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From forest to shrubland: Structural responses to different fire histories in *Prosopis flexuosa* woodland from the Central Monte (Argentina)

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ABSTRACT

We estimated post-fire population trajectories, and analyzed the effect of fire recurrence on the post-fire recovery of seven different fire histories in the Central Monte. The structure of stems showed that unburned woodlands and woodlands with the longest post-fire recovery time, presented higher proportion of stems with basal diameter (BD) > 5 cm. On sites with higher recurrence of fires, the stems with BD > 5 cm almost disappeared. Tree height and crown diameter showed a significant decrease at sites recently burned, and this pattern was reinforced in areas with recurrent fires. Results suggest that the structure of woodland in the southeast of the Province of Mendoza in Argentina has been strongly controlled by fire history. Fire generates a population dominated by individuals with numerous smaller-sized stems, which becomes more evident in environments where fire recurrence is higher. Structural changes induced by fire indicate that logging may not be possible in the area. The development of forestry practices for post-fire management is needed for the burned areas. An increase in fire frequency is expected in the area, therefore this would cause the modification in the structure of the *Prosopis flexuosa* population. Furthermore, this will lead to the conversion from woodland to shrubland, and the loss of its capacity for natural recovery.

1. Introduction

Fire has played an important role in shaping the structure, function and composition of terrestrial environments worldwide (Pausas and Keeley, 2009; Wright and Bailey, 1982). In recent decades, fires recorded in many parts of the world have affected millions of hectares. This has lead to national, regional and international action to detect, prevent and manage fires (Liu et al., 2014). Wildfires are globally considered among the primary causes of the degradation of forest ecosystems (F.A.O, 2010).

In the traditional concept of ecological succession, protection of the system from disturbance has been suggested as a tool to promote recovery of the structure and function of burned forests. Several studies, however, have suggested that modification of the disturbance regime can generate non-linear responses and new stable states, which prevent the natural recovery of forests, as well as other systems (Bestelmeyer, 2006; Rostagno et al., 2006; Suding et al., 2004). Knowledge of the post-fire trajectories of tree populations with different fire histories can help generate models of long-term dynamics applicable to the management and recovery of burned forests.

The consequences of fire on successional trajectories depend on the season, intensity, frequency, and extent of the fire event (Wells, 2004; Whelan, 1995). They also depend on the generation of new stable communities (e.g., shrublands), and on the occurrence of the processes necessary to drive the transitions between them, such as, protection from grazing, germination from surviving seed banks, seed dispersal, etc (Beckage et al., 2011; Rostagno et al., 2006).

From a forest perspective, fire modifies the population structure of woody plant species, since it causes changes in the natural regeneration and growth habits of individuals (Scholes and Walker, 1993; Álvarez et al., 2009). Resprouting of live buds in the crown, roots or trunks of the burned plants can generate a higher number of stems with lower commercial value (Barbour et al., 1998). In arid

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environments, fire combined with grazing has been suggested to promote the conversion of a woodland system to shrubland (Abril et al., 2005; Roig, 1987), thus reducing its commercial worth. The net primary productivity of woodlands may decline after a fire, reducing wood production; whereas in other cases productivity can increase because of reduced competition from understory vegetation (Carter and Foster, 2004).

In Argentina, different bioclimatic regions are affected by fire. The arid and semiarid regions are among the most affected because of the natural conditions and the widespread use of fire for vegetation management (Fischer et al., 2012; Villagra et al., 2009). In the dry Chaco region (500–700 mm of annual precipitation), it has been observed that sapling density is high (nearly 1000 per ha) in the first year following a fire, and that *Aspidosperma quebracho-blanco* has a great ability to resprout from roots (Roth and Giménez, 1997). *Prosopis nigra* is affected by fire, modifying the shape of the tree and causing wounds that reduce the volume between 60 and 90% (Gimenez de Bolzón, 1994). At a *Prosopis caldenia* woodland, it was found that a single fire event reduced the abundance and competitive ability of the woody species, while promoting regeneration of the grass layer (Bóo et al., 1997). Most woody species in this woodland resprout from the base, but very few show aerial resprouting (Cano et al., 1985). In this region, the effect of fire is related to fire intensity, plant community composition and tree age (Bóo et al., 1997).

