Forest Ecology and Management 315 (2014) 86–94

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Effects of fire on arbuscular mycorrhizal fungi in the Mountain Chaco Forest

Silvana Longo [a,*], Eduardo Nouhra [a], Bruno T. Goto [b], Ricardo L. Berbara [c], Carlos Urcelay [a]

[a] Instituto Multidisciplinario de Biología Vegetal (IMBIV), CONICET, Universidad Nacional de Córdoba, Casilla de correo 495, 5000 Córdoba, Argentina
[b] Departamento de Botânica, Ecologia e Zoologia, CB, Universidade Federal do Rio Grande do Norte, Campus Universitário, 59072-970 Natal, RN, Brazil
[c] Soil Science Department, Institute of Agronomy, Federal Rural University of Rio de Janeiro, Seropédica, RJ, Brazil

ARTICLE INFO

Article history:
Received 3 October 2013
Received in revised form 17 December 2013
Accepted 22 December 2013

Keywords:
Disturbances
Spores communities
Soil nutrients
Glomeromycota
Chaco Forest
Argentina

ABSTRACT

The aim of this study was to evaluate the fire effects on the AMF spore communities and soil chemical properties as well as the existence of possible correlations between them in the Chaco Serrano Forests of central Argentina. Our hypothesis is that the fire has a negative impact on the community of AMF spores (i.e. density, diversity, richness and evenness) and soil chemical properties. In addition, we expect to find a high correlation between changes in the communities of fungi and soil chemical properties. We selected five areas in the "Sierras Pampeanas" mountain ranges within the Chaquean region in central Argentina. In each of them we selected adjacent burned and unburned forest sites. Burned sites have all the same time since fire occurrence (August–November 2009) and soil samples were collected in autumn (April) and spring (November) in 2010. The fire events had direct negative effects on AMF spore communities. Evenness, and notably diversity and richness of AMF spores decreased in the burned sites. Density of AMF spores was not affected by fire. With the exception of C:N, nitrate and electrical conductivity, soil parameters showed significant differences between burned and unburned sites. The changes in AMF spore composition were not significantly correlated with most of the soil variables measured here. The results of this study suggest that fire occurrence negatively affect AMF communities. These effects do not seem to be mediated by changes in soil abiotic properties. Rather, they suggest direct effects of fire on soil fungi.

1. Introduction

Disturbances alter biological diversity (Bengtsson et al., 2002). Fire is among the most widespread disturbance that affects biological organisms, either directly or indirectly (Busse and DeBano, 2005). Direct effects mainly include reduction or elimination of the aboveground and belowground biomass, loss of soil organic horizon, and increase in soil temperature and ash deposition. Among the indirect effects, changes in soil properties such as organic matter, carbon, nitrogen, phosphorus, pH are frequently reported (e.g. Neary et al., 1999; Certini, 2005; Kara and Bolat, 2009; Dias et al., 2010; Longo et al., 2011; Switzer et al., 2012; Wang et al., 2012; Williams et al., 2012).

Among belowground organisms, arbuscular mycorrhizal fungi (AMF) are known to colonize the majority of land plants and provide them with access to soil nutrients in return for carbon compounds (Smith and Read, 2008). Because AMF taxa differ in their effects on plant growth, the composition of AMF communities influence the structure of plant communities (van der Heijden et al., 2008).

After severe disturbances such as fire, AMF mycelium is impaired and spores could act as source of plant colonization. Plant establishment after fire might depend on the composition of AMF spores in soil. Although many studies have evaluated the direct effects of fire on AMF the results are contradictory, reporting either negative (e.g. Dhillion et al., 1988; Valariño and Arine, 1991; Allsopp and Stock, 1994), neutral (e.g. Bellgard et al., 1994; Rashid et al., 1997; Treseder et al., 2004; Haskins and Gehring, 2004; Docherty et al., 2012), or positive effects on spore abundance (Eom et al., 1999; Moreira et al., 2006). Prescribed burning in grassland increased the total number of spores, mainly of *Glomus etunicatum* and *G. fecundisporum*, reduced the diversity and did not reduced mycorrhizal infection (Eom et al., 1999). Furthermore, in N.W. Spain wildfire reduced the number of spores in the soil and negatively affects the viability of spores of *Aculospora leavis* (Valariño and Arine, 1991). Indirect effected of fire, such as the alteration of soil nutrients availability might also cause changes in the AMF spore communities, usually reflected by a decrease in the number of AMF propagules (Allen et al., 1984). It is hard to generalize the effects of fire on the HMA. The response of this group of organisms to fire differed substantially in both the direction and magnitude of their responses. Those differences in AMF response

* Corresponding author. Tel.: +54 351 4334459x34; fax: +54 351 4331056.
E-mail address: longosil@yahoo.com.ar (S. Longo).

0378-1127/$ - see front matter © 2013 Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.foreco.2013.12.027

Table 1
Location and year of fire occurrence at each study area.

Area	Fire	Latitude (°S)	Longitude (°W)	Elevation (m a.s.l.)
Agua de Oro (AO)	2009	31° 02′ 30.95″	64° 19′ 29.73″	902
Salsipuedes (SA)	2009	31° 07′ 10.20″	64° 17′ 03.90″	743
La Serranita (LS)	2009	31° 45′ 56.75″	64° 28′ 14.92″	659
Cuesta Blanca (CB)	2009	31° 30′ 04.87″	64° 35′ 27.58″	847
Bialet Massé (BM)	2009	31° 17′ 55.46″	64° 29′ 42.59″	770

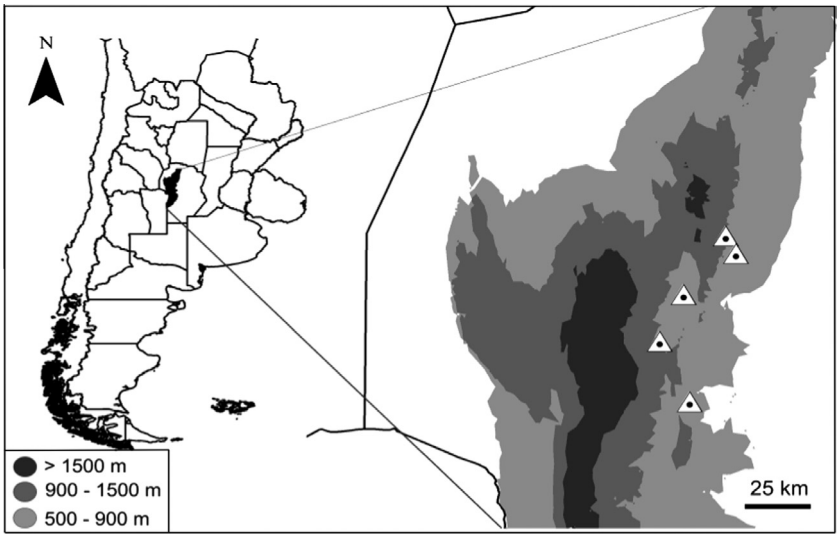

Fig. 1. Location of the five study areas in the Sierras Pampeanas within the Chaquean mountains region in central Argentina.

to fire might be related to variation in the fire characteristics (intensity, duration, wildfire vs. prescribed fire, time after burning, among other factors).

