Effects of fire and water availability on the emergence and recruitment of grasses, forbs and woody species in a semiarid Chaco savanna

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Abstract   In the semiarid Chaco savannas, the balance between herbaceous and woody species affects landscape configuration and ecosystem services such as forage production. Therefore, understanding the factors that control this balance is crucial for management. In a factorial experiment, we assessed the effects of fire and water availability on the emergence and recruitment of grasses, forbs and woody species. The results showed that the effects of fire and water availability on early regeneration stages differed among the three functional groups. For grasses, fire and water addition enhanced emergence when acted solely, but only the positive effects of fire were translated into a greater recruitment, irrespective of the water availability. For forbs, only water addition, when acted solely, promoted the emergence, although this effect was not translated into a greater recruitment. Lastly, in the case of woody species, both fire and water addition reduced emergence and recruitment. Our results support the notion that both fire and greater water availability would contribute to the maintenance and recovery of a grass-dominated state of vegetation through a positive effect of fire on grasses recruitment and a general negative effect of fire and water on woody species emergence and recruitment.

Key words: burning, plant functional group, range management, shrubland, water addition.

INTRODUCTION

Semiarid savannas have a continuous grass layer with scattered trees, sustain large populations of wild and domestic herbivores, and are periodically burned (Scholes & Archer 1997). Water availability, fire and range management are strong controls of the structure and functioning of semiarid savannas. Water availability correlates with both aerial net primary production (McNaughton 1985; McNaughton *et al*. 1993) and with the cover of woody species (Sankaran *et al*. 2004, 2005). It is also positively associated with fire frequency because vegetation accumulates greater amounts of fuel biomass as precipitation increases (Bravo *et al*. 2010). Fire has been largely invoked as a control of woody encroachment in grasslands (Bond *et al*. 2003). Therefore, a sequence of humid years would intensify the fire regime and thus promote the grass component of the savanna (Westoby *et al*. 1989; Bravo *et al*. 2010). However, high grazing intensity reduces fuel accumu-

lation, and in that case an increase of water availability may promote the establishment of seedlings of woody rather herbaceous species (Westoby *et al*. 1989).

The grass–tree coexistence has been a matter of considerable debate in the past (Scholes & Archer 1997; Jeltsch *et al*. 2000; Sankaran *et al*. 2004). It has been largely analysed from a competition-based perspective, where niche separation with respect to limiting resources such as water allowed the coexistence of both life forms, in an equilibrium state (Walter 1971; Walker *et al*. 1981). An alternative approach proposed a demographical perspective, in which tree populations were particularly limited by factors such as fire, grazing or drought. Thus, the interannual variability of these factors would allow tree–grass coexistence in a non-equilibrium state (Higgins *et al*. 2000; Jeltsch *et al*. 2000). A more recent comprehensive model combines both perspectives and explicitly considers the role of competition in the critical demographical processes (e.g. seedling establishment) that are particularly sensitive to fire or other disturbances (Sankaran *et al*. 2004). In this context, it is crucial to understand the isolated and combined effects of these factors on the demography of the main plant functional groups of savannas (i.e. grasses, forbs and woody species).

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The individual impact of fire and water availability on seedling emergence and recruitment has been extensively documented, but their combined action has received less attention. In turn, major studies in the field focus on one or a few species. In general, these studies found that fire promotes regeneration of grasses over woody species because of their faster response to capture resources released by the disturbance (Grime 1979; Veenendaal *et al.* 1996a; D'Antonio *et al.* 2001; Bond *et al.* 2005), and because seeds of some grass species tolerate high temperatures during fire (Trollope 1978; Zacharias *et al.* 1988; Overbeck *et al.* 2005). Water availability is a strong controlling influence of germination and establishment of trees and shrubs (Willams & Hobbs 1989; Wilson & Witkowski 1998; Schwinning & Sala 2004) and heavy rain events can cause episodic germination that results in alternative states of the botanical composition (Westoby *et al.* 1989; Bowers *et al.* 2004).