In the Central Monte region, large forest areas are affected by different disturbances such as logging, livestock and fire (Rojas et al., 2009; Villagra et al., 2009). Particularly in the southeast of the province of Mendoza, the fire season is between August and January. In this region, over the last 19 years, 88% of the area has been burned, with a mean fire interval of 5.7 years and a fire frequency of 0.18 (Cesca, 2011). This results in a mosaic of patches with various fire recovery times and various fire histories. This mosaic is reflected in the structure of the community and in some soil variables (Cesca, 2011). This region comprises extensive areas with open woodland of *Prosopis flexuosa* ('algarrobales'), which is the dominant tree species in the Monte region and grows on sites with where surplus water is available (Jobbágy et al., 2011). This is the most important species from an economic standpoint, and its stands have been a subsistence source of food, timber and forage for many local communities (Roig, 1993). Its main current use is for forestry and extensive livestock farming. Thus, the fire regime is expected to control the population dynamics of *P. flexuosa* and, consequently, modify its forestry potential. We propose that areas with recurrent fires will show modifications in the population structure and growth habits of *P. flexuosa* individuals, resulting in the system's conversion to shrubland and in a loss of its capacity for natural recovery. The objective of this study was to estimate post-fire population trajectories, and to analyze the effects of fire recurrence on the post-fire recovery of *P. flexuosa* woodlands in the southeast of the province of Mendoza.

2. Materials and methods

2.1. Study area

In the lowlands of Mendoza, there are three main woodland areas which originally covered approximately 40,000 km^2. We selected the Southern area, located in Travesía del Diamante-Atuel (Departments of General Alvear and San Rafael), to perform this study because this area is subjected to recurrent fires, and the status of the plant community denotes an environment that has been modified through fire. The area lying in the SE of the province of Mendoza belongs to the southern portion of the Central Monte and is bound by the Austral Monte (Rundel et al., 2007). Mean annual precipitation is 329 mm, mean annual temperature is 15.4 °C and the predominant wind regime is N–S (Weather Observatory of General Alvear, 35° S and 67°39′ W, at 465 m elevation). This region experiences water deficit most of the year. It also experiences high levels of thunderstorm and hail activity (Capitanelli, 2005). The vegetation has xerophytic features, with the upper stratum represented by *P. flexuosa* and *Geoffroea decorticans*; the shrub stratum represented by *Larrea cuneifolia* and *Larrea divaricata, Atriplex lampa, Atriplex undulata, Prosopis alpataco, Condalia microphylla*, and the herb stratum consists of *Aristida mendocina, Trichloris crinita, Panicum urvilleanum, Hyalis argentea var. latisquama*.

Extensive livestock farming is the major activity in non-irrigated areas, namely breeding of cattle and goats which feed on natural vegetation (grasses and shrubs). There are two major livestock farming systems in the plains of the province of Mendoza: the first is a subsistence system and the second a commercial ranching system. The study area lies within the second system, where producers manage their farms through tenants. Producers consider vegetation resources very important (Guevara et al., 1993).

2.2. Prosopis flexuosa D.C

Most of the species of the *Prosopis* genus occur in South America, and are among the species of highest ecological and economic value in arid and semiarid areas. Within this genus, *P. flexuosa* is a tree species that grows between 5 and 12 m tall, with a low trunk height, deciduous foliage, and which can be multi-stemmed. In Argentina, it occurs in the Monte, dry Chaco and Espinal regions (Alvarez and Villagra, 2009). In the Monte desert, which has a marked water deficit, its populations grow on sites where extra water is available from the subsoil or river beds (Rundel et al., 2007). This species has a tap root that extends vertically, enabling it to reach the water table, and a crown of surface roots that allows it to harness rainwater (Guevara et al., 2010; Jobbágy et al., 2011; Villagra et al., 2010). The 15° isotherm marks the southern border of *P. flexuosa* forest in Argentina; and to the south, the species is represented by the shrub variety *P. flexuosa* var *depressa*, forming a low shrubland.

This variety shows most of their basal branches buried in the earth, semi-buried or creeping (Roig, 1987).