In the Chaco Forest of Argentina, the effects of certain types of disturbances, such as plant removals and forest fragmentation, on AMF spore communities have been recently documented (e.g. Urcelay et al., 2009; Grilli et al., 2012). However, no studies have evaluated fire effects, which constitute one of the most frequent disturbances in the vegetation of the Chaco Forest (Zak et al., 2004). Therefore, experimental designs including replicates of the fire/non-fire situation keeping the above mentioned variables fixed are highly desirable. We selected five areas in the "Sierras Pampeanas" mountain ranges within the Chaquean region in central Argentina in order to assess the impact of fire on AMF spore communities and chemical soil properties as well as the existence of possible correlations between them. In each area we selected adjacent burned and unburned forest sites. Our hypothesis is that the fire has a negative impact on the community of AMF spores (i.e. density, diversity, richness and evenness) and soil chemical properties. In addition, we expect to find a high correlation between changes in the communities of fungi and soil chemical properties.

2. Materials and methods

2.1. Study area

The study region is located in the Chaco Serrano District in Córdoba province, Argentina. This district belongs to the Chaquean region that constitutes South America's most extensive dry seasonal forest (Cabrera, 1976; Moglia and Giménez, 1998), and covers in Córdoba, Argentina an area between 29° and 33° 30′ (S), ranging in elevation from 400 to 1300 m above sea level. Soils are lithosolic (Vázquez et al., 1979) sandy, well drained and shallow (Gorgas and Tassile, 2003). This type of forest is characterized by an open tree stratum that is up to 15 m high and is dominated by *Zanthoxylum coco Gillies ex Hook. f.* & *Arn.* (*Rutaceae*) and *Lithraea molleoides* (*Vell.*) *Engl.* (*Anacardiaceae*); shrubs (1–3 m) primarily dominated by *Celtis ehrenbergiana* (*Klotzsch*) *Liebm.* (*Celtidaceae*) and *Acacia* spp. (*Fabaceae*); herbs and grasses (0–1 m) and numerous vines and epiphytic bromeliads (Luti et al., 1979). The annual rainfall (±750 mm) is concentrated mostly in the warm season (October–April), with mean maximum and minimum temperatures of 26 °C and 10 °C respectively (Luti et al., 1979; Moglia and Giménez, 1998). In these forests most fires are human caused, either by accident or related to farming practices. It has been estimated that fires present a return interval ranging from 2 to 15 years. They generally occur at the end of the dry season, from June to November (Miglietta, 1994). In these ecosystems, woody vegetation is dominated by species that resprout after fire (Gurvich et al., 2005; Giorgis, 2012; Torres et al., 2013). Nonetheless, in the short term, burned sites show more open and lower statured vegetation than unburned ones (Giorgis, 2012). One year after fire occurrence, in unburned sites the herbaceous vegetation was dominated by grasses while burned sites are dominated by forbs (Verzino et al., 2005). Soil properties are strongly affected by fires in these ecosystems; the fire promotes lower organic matter and higher levels of nitrate in soil (Abril and González, 1999).

2.2. Sampling design and soil collection

Five study areas were selected (Table 1 and Fig. 1). In each area, nearby burned and unburned sites were studied. Burned sites have all the same time since fire occurrence (August–November 2009) and soil samples were collected in autumn (April) and spring (November) in 2010. In each site, ten samples of soil (10 replicates × site) spaced by 5 m were randomly collected in a single plot with a soil corer at 0–15 cm depth (2 sites × 5 areas × 2 seasons, total = 200).

Table 2
Relative density (%) of arbuscular mycorrhizal fungi (AMF) spores isolated from five areas of Chaco Serrano Forest, Córdoba-Argentina (n = 100). m = mean; se = standard error. Ns, non significant; $p \geqslant 0.1$; $^{*}p < 0.1$; $^{**}p < 0.05$; $^{***}p < 0.01$.

AMF					
Family	Specie	% Relative density			
		Unburned m ± se	Burned m ± se	p	Total
Glomeraceae	*Septoglomus constrictum*	0.33 ± 0.03	0.67 ± 0.07	***	20.91
	Glomus aggregatum	0.55 ± 0.1	0.45 ± 0.12	Ns	0.63
	Glomus coremioides	0.62 ± 0.14	0.38 ± 0.12	Ns	0.74
	Glomus sp. 1	0.52 ± 0.11	0.48 ± 0.13	Ns	5.41
	Glomus sp. 2	0.49 ± 0.13	0.51 ± 0.12	Ns	3.73
	Glomus sp. 3	0.49 ± 0.12	0.51 ± 0.18	Ns	2.02
	Glomus sp. 4	0.43 ± 0.06	0.57 ± 0.08	Ns	11.53
	Glomus sp. 5	0.28 ± 0.12	0.72 ± 0.29	Ns	1.11
	Glomus sp. 6	0.55 ± 0.3	0.45 ± 0.17	Ns	0.46
	Glomus sp. 7	0.47 ± 0.05	0.53 ± 0.07	Ns	15.30
	Glomus sp. 8	0.32 ± 0.16	0.68 ± 0.31	Ns	0.37
	Glomus sp. 9	0.64 ± 0.13	0.36 ± 0.09	*	3.57
	Glomus sp.10	0.52 ± 0.24	0.48 ± 0.32	Ns	0.87
	Glomus sp. 11	0.48 ± 0.23	0.52 ± 0.28	Ns	0.25
Entrophosporaceae	*Claroideoglomus claroideum*	0.4 ± 0.14	0.6 ± 0.17	Ns	1.59
	Claroideoglomus sp.	0.81 ± 0.18	0.19 ± 0.08	***	1.70
	Entrophospora infrequens	0.86 ± 0.2	0.14 ± 0.06	***	0.62
Acaulosporaceae	*Acaulospora cavernata*	0.52 ± 0.06	0.48 ± 0.08	NS	6.76
	Acaulospora rehmii	0.89 ± 0.17	0.11 ± 0.07	***	1.71
	Acaulospora scrobibulata	0.77 ± 0.12	0.23 ± 0.07	***	4.01
	Acaulospora sp. 1	0.74 ± 0.15	0.26 ± 0.08	***	1.29
	Acaulospora sp. *2*	0.48 ± 0.19	0.52 ± 0.19	Ns	1.72
	Acaulospora sp. 3	0.45 ± 0.18	0.55 ± 0.21	Ns	0.43
Dentiscutataceae	*Dentiscutata biornata*	0.66 ± 0.06	0.34 ± 0.05	***	6.20
	Fuscutata heterogama	0.93 ± 0.23	0.07 ± 0.03	***	0.42
Gigasporaceae	*Gigaspora gigantea*	0.76 ± 0.12	0.24 ± 0.09	***	1.61
	Gigaspora sp. 1	0.81 ± 0.14	0.19 ± 0.06	***	1.24
	Gigaspora sp. 2	0.55 ± 0.14	0.45 ± 0.13	Ns	1.34
	Gigaspora sp. 3	0.81 ± 0.14	0.19 ± 0.06	***	1.09
Racocetraceae	*Racocetra gregaria*	0.9 ± 0.22	0.1 ± 0.05	***	0.50
Scutellosporaceae	*Scutellospora* sp.	0.59 ± 0.18	0.41 ± 0.14	Ns	0.55
Ambisporaceae	*Ambispora jimgerdemannii*	1 ± 0.29	0 ± 0	***	0.33