Our objective was to elucidate the individual and combined effects of water availability and fire on the balance among grasses, forbs and woody species in a semiarid savanna. Unlike the most usual approach that focuses on a few species, we studied seedling emergence and recruitment of the three main plant functional groups in savannas: grasses, forbs and woody species. Our study allowed us to evaluate the role of water availability and fire on specific and critical demographical stages and to infer the role of competition among plant groups. Our hypothesis was that water availability, fire and their combined action will promote the grass component within the savanna and cause a detrimental effect on woody species and forbs. The study was performed in the South American Chaco, a vast alluvial plain where 500 years of free-ranging grazing by domestic herbivores have converted most savanna landscapes into secondary forests and shrublands, reducing their value as a forage resource, and altering fire regime and soil water balance (Adámoli *et al.* 1990; Kunst *et al.* 2006; Grau *et al.* 2008).

MATERIALS AND METHODS

Study area

The research was conducted in 'La María' Experimental Ranch, which belongs to the Agricultural Experiment Station of Santiago del Estero, National Institute of Agricultural Technology (28°3′S, 64°15′W). The climate is subtropical with seasonal rains concentrated in summer (monsoonal type) (mean annual rainfall is 569 mm). Summers are warm and humid (mean temperature in January 28°C) and winters are dry and mild (mean temperature in July 14°C), although frost events take place frequently (Boletta 1988). Soils are classified as typical Torriortent (Lorenz 1995) and the

vegetation is a mosaic of savanna, shrubland and forest. The highest topographical positions on the relatively flat landscape are associated with dry subtropical forest, whereas savannas are located in the lowest topographical positions of the landscape, next to run-off water lines. The savannas are dominated by an herbaceous–shrub community, with isolated tree individuals of *Aspidosperma quebracho-blanco*, *Acacia aroma* and *Prosopis nigra*. The herbaceous layer is composed of perennial grass species of the genera *Elionurus*, *Bothriochloa*, *Schizachirium*, *Heteropogon*, *Chloris*, *Digitaria*, *Trichloris*, *Pappophorum*, *Aristida*, *Setaria*, *Pennisetum* and *Eragrostis*. Forbs are represented by the genera *Lantana*, *Zexmenia*, *Indigofera*, *Rhynchosia* and *Bidens*. At present, most of these savannas show signs of degradation by overgrazing, and *Elyonurus muticus*, a grass of poor forage value and with flammable characteristics, is the dominant species (Kunst *et al.* 2006).

In order to encompass the spatial variability, we performed a field experiment at two sites (sites 1 and 2 hereafter) that were located 2 km apart. Both sites were protected from domestic livestock during the experimental period. Before the experiment started, compared to Site 2, Site 1 had almost twice the plant basal cover (11% *vs.* 6%) and fuel accumulation (5200 *vs.* 2300 kg ha^{-1} herbaceous dry matter biomass), and had lower plant species richness at the patch scale (0.25 m^2, 7 *vs.* 9 species).

Experimental design

At each site, we performed a complete factorial design of two manipulated factors, fire (with and without fire) and water (with and without water addition) in order to evaluate emergence and recruitment of grasses, forbs and woody species. Within each site, the four possible combinations of both factors were each randomly assigned to three 10 m × 15 m plots. The fire treatment simulated a common disturbance in these savannas (Bravo *et al.* 2001), while the water addition treatment simulated 2 years with precipitation above average and more regularly distributed. We used site (Site 1 and Site 2) as a factor that represented the intrinsic spatial variation at the landscape level. In each plot, we randomly located five permanent subplots (0.25 m^2) where emergence and recruitment of grasses, forbs and woody species were assessed throughout two growing seasons (2006 and 2007).

Fire was applied once, at the beginning of the experiment, in the spring of 2005 (November). The total area (10 m× 15 m) of the fire plots was burned. Head fires were set by two operators carrying drip torches, setting the fire line perpendicular to the prevailing wind. We measured meteorological variables in order to maintain fire within prescription (Wright & Bayley 1982). Burning was completed between 10.30 and 14.30 hours with minimal environmental variation during the procedure. Mean wind speed during fire was 8.3 km h^{-1}, mean air temperature was 28.4°C, and mean relative humidity was 27%. Mean temperatures at the soil surface and at 1 cm depth were 191 and 45°C respectively, although several records at the soil surface reached 400°C.