2.3. Experimental design and sampled vegetation units

We studied the post-fire trajectory using a chronosequence of sites with different post-fire recovery times detected by Cesca (2011), based on a multi-temporal analysis of satellite images. In addition, to assess the impact of fire recurrence, we sampled sites with different fire frequencies and similar recovery times since the last fire. Thus, the *P. flexuosa* population was sampled at sites with seven different fire histories: a) unburned (Unburned), b) sites with satellite evidence of burning before 1988 but without precision as to the year of occurrence (Burned before 1988), c) one fire event in season 1993–1994 (Fire 1993–94), d) one fire event in season 2000–2001 (Fire 2000–01), e) one fire event in season 2003–2004 (Fire 2003–04), f) burned twice in the 23 years analyzed with the last fire occurring in season 2003–2004 (2 fires), and g) burned 3–4 times over the last 23 years with the last fire occurring in season 2003–2004 (3–4 fires) (Table 1).

At least three sites were selected for each treatment, and three plots separated by approximately 100 m were established at each site. For selection of the sample sites, we chose different fire events on the map generated by Cesca (2011) at random and then sampled them according to logistic possibilities. In all cases, the distance between sites with the same treatment was over 10 km. Plot size

Table 1
Description and sample design for each fire history including number of fire events, recovery time, number of sampled sites, plot size and total sampled area and total number of stem samples.

	Unburned	Burned before 1988	Fire 1993–94	Fire 2000–01	Fire 2003–04	2 Fires	3–4 Fires
Number of fire events	–	1	1	1	1	2	3–4
Post-fire recovery time (years)	–	≥18	13	7	3	3	3
Sites sampled per unit	4	3	4	4	3	4	4
Plot size (m^2)	400–1000	600–800	400–800	400–600	400–1000	400–1000	400–800
Total sampled area (m^2)	8400	6000	6400	4600	5600	5800	6600
Number of stem samples	3332	2521	6756	11,240	5191	9472	4629

depended on tree density, since the established minimum number of individuals sampled per plot was 40. Thus, plot size varied between 0.04 ha (20 × 20 m) and 0.1 ha (50 × 20 m). In all, 26 sites and 78 plots were sampled (Table 1).

2.4. Woodland structure and conservation status

For all *P. flexuosa* individuals (saplings and adults) on each plot we recorded the number of stems and basal diameter of each stem with diameter tape and digital caliper, overall tree height with Velmex digital hypsometer, health status, growth habit and crown dimensions (largest and smallest diameter). Individuals with basal diameter (BD) smaller than 7.5 cm were considered saplings, and adults were considered those with BD larger than 7.5 cm. We selected the 7.5 cm threshold to define adult trees according to both a biological criterion (smaller individuals usually do not produce flowers) and a usage criterion (local people use stems larger than this size).

Depending on growth habit, individuals were classified as: a) erect (those with vertical growth); b) semi-erect (multi-stemmed individuals or individuals with a branched main stem but with branches not touching the ground); c) decumbent (those multi-stemmed individuals with branches touching the ground) (Pasiecznik et al., 2001); and d) *depressa*, those with most basal branches buried in the earth, semi-buried or creeping, similar to that described by Roig (1987) for *P. flexuosa* var. *depressa*. The health status of trees was classified by applying a semi-quantitative assessment: very healthy (individuals with 100% of branches alive), moderately healthy (individuals with less than 50% of dry branches), not very healthy (individuals with more than 50% of dry branches, and some live branches) and dead (individuals with 100% of dry branches).

2.5. Data analysis

Two sets of analysis were performed: one to assess the trajectory after fire comparing recovery times (chronosequence), and the other one to assess the effects of fire recurrence comparing the three treatments with the same recovery time (3 years) however with a different number of fire events during the period analyzed. We performed a Detrended Correspondence Analysis (DCA) of the sampled sites according to stem diameter structure, with the aim to find a grouping of sites related to population structure. Targeting to detect differences between treatments, we performed an Analysis of Variance for the variables overall height and crown diameter, comparing means with an LSD test (Zar, 1984). For this analysis, site was considered to be the sampling unit, first integrating the value of all three plots and then averaging the sites. For this analysis, we used Infostat software (Di Rienzo et al., 2002).