Table 3
Generalized linear mixed model outputs of AMF spores community (density, diversity, richness and evenness) in the rhizosphere of each study area (5 burned and 5 unburned) in Chaco Serrano Forest, Argentina (n = 100). Fire = F; Area = A; Unburned = Unb; Burned = Bur; m = mean; se = standard error. Ns, non significant; $p \geqslant 0.1$; $^{*}p < 0.1$; $^{**}p < 0.05$; $^{***}p < 0.01$.

	AMF	Density			Diversity			Richness			Evenness		
	Term	m ± se	F	p	m ± se	F	p	m ± se	F	p	m ± se	F	p
F	Unb	123.24 ± 2.53	3.61	*	1.81 ± 0.03	257.88	***	8.61 ± 0.2	202.71	***	0.85 ± 0.01	55.76	***
	Bur	117.76 ± 3.35			1.2 ± 0.04			5.16 ± 0.19			0.75 ± 0.01		
A	AO	115.48 ± 3.91	7.78	***	1.41 ± 0.08	5.18	***	6.25 ± 0.42	5.63	***	0.79 ± 0.02	1.01	Ns
	SA	110.02 ± 4.27			1.44 ± 0.08			6.58 ± 0.42			0.78 ± 0.02		
	LS	113.45 ± 4.31			1.43 ± 0.06			6.43 ± 0.35			0.79 ± 0.02		
	CB	142.31 ± 5.39			1.66 ± 0.07			8.05 ± 0.45			0.82 ± 0.01		
	BM	121.22 ± 3.82			1.57 ± 0.06			7.13 ± 0.37			0.82 ± 0.01		
F * A	Unb * AO	118.1 ± 4.77	0.36	Ns	1.79 ± 0.05	2.32	*	8.3 ± 0.44	1.21	Ns	0.86 ± 0.01	4.06	***
	Bur * AO	112.87 ± 6.27			1.03 ± 0.07			4.2 ± 0.27			0.73 ± 0.04		
	Unb * SA	115.73 ± 4.06			1.78 ± 0.05			8.55 ± 0.43			0.84 ± 0.02		
	Bur * SA	104.32 ± 7.41			1.09 ± 0.09			4.6 ± 0.34			0.72 ± 0.04		
	Unb * LS	113.76 ± 5.01			1.71 ± 0.06			7.8 ± 0.4			0.84 ± 0.01		
	Bur * LS	113.13 ± 7.16			1.15 ± 0.07			5.05 ± 0.39			0.73 ± 0.02		
	Unb * CB	143.75 ± 7.4			1.99 ± 0.05			9.8 ± 0.47			0.88 ± 0.01		
	Bur * CB	140.88 ± 8.02			1.33 ± 0.06			6.3 ± 0.54			0.75 ± 0.02		
	Unb * BM	124.84 ± 4.7			1.77 ± 0.05			8.6 ± 0.41			0.83 ± 0.01		
	Bur * BM	117.6 ± 6.47			1.38 ± 0.08			5.65 ± 0.41			0.82 ± 0.02		

2.3. Quantification of AMF spores

AMF spores were extracted from 50 g of soil from each sample using a wet sieving and centrifugal flotation technique (Daniels and Skipper, 1982). All spores were separated by morphotype according to microscopic features such as size, color, ornamentation type, hyphal attachment and shape. After counting, the spores were mounted on slides in polyvinyl-lactoglycerol (PVLG) and

PVLG mixed with Melzer's reagent. Glomerospores were counted and identified using a light microscope (Nikon). Sporocarpic species of *Glomus* were found in many samples and only sporocarp numbers were recorded. Only turgid and healthy looking spores were counted and then identified to genus and in many cases to species level. Taxonomic identification followed (http://invam.caf.wvu.edu/HH and http://www.lrz.de/~schuessler/amphylo/amphylo_species.html) criteria.

Spore density was expressed as the number of spores per 50 g of soil (dry weight). Relative density was calculated as the number of spores of a given species/total spores × 100. We used spores to estimate Shannon's diversity and evenness indexes for each AMF community at each site. Evenness index (E) was calculated following Pielou (1969): $E = H'/\ln(S)$, where H' is the Shannon diversity index and S is the species richness. AMF richness (S) was calculated as the total number of different AMF species encountered in each sample.