Water addition was performed on a weekly basis during the rainy season (summer), of the two experimental years. The amount of water added each season was 72 mm. Based on the second most frequent event (12 mm) observed in the

rainfall series 1981–2005, water addition was distributed in six 12-mm events between mid-summer and late summer (February to mid-March). Water was applied by sprinklers and, unlike fire, the treatment was restricted to an approximately 4-m^2 area centred on the permanent 0.25-m^2 subplots within the treatment plots due to operational restrictions.

In each permanent subplot, we recorded the number of seedlings of the three functional groups on a weekly basis and classified them into two categories, emerged and recruited. We were able to indentified newly emerged seedlings on each sampling date on the basis of some morphological characteristics. Emerged seedlings were those with height <3 cm. Additionally, in the case of grasses, we checked for the absence of adventitious roots. Forbs and woody species varied in colour, shape and size. This identification was also facilitated by the highly episodic and discrete nature of emergence, associated with rainfall events. Accumulated emergence until the end of the experiment was calculated as the sum of all emerged seedlings observed from November to April of both growing seasons. Recruited seedlings were those that remained alive at the end of each of the two growing seasons (O'Connor 1994). Accumulated recruitment was calculated as the sum of all recruited seedlings at the end of the two evaluated growing seasons.

We recorded environmental variables that described both general environmental conditions as well as specific microsite conditions of the different experimental situations. Precipitation during the experimental period was estimated by two micropluviometers in each site. In order to explore if fire affected emergence and recruitment through changes in gravimetric soil moisture, we estimated soil moisture, for control and fire plots, during the entire experimental period. Additionally, we measured the irrigated plots immediately after the water addition events, to evaluate the short-term impact of this treatment on soil moisture. We collected one composite sample per plot (five subsamples each) consisting in soil cores of 2 cm in diameter and 15 cm in depth. In each plot, soil samples were obtained in the area surrounding the 0.25-m^2 permanent subplots. Samples were oven-dried at 105°C during 48 h. Photosynthetic active radiation (PAR), measured as photon flux density, was estimated in the control and burned plots 3 months after fire (February 2006). Plots with or without water addition were not compared, because the measurements were made only once, before the water addition started. The photon sensor (Basic Quantum meter, Apogee Instruments Inc., Logan, UT, USA) was located at the soil surface in the inter tussock microsites where emergence and recruitment occur. PAR in each plot was estimated on the basis of three to five subreplicates located in the 0.25-m^2 subplots.

Statistical analyses

To test the effects of treatments on the mean accumulated emergence and recruitment of seedlings of grass, forbs and shrubs, we used a three-way ANOVA with fire (two levels) and water addition (two levels) as treatments and site (two levels) as a classification factor, and their corresponding interactions terms. Mean comparisons were performed by Tukey tests using the Bonferroni correction (Willems & Raffaele 2001). When interactions were not significant, means were compared by *a priori* contrasts of main effects (Willems & Raffaele 2001). For emergence of woody species we included the distance to the nearest adult as a covariate, because the spatial distribution of woody adults, unlike that of herbaceous species, was highly heterogeneous. Although we presented emergence and recruitment results that integrate two growing seasons, we also examined each season separately. PAR and soil moisture were analysed by two-way ANOVAs with fire and site, and their interaction term as factors. We used the Proc GLM of the SAS statistical package for mathematical calculations (SAS Institute Incorporated 1990). Although the variances of accumulated emergence and recruitment of the three plant groups were homogenous, emergence and recruitment data were not normally distributed so they were rank transformed before analysis (Conover 1980). We used $\alpha = 0.05$ for all statistical analyses.

RESULTS

Both years were similar in terms of total precipitation (611 and 600 mm for 2006 and 2007 respectively), but they differed in the magnitude and frequency of rain events. During the first year, rain events were less frequent (13 *vs.* 51 events) and more intense (mean size of rain event 47 *vs.* 12 mm respectively) than the second year (Fig. 1a). Emergence of all functional groups in the untreated (control) savanna was episodic and associated with rainfall events (Fig. 1b). Emergence of forbs and woody species was considerably higher during the first season than the second one, while the emergence of grasses was relatively similar in both seasons.