3. Results

The DCA showed that unburned sites and sites burned before 1988 were grouped to the right along axis 1, and sites recently burned and burned more than once were grouped to the left (Fig. 1 a, b). We did not observe a clear pattern of variation along the first DCA axis for different fire recurrence sites. Sites with a single fire event in 1993–94 seasons were grouped in the middle of axis 1. Unburned sites and those burned before 1988 were associated with larger *Prosopis* stems (over 10 cm BD) and with already established saplings (10 cm BD), whereas sites with frequent fires or that had been recently burned were associated with regeneration classes (0.5 and 1 cm BD) (Fig. 1 a, b).

In accordance with the DCA analysis, unburned woodlands and woodlands with longer recovery times exhibited tree population structures with a higher proportion of stems of diameter classes >10 cm (up to 60 cm in diameter), and with a lower proportion of stems of classes <5 cm BD (Fig. 2). Stem structure of the woodland burned before 1988 showed a marked decrease in stem number from the 15 cm diameter class onward (Fig. 2). Woodlands burned

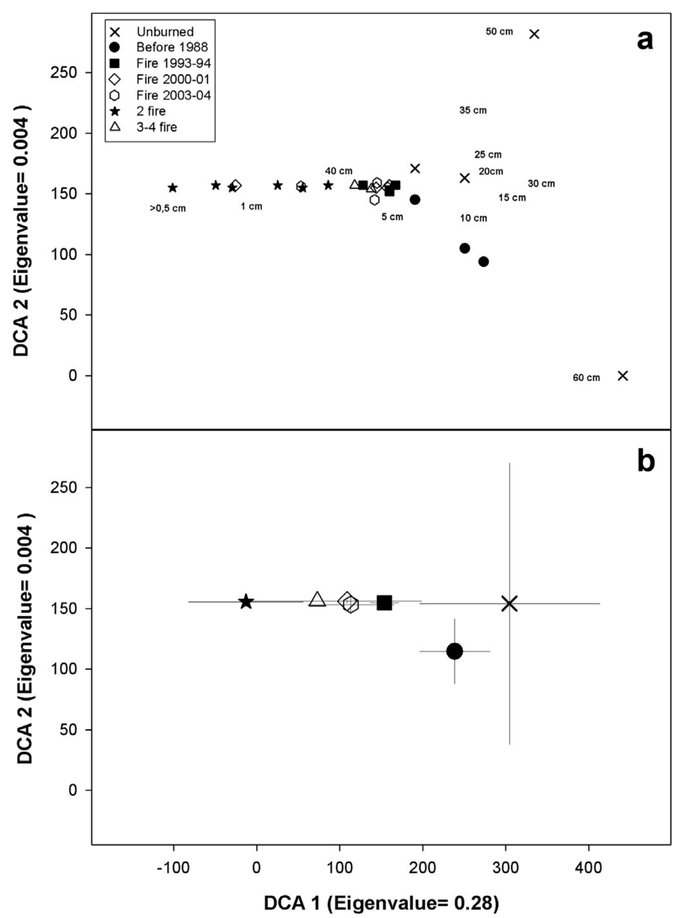

Fig. 1. a) Detrended Correspondence Analysis (DCA) according to stem basal diameter for all sampled sites. Different symbols indicate different fire histories and numbers represent the associated stem basal diameter classes. b) Mean and standard deviation of the values on DCA-axes 1 and 2 of each fire history treatment.