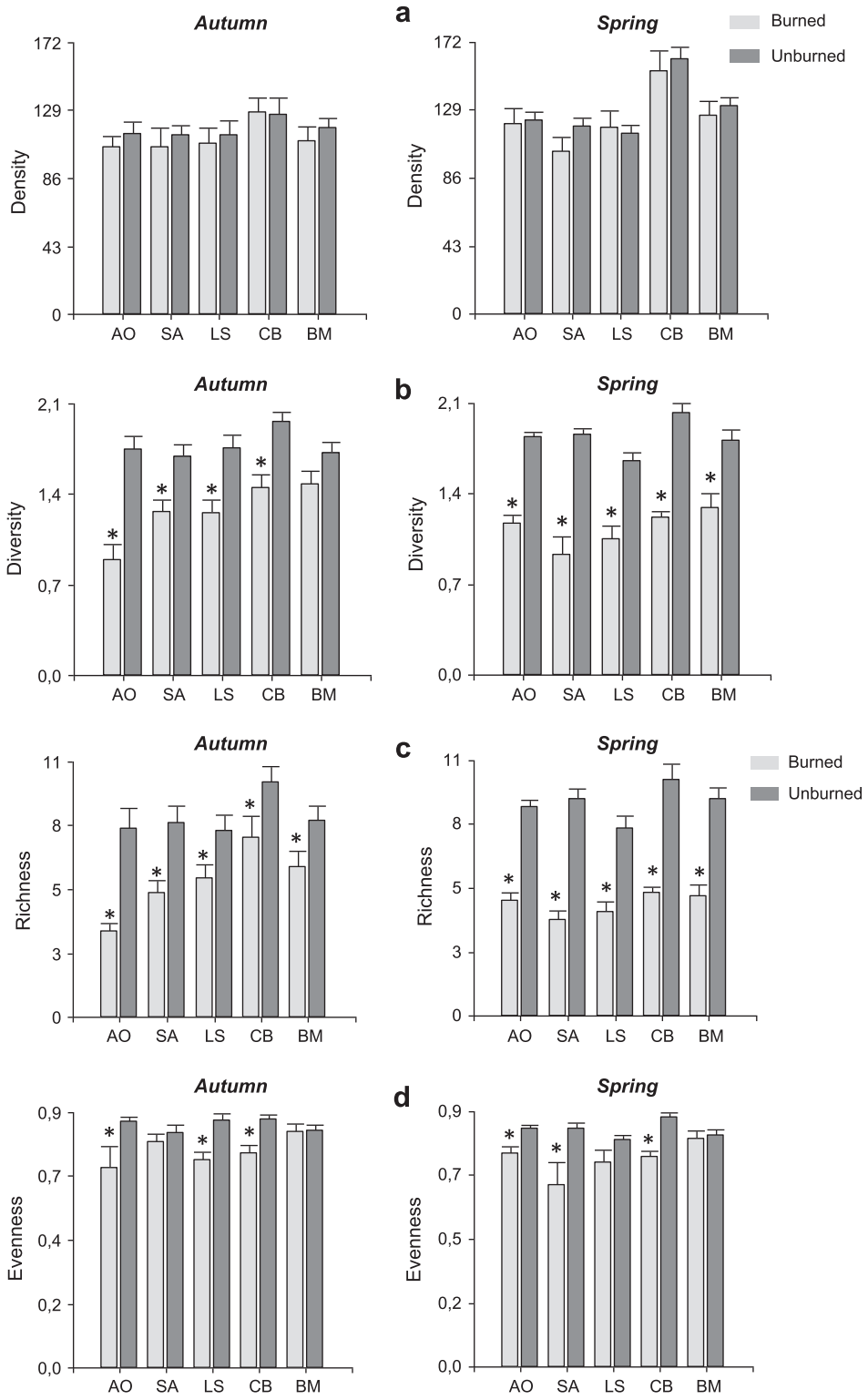

Fig. 2. Arbuscular mycorrhizal fungi (AMF) composition in burned and unburned sites in five areas of Forest Chaco Serrano, Córdoba-Argentina.(a) Density; (b) Diversity; (c) Richness and (d) Evenness ($n = 100$). *Significant differences between burned and unburned in each area.

2.4. Soil properties analysis

Ten soil samples from each study area (5 burned + 5 unburned × 5 areas = 50) were analyzed to determine:% organic matter, % total nitrogen, C:N, nitrate (mg kg^{-1}), phosphorus (mg kg^{-1}), pH 1:2.5 (w:v) and electrical conductivity (dS/m) (Sparks, 1996) at the Edaphologic Laboratory of the Faculty of Agronomic Sciences (Universidad Nacional de Córdoba, Argentina) and Secretary of Environment (Gobierno de la Provincia de Córdoba, Argentina).

2.5. Statistical analysis

All mycorrhizal and soil variables were analyzed with generalized linear mixed model with "Fire" (unburned; burned) and "Area" (AO; SA; LS; CB; BM) as fixed effects, including the interaction term and "season" (autumn; spring) as random effect. We used the Akaike's Information Criterion (AIC) and the Bayesian information criterion (BIC) to select the best-fitted model for heterogeneous variances. When data showed non normal distribution they were rank-transformed and the models was run with these data (Zar, 1999). Statistical analyses were performed in R (R Development Core Team 2009) through the interface implemented in Infostat Version 2013 (Di Rienzo et al., 2013). When the treatment effect was significant, we used Fisher LSD ($p < 0.05$) to perform mean comparisons. In addition, we performed Spearman's correlation analysis between mycorrhizal and soil variables to examine possible relationships.

3. Results

3.1. AMF community composition

In total 26327 spores belonging to 32 taxa of AMF were recovered from the 200 soil samples. Among them, 13 were assigned to known species in 8 families while the remaining were identified up to genus level.

Septoglomus constrictum (Glomeraceae) was the most abundant taxa considering all samples together but showed notably higher levels of spores in burned sites. In contrast, several species in the other families showed higher levels in unburned soils. The genera *Scutellospora* showed no differences between burned and unburned sites (Table 2). Thirty-one species were common to both sites, while *Ambispora jimgerdemannii* was present only in the unburned sites in low number.

AMF spore diversity, richness and evenness were significantly higher in unburned sites. Instead, the density was not significant between burned and unburned sites (Table 3 and Fig. 2). In addition, spore density, diversity and richness but not evenness significantly varied between areas. Site CB tended to have higher values than BM; SA; AO and LS (Table 3 and Fig. 2a–c). There was a significant interaction term between fire and area on evenness (Table 3). Despite these interactions between factors, diversity, richness and evenness were consistently higher in unburned sites in most areas in autumn and spring (Fig. 2).

3.2. Soil properties and their relationship with AFM community

With the exception of C:N, nitrate and electrical conductivity, soil parameters showed significant differences between burned and unburned sites (Table 4). However, the observed trends for burned and unburned sites among areas were not as consistent as for fungal variables. In autumn, unburned sites had higher values of organic matter and total nitrogen in AO, SA and BM but not in LS and CB, and in spring SA had higher values in the burned site

Table 4
Generalized linear mixed model outputs outputs of soil properties of each study area (5 burned and 5 unburned) in Chaco Serrano Forest, Argentina ($n = 50$) Fire = F; Area = A; Unburned = Unb; Burned = Bur; m = mean; se = standard error, Ns, non significant; $^{*}p > 0.1$; $^{**}p < 0.1$; $^{***}p < 0.05$; $^{****}p < 0.01$.