The mean accumulated emergence of grasses revealed an interactive effect of fire and water addition (Fig. 2, Table 1). Both factors promoted emergence when acting separately but had no effect when acting together. This response was similar for both seasons, separately analysed (water × fire $P < 0.02$ in both seasons). The mean accumulated recruitment of grasses was about three orders of magnitude lower than emergence, and was consistently promoted by fire, solely or combined with water addition (Fig. 2, Table 1). Water addition had a positive, but statistically marginal effect ($P = 0.08$) when applied on unburned plots (Fig. 2, Table 1). In the case of recruitment, fire and water effects documented after two growing seasons were exclusively explained by differences during the first growing season, because a separate analysis on the second growing season did not show significant differences among treatments ($P = 0.4$ and 0.9 for fire and water respectively, data not shown).

The mean accumulated emergence of forbs revealed an interactive effect of fire and water addition that consisted of a positive effect of water addition when acting solely and a neutral effect when acting combined with fire (Table 1, Fig. 2). This response was significant in both seasons separately ($P < 0.03$ for
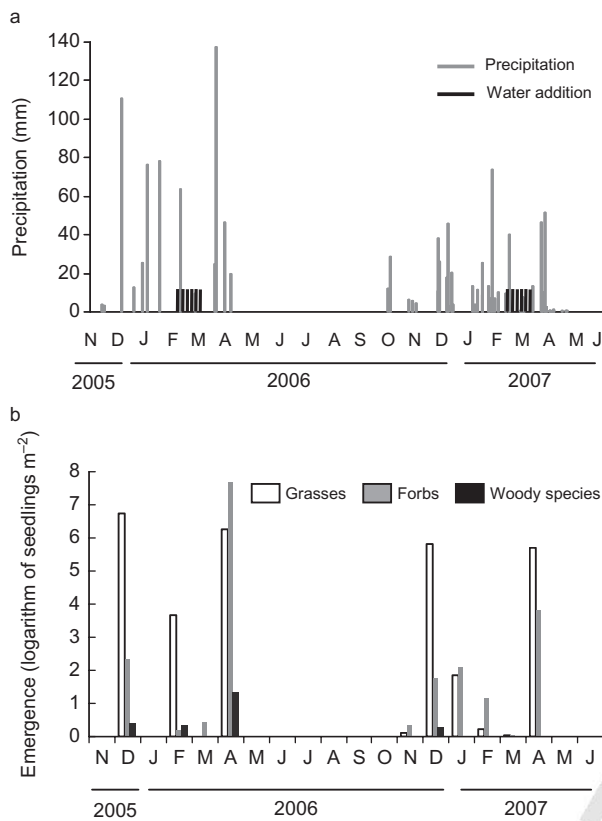
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Fig. 1.   (a) Precipitation per rain event and experimental irrigation throughout a 2-year experiment of fire and water treatments. (b) Emergence episodes of grasses, forbs and woody species in control plots over 2 years.
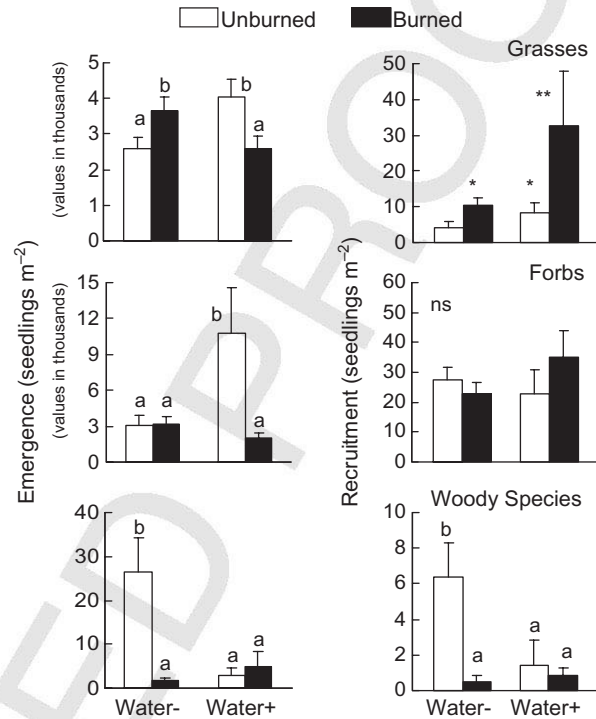