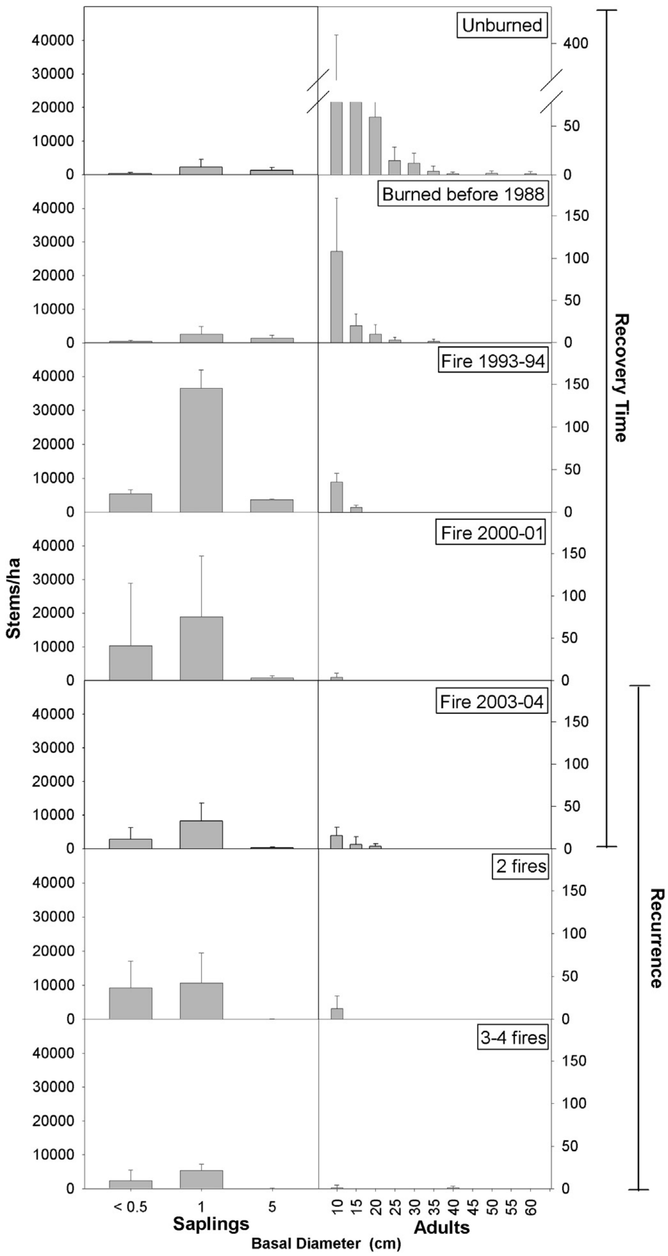

Fig. 2. Stem basal diameter structure for each treatment. The first column corresponds to stems shorter than 7.5 cm BD (saplings) and the second column to stems longer than 7.5 cm BD (adults). Note the change in scale between plots of saplings and adults and in the unburned treatment among plots of adults. Bars represent means, lines denote standard deviation. Vertical lines show the treatments included in the analysis of the effect of recovery time and fire recurrence.

only once in the seasons 1993–94, 2000–01 and 2003–04 had a relatively similar structure, with a high concentration of stems of the first classes and very few stems of diameter classes >5 cm BD (Fig. 2). Woodlands with recurrent fires (2 and 3–4 fires) had the most extreme differences with respect to the unburned site, showing a large stem density in the two first diameter classes (<0.5 and 1-cm BD) and very few stems in the subsequent classes, with the stems of BD >5 cm having almost disappeared (Fig. 2).

Sites unburned or with longer recovery times supported the tallest trees, with some individuals reaching 8 m in height, whereas at sites recently burned, the trees rarely exceeded 3 m (Fig. 3). ANOVA results for tree height indicated that individuals on unburned sites and on sites burned before 1988, attained greater mean height than on the other treatments (*F*: 4.25; *P*: 0.02). Also, the treatment with the highest recurrence of fire had the lowest tree height with the same recovery time (*F*: 4.5; *p*: 0.049) (Fig. 4). Average crown diameter decreased with diminishing recovery times (*F*: 4.97; *P*: 0.01), while no significant effect was detected with increasing fire recurrence (*F*: 2.38; *P*: 0.15) (Fig. 4).

All woodlands had a high percentage of very healthy trees (more than 55%) and a low percentage of dead individuals (the highest was 12% for the 2003–2004 woodland). The highest percentage of very healthy trees was found in the unburned woodland and the woodland which was subjected to two fires, with 90% and 88% respectively (Table 2). For all woodlands, the most frequent tree growth habits were semi-erect and decumbent. The unburned woodland had the highest percentage of semi-erect and erect trees (55% and 21% respectively). The highest percentage of decumbent trees was found in the 2-fire treatment (70%) (Table 2). The *depressa* form showed highest values in the woodlands burned during seasons 1993–1994 and 2000–2001 (29% and 22% respectively).