Soil variables		Organic matter			Total nitrogen			C:N			Nitrate			Phosphorus			pH			Electrical conductivity		
Term		m ± se	F	p	m ± se	F	p	m ± se	F	p	m ± se	F	p	m ± se	F	p	m ± se	F	p	m ± se	F	p
F	Unb	7.75 ± 0.4	19.5	***	0.4 ± 0.02	17.06	***	11.4 ± 0.18	2.23	Ns	69.66 ± 9.17	0.47	Ns	12.67 ± 2.81	15.67	***	6.43 ± 0.09	0.51	Ns	0.74 ± 0.1	0.51	Ns
	Bu	5.84 ± 0.4			0.3 ± 0.02			11.08 ± 0.19			64.57 ± 8.66			21 ± 3.64			6.79 ± 0.08			0.69 ± 0.1		
A	AO	7.39 ± 0.73	9.93	***	0.37 ± 0.04	10.29	***	11.42 ± 0.31	2.32	*	56.4 ± 9.45	0.64	Ns	13.63 ± 4.58	3.02	**	6.62 ± 0.1	10.7	***	0.57 ± 0.1	2.31	*
	SA	9.1 ± 0.62			0.48 ± 0.03			11.08 ± 0.34			74.21 ± 12.3			21.17 ± 6.87			7.1 ± 0.13			0.77 ± 0.16		
	LS	6.42 ± 0.63			0.32 ± 0.03			11.45 ± 0.18			89.81 ± 22.06			12.71 ± 3.85			6.6 ± 0.12			0.89 ± 0.21		
	CB	4.61 ± 0.56			0.25 ± 0.03			10.67 ± 0.3			64.68 ± 13.36			19.48 ± 5.2			6.57 ± 0.15			0.77 ± 0.16		
	BM	6.45 ± 0.36			0.33 ± 0.02			11.56 ± 0.26			50.49 ± 8.47			17.19 ± 5.29			6.14 ± 0.12			0.56 ± 0.11		
F * A	Unb * AO	9.83 ± 0.7	2.75	**	0.49 ± 0.04	2.65	Ns	11.75 ± 0.27	6.62	Ns	75.78 ± 13.95	4.41	***	5.55 ± 1.3	11.56	***	6.52 ± 0.14	1.82	Ns	0.66 ± 0.16	2.46	*
	Bur * AO	4.94 ± 0.68			0.25 ± 0.03			11.1 ± 0.56			37.01 ± 9.96			21.7 ± 8.52			6.73 ± 0.15			0.49 ± 0.14		
	Unb * SA	9.97 ± 0.76			0.53 ± 0.05			11.25 ± 0.57			68.04 ± 13.57			6.55 ± 0.94			6.92 ± 0.17			0.72 ± 0.23		
	Bur * SA	8.23 ± 0.93			0.44 ± 0.05			10.92 ± 0.41			0.41 ± 21.13			35.79 ± 12.28			7.29 ± 0.18			0.83 ± 0.24		
	Unb * LS	6.67 ± 0.81			0.33 ± 0.04			11.61 ± 0.17			60.15 ± 32.5			2.99 ± 0.32			6.42 ± 0.19			0.68 ± 0.22		
	Bur * LS	6.16 ± 1.01			0.32 ± 0.05			11.29 ± 0.32			119.46 ± 28.32			22.44 ± 6.43			6.78 ± 0.12			1.1 ± 0.36		
	Unb * CB	5.45 ± 0.81			0.28 ± 0.04			10.96 ± 0.4			79.97 ± 24.15			22.65 ± 7.94			6.17 ± 0.2			0.94 ± 0.29		
	Bur * CB	3.77 ± 0.71			0.21 ± 0.04			10.37 ± 0.45			49.4 ± 10.86			16.3 ± 7			6.97 ± 0.13			0.61 ± 0.16		
	Unb * BM	6.83 ± 0.44			0.36 ± 0.03			11.41 ± 0.48			64.35 ± 15.58			25.63 ± 9.95			6.12 ± 0.24			0.69 ± 0.2		
	Bur * BM	6.07 ± 0.56			0.3 ± 0.03			11.7 ± 0.25			36.62 ± 4.17			8.76 ± 1.77			6.16 ± 0.09			0.44 ± 0.11		

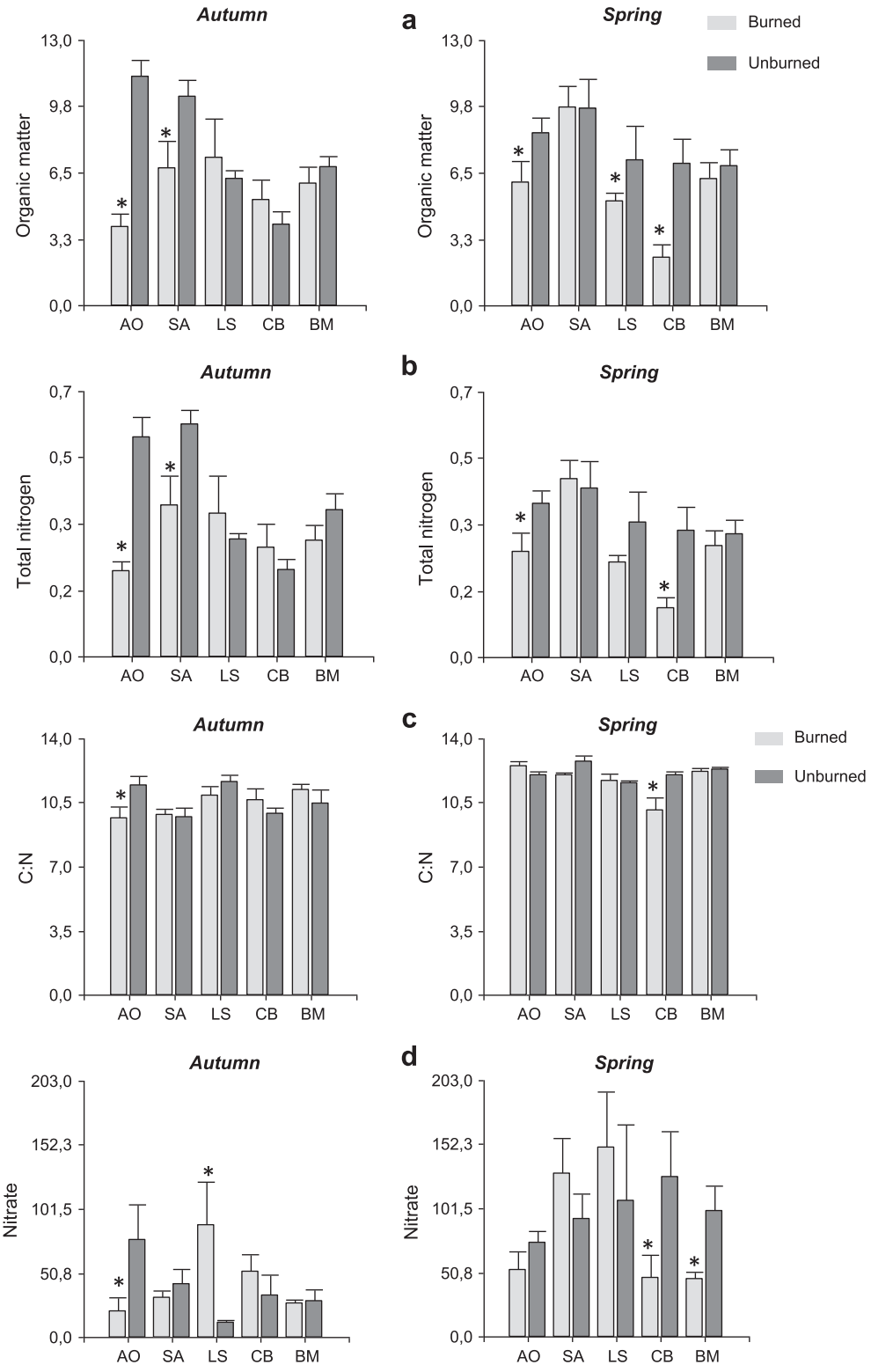

Fig. 3. chemical parameters in burned and unburned soils in five areas of Forest Chaco Serrano in Córdoba-Argentina. (a) organic matter, (b) total nitrogen, (c) C:N, (d) nitrate, (e) phosphorus, (f) pH and (g) electrical conductivity ($n = 50$). *Significant differences between burned and unburned in each area.

