.

Burns conducted in 2009 generated a larger mean flame length and larger mean height of bark char than those performed in 2008. As discussed early, this was probably due to differences in fine fuel desiccation, a result particularly evident in the July 2009 burns.

Table 4
Mean thickness (LS Means) and mean density of total, inner and outer bark at three cross sections in three native woody species of Argentine Chaco. Standard deviations between brackets.

Species	Cross section height (m)	N	Age mean of section (years)	Mean diameter of section (cm)	Mean bark thickness (cm)			Mean bark density (kg cm^{-2})[B]
					Total	Inner	Outer	
Aspidosperma quebracho-blanco	0.3	10	26.5 (12.66)	8.42 (5.1)	0.88 (0.08) a[2]	0.48 (0.02) a	0.43 (0.06) a	0.57 (0.13) a
	1.3	10	24.1 (13.3)	7.41 (4.78)	0.78 (0.08) a[2]	0.47 (0.21) a	0.26 (0.26) a	
	2.3	7	26 (12.63)	7.91 (4.23)	0.77 (0.09)	0.54 (0.03)	0.23 (0.07)	
Schinopsis lorentzii	0.3	12	26.25 (14.6)	8.18 (4.44)	0.46 (0.04) b	0.23 (0.02) b	0.22 (0.02) b	0.70 (0.16) b
	1.3	12	21 (12.7)	6.43 (3.83)	0.46 (0.04) b	0.22 (0.02) b	0.24 (0.07) b	
	2.3	10	20.5 (9.56)	6.23 (3.21)	0.47 (0.05)	0.23 (0.02)	0.23 (0.03)	
Ziziphus mistol	0.3	15	28.5 (8.88)	8.5 (3.5)	0.37 (0.04) c	0.22 (0.02) c	0.15 (0.03) c	0.84 (0.23) c
	1.3	12	23.75 (8.53)	6.11 (2.7)	0.29 (0.04) c	0.22 (0.02) b	0.07 (0.04) c	
	2.3	11	17.73 (6.52)	4.29 (1.8)	0.32 (0.04)	0.25 (0.02)	0.07 (0.04)	

[A] Different letters within a mean bark thickness column at cross section 0.3 m and DBH indicate significant pairwise differences, *t*-test ($p < 0.05$).
[B] Different letters within mean bark density column indicate significant pair wise differences, *t*-test ($p < 0.05$).

Climate exerts a clear control on the production and desiccation of fine fuels (Grau and Veblen, 2000; Kunst et al., 2000; Bravo et al., 2010) and therefore on fire severity (Robbins and Myers, 1992). Variations among ignition techniques, fuel characteristics (flammability, density, and moisture content, among others) and temperature recording methods (Tempilaq paints, thermocouples) prevent considering two fire events as equal physical phenomena. However, fires in our study could be considered as medium to high fire intensity given the average flame length and temperature range observed on the soil surface and both at the windward and leeward sides of boles.

5.2. First order fire effects

The significant effect of species on the height of bark char suggests the influence of bark features of the species in their response to fire. Bark thickness is the main barrier against heat (Michaletz and Johnson, 2007); therefore, we consider appropriate to discuss results of charring height together with bark features. *A. quebracho-blanco* showed the highest bark char height throughout the study; the greatest total, inner and outermost bark thickness; and the lowest bark density of the three species. These results could be related to its low density bark, added to other factors such as fire behavior and fine fuel load. Henst and Dawson (1994) observed a shorter time to ignition in thick and low density bark species than in thin and high density bark species, respectively. On the other hand, *S. lorentzii* and *Z. mistol* had lower bark char height, lower total bark thickness and higher bark density than *A. quebracho-blanco* .Thermal diffusivity of the bark decreases with increasing bark density and moisture content, the latter principally related to the proportion of the inner bark layer (Reifsnyder et al., 1967; Hare, 1965; both cited by Van Mantgem and Schwartz, 2003). This fact could partially explain the lower charring height in *S. lorentzii* and *Z. mistol* since thin and high density barks could have delayed combustion.

Inner bark thickness represented above 50% of the total bark thickness in the three species and this proportion persisted nearly 30 years giving to seedlings and pole individuals a great resistance to fire such as have been observed by Van Mantgem and Schwartz (2003).

Pinard and Huffman (1997) considered that a threshold of 18 mm of bark thickness could give tree species in the Bolivian dry forest the ability to withstand lethal cambial temperatures during low intensity fires. Vanderweide and Hartnett (2011) found a lower threshold, 8.6 mm, in species of the American gallery forest. Hoffmann et al. (2003) reported that a bark thickness of 6–5 mm allows bole survival in low-intensity savanna fires and a bark thickness of 11–14 mm in high intensity fires. In our study, only individuals of *A. quebracho-blanco* and *S. lorentzii* reached bark thicknesses similar to the thresholds mentioned above. The greater mortality observed in *Z. mistol* (10%) despite of this low mean bark char height observed in our prescribed burns seems to reaffirm the influence of bark thickness on the response to fire.