4. Discussion

The data from the structural analysis performed in this study suggest that the structure of *P. flexuosa* woodlands is controlled by the fire history of each site. For all treatments in the study area, we found that the stem structure of *P. flexuosa* reflects a fire-modified environment, and the stem structure variability that was observed would be related to the different recovery times following fire, and can be interpreted as the successional trajectory after fire. It should be noted that stem structure in the unburned treatment, despite being the best preserved woodland, also showed evidence of past fire events. Furthermore, the higher recurrence of fire results in a highly affected tree stratum. The stronger structural modification observed on sites with high fire recurrence suggests that forest recovery in the area is not linear with recovery time, which is consistent with the proposed hypothesis stating that loss of the recovery capacity is a consequence of recurrent fires. In this case, as has been observed in other woody communities, a process that triggers recovery of the original structure will be necessary (Rostagno et al., 2006; Suding et al., 2004).

Our results showed that fire modified both stem density and growth habits of the tree, generating an environment dominated by individuals with numerous smaller sized stems (<0.5–5 cm BD). This was particularly evident in the loss of adult classes and the reduction of tree height, in environments with high fire recurrence. This is consistent with previous studies that indicate that Prosopis species resprout both from the base and from aerial parts as a response to fire. In North America, *Prosopis juliflora* can develop new aerial, basal or subterranean shoots depending on the level of damage caused by fire to the plant. If the fire is of low intensity, only a proportion of the aerial part of the individual dies, and plants resprout from axillary buds on crown branches. However, when fires are severe, the crown is completely consumed, the entire aerial part of the plant dies and a large number of basal resprouts are produced (Cable, 1965; Danthu et al., 2003; Gould et al., 2002; White, 1969). Generation of basal resprouts following fire has been reported by Cano et al. (1985) for *P. flexuosa* in La Pampa province. This could explain the particular structural pattern of the woodlands burned in seasons 1993–1994 and 2000–2001, where trees contain numerous basal resprouts. Although fire severity was not measured in this study, the data from the fire department of the Direction of Renewable Natural Resources of General Alvear indicates that both of those seasons showed highly severe fires, which affected the whole plant community and, that a large number of basal resprouts emerged, probably due to the aerial part of the plant being consumed.