(Table 4 and Fig. 3a–b). Phosphorus was higher in burned sites from three areas in spring (AO, SA and LS) and the inverse pattern was observed in the other two. In autumn, higher phosphorus in burned sites was observed only in two sites (AO and LS) but had considerably lower values than spring (Fig. 3e). The pH was higher in burned sites (Fig. 3f). Electrical conductivity was not significantly affected by fire, but differed between areas (Table 4 and Fig. 3g).

There were no significant correlations between soil properties and fungal variables. The only exception was a significant negative correlation ($r = -0.46$; $p = 0.04$) between pH and spore diversity.

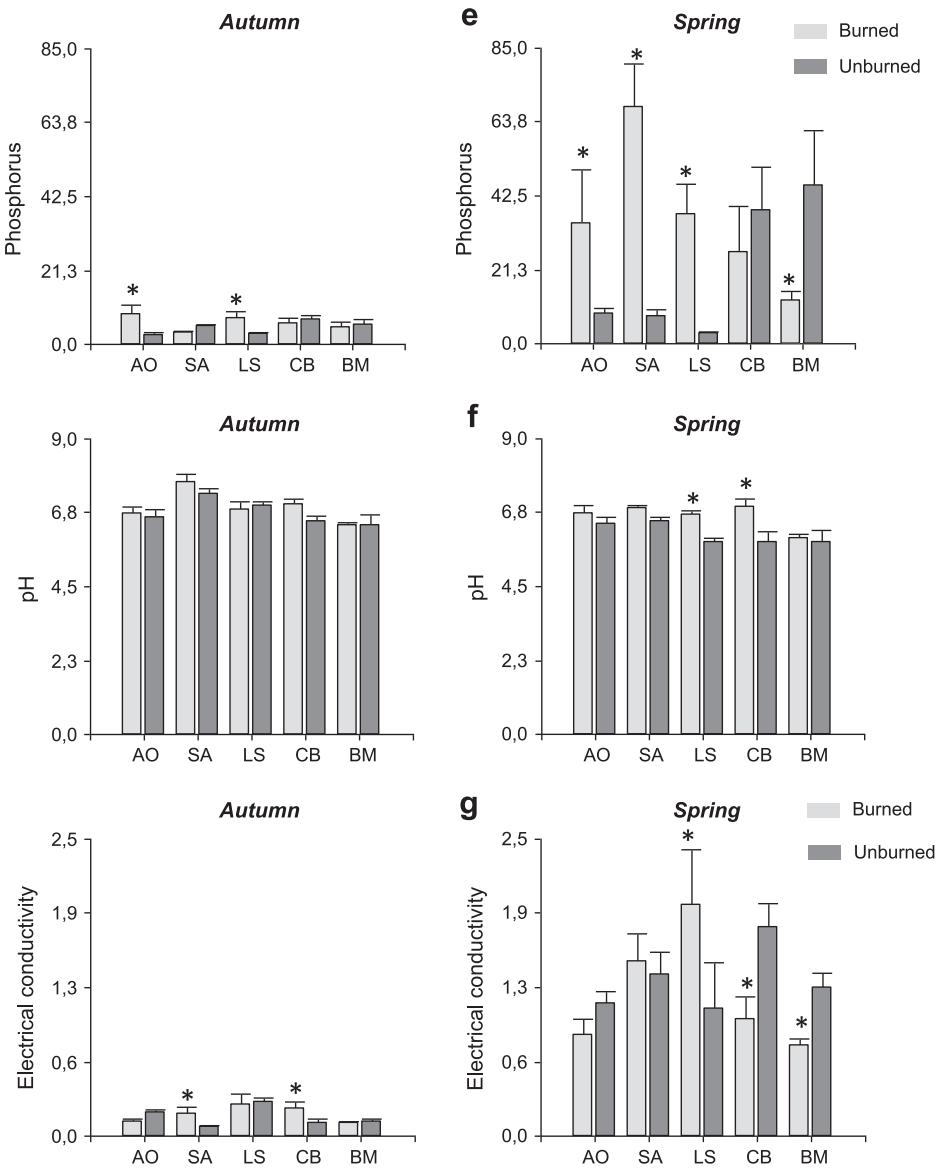

Fig. 3 (*continued*)

4. Discussion

4.1. Effects of fire on AMF composition

Fire events had direct negative effects on AMF spore communities in the Chaco Forests of central Argentina, as evenness, diversity and richness of AMF spores decreased in the burned sites. Contrary to what we expected, one year after fire occurrence spore abundance did not differ between unburned and burned sites. Despite some interactions between the factors, these results were mostly consistent for the five studied areas and both sampling seasons. These findings supported our prediction of negative effects of fire on AMF spore communities and agree with recent a meta-analysis that showed overall negative effects of fire on soil microbial communities (Wang et al., 2012).

Tests of the fire effects on AMF spores in previous studies have had contrasting results (see introduction). These disparities might be related to differences in the geographic location, experimental designs, variation in fire intensity, duration of fire, vegetation types (forest, shrubland, grassland), fire types (wildfire or prescribed fire) time after burning, and, certainly, different climates (see Wang et al., 2012). For example, in the tallgrass prairies of North America, under sampling conditions similar to ours, but differing in the geographic location, climate, and vegetation types, Eom et al. (1999) found negative fire effects on spore diversity but positive effects on spore density. In contrast, Valariño and Arine (1991) found negative effects on spore density in two studied areas in northern Spain. However, results from similar studies in terms of geographic location (19–35° latitude N), altitude (<900 masl), vegetation type (forest-shrubland), precipitation (mean annual 500–1500 mm), and time after burning (within the first 14 months after fire occurrence), contrast with our findings since they showed no fire effect on the spore diversity and density (Aguilar-Fernández et al., 2009; Bellgard et al., 1994; Rashid et al., 1997).

A distinguishing feature of our study design is that includes fire events selected on a regional basis, that occurred in the same season and year, replicated in five independent areas with similar altitude, vegetation type, climatic conditions, and, presumably, fire intensity and duration.

It has been suggested that AMF might be grouped according to their life history strategies (e.g. Hart and Reader, 2002; Chagnon et al., 2013). According to this framework, taxa from Glomeraceae

are regarded as ruderals that would be favored by disturbances. In turn, members in families such as Gigasporaceae, Acaulosporaceae and Entrophosporaceae would be disfavored by disturbances. In line with this, we found that the dominant species in Glomeraceae, *Septoglomus constrictum*, had significantly higher spore abundance in burned sites while taxa in other families such as *Entrophospora infrequens*, *Claroideoglomus* sp., *Acaulospora rehmii*, *Acaulospora scrobibulata*, *Acaulospora* sp. 1, *Dentiscutata biornata*, *Fuscutata heterogama*, *Gigaspora gigantea*, *Gigaspora* sp. 1, *Gigaspora* sp. 3, *Racocetra gregaria* decreased after fire.