Fig. 2.   Accumulated emergence (left panels) and recruitment (right panels) of grasses, forbs and woody species in plots subjected to a complete factorial experiment of fire and water addition. Different letters indicate significant differences ($\alpha = 0.05$; Tukey) and in recruitment of grasses, the asterisks indicate significant differences among burned and unburned plots ($\star = 0.05$ and $\star\star = 0.01$).

both seasons), but the pattern was more evident during the first growing season (data not shown). The mean accumulated recruitment of forbs was about two orders of magnitude lower than their emergence, and it was not affected by fire or water (Table 1, Fig. 2).

The mean accumulated emergence of woody species was considerably lower than those of the other groups, strongly depended on the distance to the nearest adult (Table 1) and revealed a negative effect of both fire and water (Fig. 2). This pattern was also observed for both growing seasons, separately analysed ($P < 0.03$ for both seasons). The mean accumulated recruitment of woody species represented approximately 30% of the seedlings emerged. Even though Site 1 exhibited greater seedling recruitment than Site 2, in both cases it was negatively affected by fire and water. In this case, fire and water effects documented after two growing seasons were exclusively explained by differences during the first growing season, because a separate analysis on the second growing season did not show significant differences among treatments ($P = 0.6$ and 0.2 for fire and water respectively).

Gravimetric soil moisture in the top 15 cm had a strong seasonal variation that ranged between 1 and 27% and accounted for most of variation ($P < 0.0001$, Fig. 3). Fire slightly but significantly affected soil moisture, reducing it during the first experimental season (P of interaction = 0.004, Fig. 3). Site 1 had slightly greater soil moisture than Site 2 (10 *vs.* 8.9% respectively, $P < 0.001$). The water addition temporarily increased soil moisture ($P < 0.0001$, Fig. 3). Three months after fire, burned plots of Site 1 had lower PAR at the soil surface than their unburned controls, whereas PAR was similar in burned and unburned plots of Site 2 (fire × site interaction $P = 0.002$; Fig. 4).

DISCUSSION

This study showed that fire and water addition promoted the regeneration of grasses and reduced that of woody species, whereas regeneration of forbs was less responsive to the experimental treatments. This suggests that grasses constitute the functional group that more efficiently captured the released resources after disturbance and supports the accepted notion that, in the absence of grazing, fire and greater water availability

Table 1. ANOVA results (*F*-values) for emergence and recruitment accumulated during two growing seasons, of grasses, forbs and woody species

Source of variation	Grasses		Forbs		Woody species	
	Emergence	Recruitment	Emergence	Recruitment	Emergence	Recruitment
Fire	0.06	**6.51***	**6.61***	0.41	**10.6****	**4.2***
Water	0.04	3.28	**4.47***	0.49	**6.32***	**13.3****
Site	0.1	2.28	0.03	1.87	2.19	**9.4****
Fire × water	**8.17****	0.45	**16.4****	0.76	**4.73***	**8.23***
Fire × site	0.2	0.6	2.76	0.19	0.58	0.6
Water × site	1.95	1.38	3.49	2.21	0.75	0.21
Fire × water × site	1.31	0.5	3.97	1.43	0.18	0.01
Covariable					**26.1****	

*P < 0.05, **P < 0.01. Values in bold indicate significant differences. Degrees of freedom of the numerator and denominator are 1 and 16 respectively, except for emergence of woody species, which are 1 and 15 respectively.
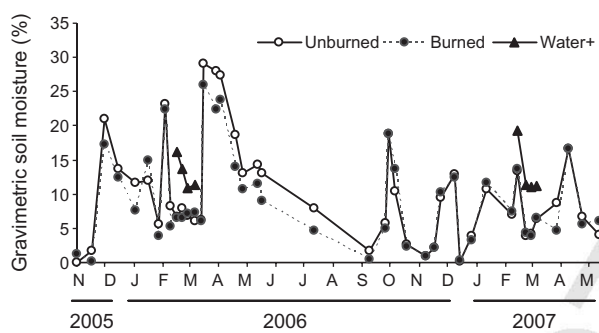

Fig. 3. Gravimetric soil moisture in the top 15 cm of the soil profile of unburned and burned plots during the entire experimental period. Triangles indicate the gravimetric soil moisture of plots receiving water addition, documented immediately after each addition. Data of both sites are pooled.