Bark properties such as density, total bark thickness and inner bark proportion are not often considered in post-fire evaluations using bark char height as an indicator of fire severity. High charring heights in species with thick and low density bark may not always indicate higher fire severity. This bark type may inflame quickly, but has an excellent insulating property, thus limiting the cambial damage such as been reported for *Quercus suber* L. (cork tree), a species that present low density bark and remarkable fire resistance (Catry et al., 2009). Pinard and Huffman (1997) and Vanderweide and Hartnett (2011) considered negligible the effect of density and inner bark proportion on the heat transference through bark tissues. However, they undoubtedly influence both the time to reach ignition and the exposition time of cambium to lethal temperatures (Henst and Dawson, 1994).

According to the different combinations of bark thickness and density, our results suggest a high protection level of bark in saplings and pole individuals of *A. quebracho-blanco* and *S. lorentzii*, and intermediate in *Z. mistol*. The mortality observed in *Z. mistol* may reflect these bark protection levels and our results agree with available about fire resistance (Giménez et al., 1998; Bravo et al., 2001a,b; Bravo et al., 2008; Tálamo and Caziani, 2003) and confirm our first hypothesis.

In the overall ANOVA, the significant effect of both fuel load and the interaction year of burning × species × date of burn on the bark char height in *A. quebracho-blanco* and *S. lorentzii* seems to indicate the complexity of factors determining tree responses to fire, including specific features, environmental conditions and fire behaviour (Drewa, 2003).

Burns conducted in 2009 generated a larger mean flame length and larger mean bark char height than those performed in 2008. As discussed early, this was probably due to differences in fine fuel desiccation, a result particularly evident in the July 2009 burns carried out after a growing season with below-average precipitations (Bravo et al., 2010). In the three species studied, the late burns in 2008 produced a higher mean flame length and bark char height than the early burns. This fact affirms the close relationship between this variable and fire behaviour, particularly with intensity and severity (Ryan and Steele, 1989; Agee, 1993; Moreira et al., 2009; Cochrane, 2009). Williams et al. (1998) informed that fires in the early dry season in a tropical savanna of northern Australia were significantly less severe than late dry season fires, attributing this to high fuel desiccation, more leaf litter and more extreme fire weather in the latter. Kunst et al. (2003) and Ledesma (2011) obtained similar results with prescribed fires within grasslands and shrublands of the Argentine western Chaco region.

The low bark char height observed in our study in October 2009 in both the low and high load plots could be attributed to changes in environmental conditions during fires such as wind speed, air temperatures or fuel density that may obscure seasonal differences of fire severity (Rothermel, 1991; Robbins and Myers, 1992; Vega et al., 2000).

The significant effect of DBH on the bark char height in *A. quebracho-blanco* and *Z. mistol* could be attributed to a greater fuel accumulation and residence time of the fire caused by a greater tree size and bole volume (Dickinson and Johnson, 2001; Lloret, 2004). Barlow et al. (2003) found that a deep leaf litter accumulation at the tree base generates greater char heights of bole in buttressed trees in Central Amazonian forests.

5.3. Second order fire effects

The significant differences in mortality among the three species studied reaffirm the influence of bark thickness on fire resistance since the higher probability of mortality corresponded to *Z. mistol*, which presented the lowest bark thickness in this study. Ryan and Reinhardt (1988) using logistic regression models determined that the probability of mortality decreased as bark thickness increased in seven species of the North American western conifer forest. Barlow et al. (2003) considered that thin bark tree species are more prone to selective mortality induced by heat stress and the bark char height is one of the variables better explaining tree mortality. The lack of a significant effect of DBH on the tree mortality in our research differs with reports informing high mortality associated with a small tree size (Gignoux et al., 1997; Barlow et al., 2003; Fernandes et al., 2008). The low R^2 of the logistic model for mortality agrees with Catry et al. (2010) who reported that the low mortality of broadleaved species difficult the fitting of predictive models.

The lowest probability of top-kill observed in late burns in our study suggests the importance of post fire environmental conditions on tree survival (Robbins and Myers, 1992; Catry et al., 2010). In the Chaco region, environmental conditions after late burns (higher temperatures and water availability) could promote a more rapid recovery of damaged structures, accompanied by a profuse mobilization of reserves destined to foliage recovery (Miller, 2000; Lawes and Clarke, 2011; Juárez et al., 2012). Lloret (2004) considered that greater resource availability and lower plant competition characterize post fire environments in Mediterranean ecosystems. Early burns probably impose a synergic stress produced both by heat shock, damages on aerial structure (buds, foliage, bole and branches) and the lower temperatures and water availability typical of winter season, contributing to greater top-kill.