4.2. Fire effects on soil properties and their relationship with AMF community

Patterns in soil properties among burned and unburned sites and areas were not as consistent as those for fungi. In accordance with previous reports for other ecosystems (Jackson and Caldwell, 1993; Ritz et al., 2004; Dias et al., 2010), our findings show noticeable levels of spatial heterogeneity. Despite this, burned sites had overall lower contents of organic carbon and total nitrogen, albeit some of the areas showed no differences, depicted by the significant interaction term. Recently, Wang et al. (2012) observed that within 3–12 months after fire occurrence, soil organic carbon were not affected while total nitrogen decreased in burned sites. In turn, within 1–3 years, organic carbon decreased but total nitrogen increased after fire occurrence. Considering the time factor in our study (i.e. 8 and 15 months after the occurrence of the fire), our results fall in both categories and are partially consistent with those analyzed there.

We found a general trend of higher pH and phosphate availability in burned sites. This trend was consistent among the 5 areas and in both seasons which can be a consequence of soluble cations liberation from burned organic matter (Certini, 2005; Knoepp et al., 2005). Altogether the results suggest, with nuances, that carbon and nitrogen decreased in burned sites while phosphorus and pH increased.

Contrary to our expectations, changes in species composition of AMF were not significantly correlated with most of the soil variables measured. Nonetheless, a significant negative correlation between pH and spore diversity was observed. In line with this, Switzer et al. (2012) suggested that the negative effects of fire on AMF (measured as abundance of fatty acids in soils) could be attributed to increased pH levels which negatively correlated with AMF abundance. Although we cannot rule out this possibility, in our study the variation in pH levels among sites was small and the correlation with the diversity of spores was not high, making the relationship inconclusive.

All in all, these results suggest that fire occurrence affected some soil abiotic properties but these were not clearly associated with changes in AMF. The changes in AMF spore communities might be a direct effect of fire and/or of changes in vegetation, such as the increase in ruderal forbs observed in burned sites.

5. Conclusions

Fire occurrence negatively affected AMF spore communities, but the effects did not seem to be mediated by changes in soil abiotic properties. Rather, they suggest direct effects of fire and/or vegetation on soil fungi. The observed changes in AMF composition after fire occurrence may consequently affect plant succession and productivity. Moreover, the degradation of AMF communities after fire occurrence could be also associated with exotic plant success in disturbed sites. This issue will be explicitly tested in future studies.

Acknowledgments

The authors wish to acknowledge the assistance of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET) and the Universidad Nacional de Córdoba, both of which have provided facilities used for this study. CNPq-National Council for Scientific and Technological Development-SISBIOTA Program, Brazil, is acknowledged for financial support. Field assistance by Lescano JN, Hernadez-Caffot L; Longo G and Longo R is appreciated. Nori J assisted in the preparation of the map. Dr. Cindy Prescott and two anonymous reviewers made useful comments on the manuscript. C.U. and E.N. are researchers of CONICET, and serving professors at the U.N.C. L.S. is a CONICET fellowship holder and is doctoral student at the U.N.C.

References

Abril, A., González, C., 1999. Dinámica de la fertilidad y de las poblaciones microbianas en suelos afectados por incendios en las sierras de Córdoba (Argentina). Agriscientia XVI, 63–70.

Aguilar-Fernández, M., Jaramillo, V.J., Varela-Fregoso, L., Gavito, M.E., 2009. Short-term consequences of slash-and-burn practices on the arbuscular mycorrhizal fungi of a tropical dry forest. Mycorrhiza 19, 179–186.

Allen, M.F., MacMahon, J.A., Anderson, D.C., 1984. Re-establishment of Endogonaceae on Mount St. Helens: survival of residues. Mycologia 76, 1031–1038.

Allsopp, N., Stock, W.D., 1994. VA mycorrhizal infection in relation to edaphic characteristics and disturbance regime in three lowland plant communities in the south-western Cape, South Africa. J. Ecol. 82, 271–279.

Bellgard, S.E., Whelan, R.J., Muston, R.M., 1994. The impact of wildfire on vesicular–arbuscular mycorrhizal fungi and their potential to influence the re-establishment of post-fire plant communities. Mycorrhiza 4, 139–146.

Bengtsson, J., Nilsson, S.G., Franc, A., Menozzi, P., 2002. Biodiversity, disturbances, ecosystem function and management of European forests. For. Ecol. Manage. 132, 39–50.

Busse, M.D., DeBano, L.F., 2005. Soil biology, in: Neary, D.G., Ryan, K.C., DeBano, L.F. (Eds.), Wildland Fire in Ecosystems: Effects of Fire on Soil and Water. Gen. Tech. Rep. RMRS-GTR-42-vol. 4. USDA Forest Service, Rocky Mountain Research Station, Ogden, UT, pp. 73–91.

Cabrera, A., 1976. Regiones fitogeográficas Argentinas, second ed. Enciclop. Arg. Agric. Y Jardinería. ACME, Buenos Aires, Argentina.

Certini, G., 2005. Effects of fire on properties of forest soils: a review. Oecologia 143, 1–10.

Chagnon, P.-L., Robert, L., Bradley, R.L., Maherali, H., Klironomos, J.N., 2013. A trait-based framework to understand life history of mycorrhizal fungi. Trends Plant Sci. 18 (9), 484–491.

Daniels, B.A.D., Skipper, H.D., 1982. Methods for the recovery and quantitative estimation of propagules from soil. In: Schenck, N.C. (Ed.), Methods and principles of mycorrhizal research. The American Phytopathological Society, St. Paul, MN.

Dhillion, S.S., Anderson, R.C., Liberta, A.E., 1988. Effect of fire on the mycorrhizal ecology of little bluestem (*Schizachyrium scoparium*). Can. J. Bot. 66, 706–713.

Di Rienzo, J.A., Casanoves, F., Balzarini, M.G., Gonzalez, L., Tablada, M., Robledo, C.W. InfoStat versión 2013. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina. URL <http://www.infostat.com.ar>.

Dias, J.M., Oliveira1, R.S., Franco, A.R., Ritz, K., Nunan, N., Castro, P.M.L., 2010. Assessment of mycorrhizal colonisation and soil nutrients in unmanaged fire-impacted soils from two target restoration sites. Span. J. Agric. Res. 8 (S1), S86–S95.

Docherty, K.M., Balser, T.C., Bohannan, B.J.M., Gutknecht, J.L.M., 2012. Soil microbial responses to fire and interacting global change factors in a California annual grassland. Biogeochemistry 109, 63–83.

Eom, A.H., Hartnett, D.C., Wilson, G.W.T., Deborah, A.H., Figge, D.A.H., 1999. The effect of fire, mowing and fertilizer amendment on Arbuscular Mycorrhizas in tallgrass prairie. Am. Midl. Nat. 142 (1), 55–70.