Fig. 4. Photosynthetic active radiation (PAR; measured as photon flux density), at the soil surface, of unburned and burned plots. Measurements were obtained 3 months after the fire treatment (February 2006).

would promote the state of grassland and preclude woody encroachment. Emergence of woody species was associated with the vicinity of adult plants. The greater grass recruitment in burned plots, together with the lower PAR (at Site 1) at the soil surface and lower soil moisture (at both sites), suggest that competition among grass and woody species partially control vegetation structure. Finally, the temporal dynamics and the magnitude of emergence was episodic and responded to soil water content variation after rain events.

In grasslands and savannas, the recruitment of seedlings of grasses and forbs occurs when disturbances in general (Platt & Weiss 1985; Aguilera & Laurenroth 1993; Hook *et al.* 1994) or fire in particular (D'Antonio *et al.* 2001; Laterra & Solbrig 2001) relax competition for resources. The positive effects of fire on the emergence and recruitment of grasses have been documented in experimental and accidental fires in a variety of ecosystems (Silva *et al.* 1991; Canales *et al.* 1994; Snyman 2004; Brys *et al.* 2005; Jacquemyn *et al.* 2005; Glasgow & Matlack 2007). Other studies
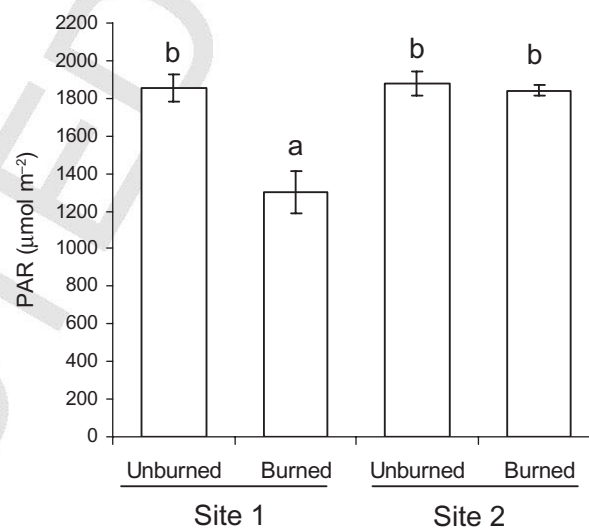
emphasize that the effects of fire may also operate through other demographical mechanisms such as the reduction of tuft mortality by self-shading, which may counteract immediate negative effects of fire (Zimmermann *et al.* 2010). For semiarid savannas of the Chaco, fire was also found to increase the emergence of two palatable grasses, *Heteropogon contortus* and *Pappophorum pappiferum* (Kunst *et al.* 2003).

The lower emergence and recruitment of woody species caused by fire, and the general lack of response of forbs could be explained by direct effects of fire such as seed mortality or by indirect effects (e.g. drying of the shallow soil profile at different periods) in combination with common strategies for the species of these functional groups. On the one hand, soil temperatures during experimental fire (in some plots over 400°C)

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are lethal for the seeds of most woody species (Auld & O'Connell 1991; Shackleton 2007). In experimental burns on Australian savannas Setterfield (2002) attributed the lower emergence of woody species to a negative indirect effect of fire mediated by greater seed predation by ants and greater resource competition. In this study, although predation was not documented, we believe that the greater magnitude of short-term emergence of grass seedlings may have been strong enough to reduce the emergence of woody species by competition. Hence, pre-emptive competition (Platt & Weiss 1985) after fire by grass seedling could be invoked as the underlying mechanism of our results. On the other hand, some genera of forbs (in ex. *Bidens*) are typically annual herbs, present ruderal life strategies and hence respond quickly to disturbances (Grime 1979), while other genera mainly of the *Verbenaceae* family such as *Aloysia* or *Lantana* are small subshrubs, and probably less ruderal than the annual herbs. In this sense, the lack of response in recruitment of forbs to manipulation of fire and water could also be explained by the heterogeneity of life strategies within this functional group.