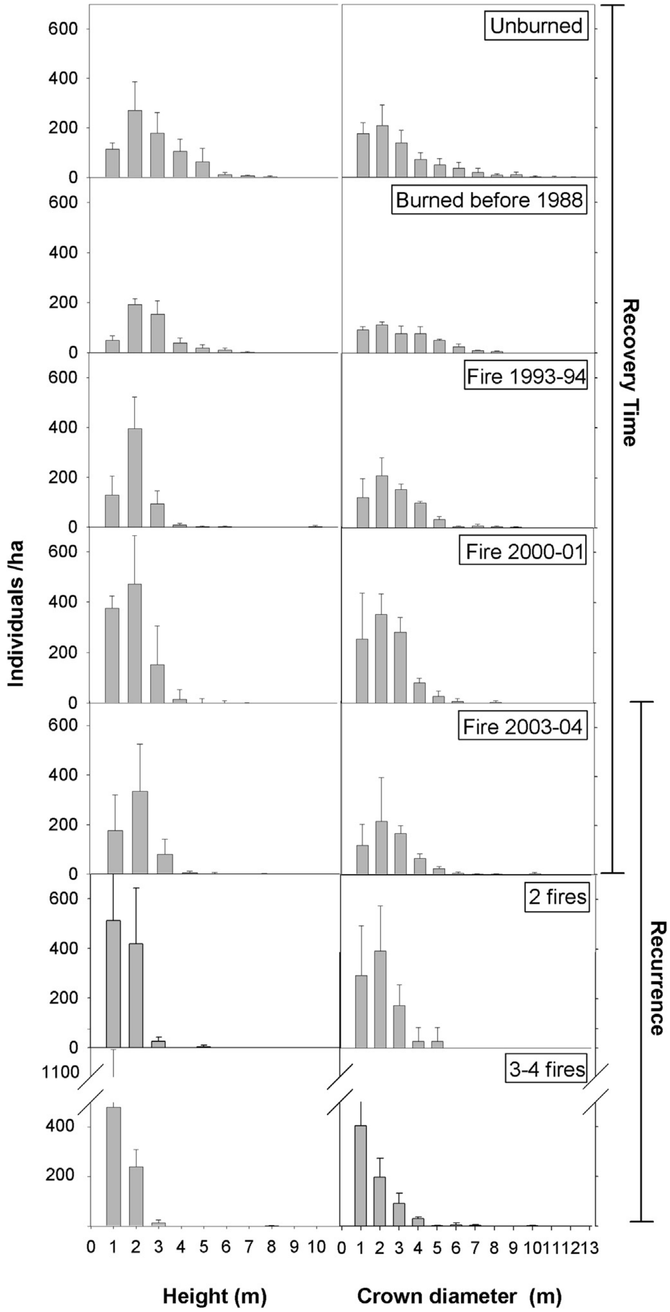

Fig. 3. Frequency histogram of total tree height and crown diameter of individuals in the different treatments. Bars represent means, lines denote standard deviation. Vertical lines show the treatments included in the analysis of the effect of recovery time and fire recurrence.

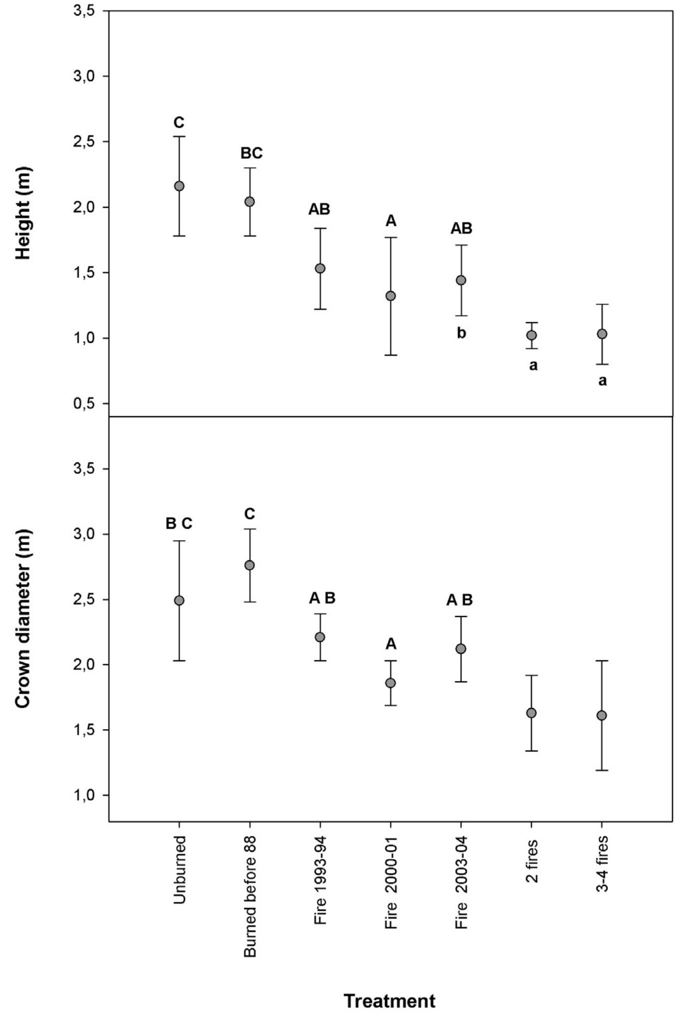

Fig. 4. Mean overall tree height and crown diameter for the different treatments. Circles represent the mean and vertical lines denote standard deviation. Different capital letters indicate significant differences at $p < 0.05$ among recovery time treatments and different lower case letters indicate significant differences at $p < 0.05$ among fire recurrence treatments.

The change in the growth habits of the trees induced dominance of decumbent and short individuals. In southeastern Mendoza we found that *Prosopis* stands, with longer recovery times and low fire recurrence, were dominated by tall and semi-erect trees with a low number of stems; whereas a large number of 1 m tall decumbent individuals with a large number of stems, predominated in woodlands with shorter recovery times and higher fire recurrence. Fisher (1977) showed that *P. juliflora* is multi-stemmed as a consequence of the destruction of the main stem or apical meristem by animal attacks, cattle trampling or frost. Our analysis suggests that the same mechanism could be induced by fire. Hicke et al. (2012) demonstrated the importance of indirect consequences of fire on post-fire mortality of woody plants. In our study, we found no clear evidence of this effect since we did not find a clear increase in the number of trees dead from fire, and both the unburned woodland and the woodland with recurrent fires exhibited a high percentage of healthy trees. However, most healthy trees in the first woodland were adults, whereas trees in the second one were juveniles or saplings.

