Forest Ecology and Management 262 (2011) 348–354

Contents lists available at ScienceDirect

Forest Ecology and Management

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

Long term effects of fire on ectomycorrhizas and soil properties in *Nothofagus pumilio* forests in Argentina

M. Silvana Longo *, Carlos Urcelay, Eduardo Nouhra

Instituto Multidisciplinario de Biología Vegetal, CONICET, Universidad Nacional de Córdoba, Casilla de correo 495, 5000 Córdoba, Argentina

ARTICLE INFO

Article history:
Received 16 December 2010
Received in revised form 28 February 2011
Accepted 26 March 2011
Available online 12 May 2011

Keywords:
Ectomycorrhizas
Soil properties
Fire effects
Nothofagus pumilio

ABSTRACT

The forests of *Nothofagus pumilio* have historically been affected by forest fires. The effects of fire on certain above and belowground, biotic and abiotic components of these ecosystems have been previously documented, albeit belowground components have received much less attention. It has been suggested that the effects observed in the short-term after a fire usually differ from the longer-term effects. The long-term effects of fire (i.e. >5 years after burning) on belowground components in *Nothofagus* forests are currently unknown. In the present study we evaluated the long-term effect of fire on ectomycorrhiza (ECM) colonization and morphotype composition in *N. pumilio* roots, as well as soil chemical properties in temperate forests in Patagonia. Sampling was conducted in three mature monospecific forests. In each, nearby burned and unburned sites were selected. The time since the occurrence of fires differed between areas (i.e. 6–10 years). Within each site, 3 transects of 40 m were established randomly along which 5 samples of roots and soil were collected in spring and autumn. The main results were: (1) in comparison with the unburned site, ECM colonization was lower in the burned site in the area with the shorter time length since fire occurrence and no effects in the other two areas were observed; (2) richness and diversity were not significantly affected by fire but there was a significant effect of season for both parameters, being higher in spring; (3) ECM dominance was significantly higher in the unburned than in the burned site in Tronador, while in Challhuaco the opposite was observed, mainly in autumn; (4) in general carbon, nitrogen and phosphorous decreased while pH increased in the burned sites; (5) ECM colonization positively correlated with NH^{4+} and phosphorus and negatively with pH but was not significantly correlated with organic matter or any other soil variable. Altogether the results suggest that effects of fire on ectomycorrhiza and soil properties in *N. pumilio* forests are probably related to the time elapsed since fire occurrence combined with site characteristics. In addition, the direct and indirect effects of fire in these forest systems may persist for more than 10 years.

1. Introduction

The important role played by disturbance in shaping stand-level and landscape-level forest patterns has been recognized (Attiwill, 1994). Among disturbances, fire is one of the most far-reaching, either in space or time (Bond and Keeley, 2005). Fire generates spatio-temporal changes that affect the structure and functioning of communities in many ecosystems (Sousa, 1984). In southern South-America, fire constitutes the main disturbance factor of the Andean–Patagonian forests (Veblen and Lorenz, 1987, 1988; Veblen et al., 1992, 1996). In particular, the forests of *Nothofagus pumilio* which range attitudinally from 38 to 55° north–south, have historically been affected by forest fires (Veblen et al., 2003). The effects of fire on some above and belowground biotic and abiotic components of these ecosystems have been previously documented (Veblen et al., 2003), although belowground components have received much less attention. Alauzis et al. (2004) examined soil chemical and microbial properties in burned and undisturbed forest stands during the 4 years immediately after burning. They found that fire significantly increased pH, electrical conductivity, extractable phosphorus, and cations. In turn, a significant reduction in organic C and total N was observed. Among biotic components, a decline of microbial activity and microbial biomass was also observed (Alauzis et al., 2004). However, due to successional dynamics, short-term effects usually differ from long term effects (Neary et al., 1999).