While in other field experiments water promoted the emergence and recruitment of both grasses and forbs (Isselstein *et al.* 2002; Sher *et al.* 2004; Lenz & Facelli 2005), this study allowed to indicate some differences between both groups. Water addition during February–March, before the start of the late-summer rains generated massive emergence in forbs that did not necessarily translate into higher recruitment. In contrast, the increased availability of water seems to have been more efficiently used by grasses, because the positive effect on emergence was also translated into greater seedling recruitment. Coinciding with our findings, C_4 grasses from semiarid African savannas and arid shrublands with summer rains of South America show an important emergence throughout the entire wet season (Veenendaal *et al.* 1996b; Marone *et al.* 2000). In this regard, Maze and Watt (1993) mentioned that some grass species of African and Australian savannas germinate with lower soil water availability than is generally required by the grasses of Australian grasslands. This suggests that C_4 grasses of semiarid savannas are adapted to germinate and recruit from a wider range of moisture conditions than forbs and do not depend on special conditions of large amounts of soil water.

Water addition had a negative influence on the recruitment of woody plants, a result that differs from the other studies in savannas (Hoffmann 1996; Brown & Archer 1999). Barbera *et al.* (2006) found that rainfall events even smaller than those simulated in our study triggered emergence of the woody species *Rhamnus lycioides* when they were preceded by a reduction of the incident radiation and temperature, coupled with an increase in the air relative humidity.

Moreover, in some arid ecosystems, episodic or massive emergence of woody species is triggered by intense rainfall events during the autumn (Bowers *et al.* 2004). The amount of water added in this study was small compared with the autumn rain events and, additionally, water was not added under the typical conditions of lower irradiance, low air temperature and higher relative humidity that are associated with storms. We believe that these facts might have contributed to reduce the effectiveness of the irrigation treatment, beyond the greater soil moisture documented for the irrigated plots immediately after water addition. As evidence, soil water contents after experimental irrigation were lower than those registered after rainfall events that triggered episodic emergence.

It has been proposed that relative increases in precipitation during winter due to global warming would explain changes in the grass : woody ratio favouring woody species (Brown *et al.* 1997). If the rainfall seasonal pattern in the semiarid Chaco tends to have more precipitation during autumn, we might expect an increase in cover of woody species by an increase in their recruitment success (Sankaran *et al.* 2005). Moreover, recent evidence (Schwinning *et al.* 2005) suggests that just the increase in precipitation variability predicted by global warming might affect the balance in favour of woody species. This positive effect on woody plant recruitment was also envisioned in this study because during the first wet season, when rainfall events were more variable in time and magnitude, we detected a greater emergence of woody species.

High spatial heterogeneity is an inherent characteristic of the recruitment of woody species in arid environments (Watson *et al.* 1997). In the grassland–forest mosaic of central Spain, Arrieta & Suárez (2005) found that the spatial distribution of the emergence of *Ilex aquifolium* depended on the spatial pattern of seed rain. This observation agrees with our finding of significant effects of the nearest adult woody plant on emergence. Initial spatial variation in seed bank and other associated processes (e.g. granivory) were not evaluated in this study, although, in semiarid grasslands, temporal variation of the seed bank could be even larger than spatial variation (Coffin & Laurenroth 1989). In general, fire and water interactions were significant only for emergence data. This suggests that the combined effect of both factors on recruitment could be different than the combined effect observed during emergence according to the precipitation pattern in the following wet seasons after fire occurrence.

In conclusion, the positive responses of grass emergence and recruitment to manipulated factors with respect to the other functional groups suggest that, in a grass dominated savanna, fire and water may contribute to maintain savanna over shrubland state. New research that studies topics such as the autecology of key species of these savannas, spatial variability, interactions

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among factors, climate change and herbivory are necessary for continued understanding, conservation and management of semiarid Chaco savannas.

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