Giorgis, M.A., 2012. Caracterización florística y estructural del Bosque Chaqueño Serrano (Córdoba) en relación a gradientes ambientales y de uso. Tesis doctoral, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Córdoba, Argentina.

Gorgas, J.A., Tassile, J.L., 2003. Los suelos. Agencia Córdoba DACyT-INTA.

Grilli, G., Urcelay, C., Galetto, L., 2012. Forest fragment size and nutrient availability: complex responses of mycorrhizal fungi in native–exotic hosts. Plant Ecol. 213, 155–165.

Gurvich, D.E., Enrico, L., Cingolani, A.M., 2005. Linking plant functional traits with post-fire sprouting vigour in woody species in central Argentina. Austral Ecol. 30, 789–796.

Hart, M.M., Reader, R.J., 2002. Taxonomic basis for variation in the colonization strategy of arbuscular mycorrhizal fungi. New Phytol. 153, 335–344.

Haskins, K.E., Gehring, C.A., 2004. Long-term effects of burning slash on plant communities and arbuscular mycorrhizae in a semi-arid woodland. J. Appl. Ecol. 41, 379–388.

Jackson, R.B., Caldwell, M.M., 1993. The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. Ecology 74, 612–614.
Kara, O., Bolat, I., 2009. Short-term effects of wildfire on microbial biomass and abundance in black pine plantation soils in Turkey. Ecol. Indic. 9, 1151–1155.
Knoepp, J.D., DeBano, L.F., Neary, D.G., 2005. Chapter 3: Soil Chemistry, in: Neary D.G., Ryan, K.C., DeBano, L.F., Wildland (Eds.), 2005. Fire in ecosystems effects of fire on soil and water. Gen. Tech. Rep. RMRS-GTR-42-vol.4. Ogden, UT: US Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 250.
Longo, S., Urcelay, C., Nouhra, E., 2011. Long term effects of fire on ectomycorrhizas and soil properties in *Nothofagus pumilio* forests in Argentina. For. Ecol. Manage. 262, 348–354.
Luti, R., Bertrán de Solís, M.A., Galera, M.F., Müller de Ferreira, N., Berzal, M., Nores, M., Herrera, M.A., Barrera, J.C., 1979. Vegetación, in: Vázquez, J., Miatello, R., Roque, M. (Eds.), Geografía Física de la provincia de Córdoba. Ed. Boldt, Buenos Aires.
Miglietta, S., 1994. Patrón de ocurrencia de fuegos y su efecto sobre la vegetación en el bosque Serrano de Córdoba. Tesis de Maestría, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba, Córdoba, Argentina.
Moglia, G., Giménez, A.M., 1998. Rasgos anatómicos característicos del hidrosistema de las principales especies arbóreas de la región chaqueña argentina. Invest Agrar-Sist R. 7, 53–71.
Moreira, M., Baretta, D., Tsai, S.M., Cardoso, E.J.B.N., 2006. Spore density and root colonization by arbuscular mycorrhizal fungi in preserved or disturbed Araucaria angustifolia (Bert.) O. Ktze. ecosystems. Sci. Agric. (Piracicaba, Braz.), 63(4), 380–385.
Neary, D.G., Klopatek, C.C., DeBano, L.F., Ffolliott, P.F., 1999. Fire effects on belowground sustainability: a review and synthesis. For. Ecol. Manage. 122, 51–71.
Pielou, E., 1969. An introduction to mathematical ecology. Wiley Interscience, New York.
Rashid, A., Ahmed, T., Ayub, N., Khan, A.G., 1997. Effect of forest fire on number, viability and post-fire re-establishment of arbuscular mycorrhizae. Mycorrhiza 7, 217–220.
Ritz, K., Mcnicol, J.W., Nunan, N., Grayston, P., Millard, P., Atkinson, D., Gollote, A., Habeshaw, D., Boag, B., Clegg, C.D., Griffiths, B.S., Weatley, R.E., Glover, L.A., Mccaig, A.E., Prosser, J.I., 2004. Spatial structure in soil chemical and microbiological properties in an upland grassland. FEMS Microbiol. Ecol. 49, 191–205.
Smith, S.E., Read, D.J., 2008. Mycorrhizal Symbiosis, third ed. Academic Press, London.
Sparks, D.L., 1996. Methods of soil analysis. Part 3. Chemical methods. ASA, SSSA, CSSA, Madison, WI.
Switzer, J.M., Hope, G.D., Grayston, S.J., Prescott, C.E., 2012. Changes in soil chemical and biological properties after thinning and prescribed fire for ecosystem restoration in a Rocky Mountain Douglas-fir forest. For. Ecol. Manage. 275, 1–13.
Torres, R.C., Giorgis, M.A., Trillo, C., Volkmann, L., Demaio, P., Heredia, J., Renison, D., 2013. Post-fire recovery occurs overwhelmingly by resprouting in the Chaco Serrano forest of Central Argentina. Austral Ecol.. http://dx.doi.org/10.1111/aec.12084.
Treseder, K.K., Mack, M.C., Cross, A., 2004. Relationships among fires, fungi, and soil dynamics in Alaskan boreal forests. Ecol. Appl. 14, 1826–1838.
Urcelay, C., Díaz, S., Gurvich, D.E., Chapin, F.S., Cuevas, E., Domínguez, L.S., 2009. Mycorrhizal community resilience in response to experimental plant functional type removals in a woody ecosystem. J. Ecol. 97, 1291–1301.
Valariño, A., Arine, J., 1991. Numbers and viability of vesicular–arbuscular fungal propagules in field soil samples after wildfire. Soil Biol. Biochem. 23, 1083–1087.
van der Heijden, M.G.A., Bardgett, R.D., van Straalen, N.M., 2008. The unseen majority: soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. Ecol. Lett. 11, 296–310.
Vázquez, J.R., Miatello, R., Roque, M., 1979. Geografía Física de la provincia de Córdoba, eds. Ed. Boldt, Buenos Aires.
Verzino, G., Joseau J., Dorado, M., Gellert, E., Rodríguez-Reartes, S., Nóbile, R., 2005 Impacto de los incendios sobre la diversidad vegetal, sierras de Cordoba, Argentina. Ecol. Appl. 4(1,2) 25–34.
Wang, Q., Zhong, M., Wang, S., 2012. A meta-analysis on the response of microbial biomass, dissolved organic matter, respiration, and N mineralization in mineral soil to fire in forest ecosystems. For. Ecol. Manage. 271, 91–97.
Williams, R.J., Hallgren, S.W., Wilson, G.W.T., 2012. Frequency of prescribed burning in aupland oak forest determines soil and litter properties and alters the soil microbial community. For. Ecol. Manage. 265, 241–247.
Zak, M.R., Cabido, M., Hodgson, J.G., 2004. Do subtropical seasonal forests in the Gran Chaco, Argentina, have a future? Biol. Conserv. 120, 589–598.
Zar, J.H., 1999. Biostatistical Analysis, fourth ed. Prentice Hall, New Jersey.