Although our study did not focus on commercial forestry, it is known that by combining health status and tree shape it is possible to determine what uses can be made of the timber produced from the woodland. These uses include manufacturing of furniture, production of posts, firewood and charcoal (Alvarez and Villagra, 2009; Alvarez et al., 2011a, 2011b). The fire-induced structural transformations observed suggest that forest harvesting may not be possible in the burned areas. This is particularly evident at sites with high fire recurrence where very few stems over 7.5 cm BD were recorded. An increase in fire frequency, as would be expected from predictions by climate change models (Labraga and Villalba, 2009) and from the factors that predispose fire in the area (Cesca, 2011), might threaten such forestry potential and prevent recovery of the *P. flexuosa* population. Development of appropriate management practices is necessary for the recovery of the forestry potential of burned woodlands. Pruning and differential use of stems from multi-stemmed trees have been suggested as useful

Table 2
Health status and tree classification according to growth habit of *P. flexuosa* population in woodlands with different fire histories. Values represent the mean percentage for each treatment.

	Unburned	Burned before 88	Fire 1993–94	Fire 2000–01	Fire 2003–04	2 Fires	3–4 Fires
Health status							
Very healthy	90	71	57	63	79	88	83
Moderately healthy	1	15	29	23	7	4	6
Not very healthy	3	5	12	9	2	2	2
Dead	6	9	2	5	12	6	9
Tree growth habit							
Erect	21	13	5	7	4	2	3
Semi-erect	55	41	33	43	34	26	53
Decumbent	23	39	33	28	56	70	33
Depressa	1	7	29	22	6	2	11

techniques for obtaining some products, while at the same time improving the growth habit in these types of trees (Alvarez et al., 2011a). However, further studies are necessary to better understand the potential of these techniques for post-fire management of burned areas. From the standpoint of livestock farming, a fire-induced increase in stem number may hinder livestock access to forage, reducing the actual grazing area (personal observation). In contrast, reduced tree height would make available *P. flexuosa* leaves and fruits of high forage value. Therefore new studies are required to properly assess the effects on livestock production from changes brought by fire.

The strong modification that fire causes to the population structure of *P. flexuosa* woodland can have functional consequences for this ecosystem. *P. flexuosa* is known to facilitate the recolonization and establishment of other colonizing species in the area (Cesca et al., 2012). The loss of woody species may therefore result in reduced establishment and productivity of some grasses (Aguiar and Sala, 1999; Cesca et al. (2012); Villagra et al., 2009). The effects of shade from *P. flexuosa* may ameliorate environmental conditions beneath the canopy to favor understory species (Rossi and Villagra, 2001). The modifications to growth habits induced by fire could affect these functional mechanisms, therefore it is important that further research evaluate this effect.

Finally, it is worth highlighting the fact that the response to fire was not linear; suggesting that recovery time is not the only factor determining the successional status of the *P. flexuosa* population. This might include characteristics of the last fire, such as amount and status of the fuel present, fire intensity, and the capacity of individual species to resprout after fire (Cable, 1965; Causin et al., 2004; White, 1969). Fire recurrence can induce positive feedback that generate new stable states, commonly dominated by grasses or small shrubs (Rostagno et al., 2006) This process could be occurring in the study area, where the sites with a higher dominance of herbs coincide with those with a higher recurrence of fire (Cesca, 2011). Such higher fire recurrence would reduce the availability of combustible material, which would decrease fire intensity, and allow the development of herbs and grasses, which would finally favor the occurrence of low-intensity fires. A possible increase in fire frequency across the Monte region as a response to climate changes and to higher grass productivity (Villagra et al., 2009) may lead some woody communities to be transformed into ecosystems with a simplified structure, as it has been observed in other areas of the world (Archer, 1995; Rostagno et al., 2006).

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