The proportion of sprouting individuals in *A. quebracho-blanco* and *Z. mistol* could be considered low, taking into account information from semiarid environments reporting 90–70% of resprouting individuals after wildfires (Quevedo Dalmau et al., 2007; Catry et al., 2009). The resprouting strategy is determined both by anatomical and physiological characteristics of species, the bud bank, level of reserves but also by fire behaviour and post fire conditions (Robbins and Myers, 1992; Lloret, 2004). Bud bank is defined as the pool of buds available for resprouting on bole and branches (Harper, 1977). Sennerby-Forsee and Zsuffa (1995) indicated that differences in the resprouting intensity among woody species are related to size of the bud bank. However, the ability to form adventitious buds at basal bole level or from other underground organs contributes to the aerial bud bank and increases the possibility of resprouting (Clark et al., 2012).

A. quebracho-blanco exclusively produced basal sprouts, even with different fuel loads and fire times (Fig. 4). This result added to the data of bark char height could indicate the loss of axillary and epicormic buds by heat, thus rejecting our second hypothesis. However, Clark et al. (2012) communicated that thicker barks may hamper the emergence of epicomic buds, thus limiting resprouting. Assessment of resprouting 4 months after fire, as those performed in this study, could be considered as a short time, especially in thick bark species. On the other hand, the presence of both sprout types in *S. lorentzii* and *Z. mistol* seems to indicate that their barks preserve axillary and epicormic buds from fire allowing them resprouting profusely from epicormic buds such as those observed in *S. lorentzii,* in the early burns of 2008, characterized by low intensity and severity (Fig. 4).

The increase of percentage of individuals with basal resprouts and the absence of epicormic resprouts in all species studied after the late burns suggest the effect of fire severity on resprouting pattern. More severe fires could eliminate aerial buds limiting the epicormic sprouts and promoting basal sprouts. These results affirm the second hypothesis about the role of bark in protecting the aerial bud bank. However, the bark thicknesses of species studied seem to protect efficiently the aerial bud bank in low to medium intensity fires, whereas more severe fires (such as in late burns) may obligate the individuals to resprout by basal and adventitious buds.

The lower average DBH of resprouting individuals allow us also to suppose that, in this study, the effect of age and vigour of a individual on the formation of new shoots and leaves. Ky-Dembely et al. (2007) informed a decrease in seedling resprouts with an increase of the size class of individuals in West African savanna-woodlands, associated to loss of vitality with ageing. The average DBH of no resprouting individuals (9.2 ± 3.68 cm) in our study corresponds to individuals of 28–30 years (Table 4) which could have high costs of maintenance of aerial structures, limiting the energy resources for resprouting.

6. Conclusions and management implications

The saplings and pole-sized trees of the species studied have bark features giving them both high resistance and tolerance to medium and high intensity surface fires. Species with thick and low density bark had higher charring height of bole than species with thin and high density barks in fires with similar intensities and severities. Mortality of more thick bark species (*A. quebracho-blanco* and *S. lorentzii*) was lower than in the thinnest bark species (*Z. mistol*). Therefore, bark density should be taken into account in post fire evaluations to avoid an overestimation of fire damage.

High fuel loads produced more severe fires than low fine fuel loads and the significant interaction of date of fire and year of study, suggests an important effect on fine fuel desiccation on fire intensity and severity. The three species studied showed a significant resprouting ability after fires of medium to high severity and the resprouting pattern seems to be influenced by specific features and also by fire intensity and severity. The late burns (October) seem to be the more appropriate date of fire application with high likelihood for survival of small saplings and pole-sized individuals due to the better post fire environmental conditions.

Our results improve the interpretation of fire as ecological process in the ecosystem of the Argentine Chaco region. Saplings and pole-sized trees of species studied are often the target of several silvicultural treatments since the natural regeneration is a critical phase of forest management. The low mortality observed 4 months after fire suggests that prescribed fires could be used as a forest management tool in the Argentine Chaco forests.

However, research on other tree species of the Chaco is desirable in order to achieve a better understanding of forest dynamics in relation to fire. The approach used here permitted the description of fire features more precisely, since surface fires were lit using two different fuel loads at two times of application. Because these data were gathered in a manipulated experiment, they will contribute to enhance the existing prescribed fire protocols, promoting a more sustainable use of the natural resources.

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