The long-term effects of fire (i.e. >5 years after burning) on belowground components in *Nothofagus* forests have not been studied. Moreover, despite the fact that this deciduous tree species depends on ectomycorrhiza (ECM) for nutrient uptake and that ectomycorrhizal associations are a key soil biotic component in temperate ecosystems (Smith and Read, 2008), the impacts of burning on ectomycorrhizal fungi associated with *Nothofagus* have

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

0378-1127/$ - see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.foreco.2011.03.041

not been studied. Numerous studies in other systems have shown that mycorrhizal symbiosis can be directly affected with increasing levels of anthropogenic disturbance (Allen, 1988; Klopatek et al., 1991, 1994). Forest fires can cause direct and indirect effects on ECM communities (Neary et al., 1999). Direct effects could be related, for example, to increases in soil temperature which eliminate the fungal biomass present in the organic horizon (Stendell et al., 1999). However, since mycorrhizal fungi mediate the access to soil resources by the plant, indirect effects are to be expected due to changes in chemical properties of soil (Neary et al., 1999). Most studies of the impact of fire on ECM fungi conducted in conifer forests, mostly involving *Pinus* spp.; have reported negative to neutral effects (Danielson, 1984; Visser, 1995; Baar and Kuyper, 1998; Horton et al., 1998; Baar et al., 1999; Jonsson et al., 1999; Stendell et al., 1999; Grogan et al., 2000; Dahlberg et al., 2001; Mah et al., 2001; Purdy et al., 2002; Rincón and Pueyo, 2010). In addition, the experimental designs of these studies vary considerably with respect to fire intensity, duration of fire, and time after burning. Also, since these studies involve north temperate forests, it is difficult to extrapolate their results to the south temperate deciduous forests.

In the present study we compared ECM colonization, morphotype composition in roots of *N. pumilio*, and chemical soil properties in burned and unburned areas in the Patagonian temperate forest region of Argentina.

2. Materials and methods

2.1. Study area

The study region is located within the Nahuel Huapi National Park in Patagonia (705.000 ha), Argentina (Table 1). Sampling was conducted in spring (from November 29 to December 3, 2005) and autumn (from April 4 to 8, 2006) in mature monospecific forest of *N. pumilio* (deciduous broad-leaf species). Three study areas were selected (C° Challhuaco, C° Otto, C° Tronador). In each of them, nearby burned and unburned sites were selected. The areas have different time spans, 6–10 years, since the occurrence of fires (Table 1).

Climate is characterized by a mean annual precipitation ranging from 500 to 2300 mm (increasing from E to W), and a mean annual temperature of 5–10 °C (increasing from S to N). Precipitation, rain and snow, is concentrated in autumn and winter (March–September). Summer is generally dry in this region. Soils are Andisols with a low degree of development, characterized by a high capacity to stabilize organic matter and store water (Mazzarino et al., 1998).

2.2. Sampling design

In each area, one burned and one unburned site was selected and, within each site, 3 transects of 40 m were randomly established but separated by at least 50 m. In each transect, 5 samples (8 m apart) of roots and soil were collected in two seasons, spring and autumn (30 samples/area/season, total = 180). In this study each transect is the sampling unit. Samples were collected with a soil corer, 15 cm deep and 8 cm in diameter, at approximately 15–30 cm from the base of a tree. This sampling distance, established in order to standardize root sampling in each transect, is within the range suggested in the literature for mycorrhizal sampling (e.g. Cornelissen et al., 2003; Avis et al., 2003). If a tree was not present at a point, then we selected the closest tree. Roots and soil samples collected in sites affected by fire were taken from living trees; some of these were in poor condition. We always selected mature trees (>30 cm diameter), thus many of them still had signs of damage in burned sites. The root systems and soils samples were placed separately in plastic bags and kept at 4 °C until processing.

2.3. Ectomycorrhizal morphotype identification

In the laboratory, the ECM were extracted carefully from soil samples and were sorted into morphotypes according to their morphological and anatomic features using a Wild M5A stereo microscope at 10–40× magnification. Criteria for sorting included color, mantle layers, branching pattern, emanating hyphae, characteristics of rhizomorphs, and cystidia, following accepted methodology (Agerer, 1991, 1999).

2.4. Colonization and composition of ECM morphotypes

The percentage of ECM colonization was calculated as the number of ECM root tips divided by the total number of root tips (Gehring and Whithan, 1994). The percentage of colonization by each ECM morphotype was calculated for each sample by dividing the number of root tips colonized by each ECM morphotype by the total number of root tips and multiplying by 100 (Helm et al., 1999). Diversity of morphotypes was calculated by the reciprocal of Simpson's dominance index (Magurran, 1988) using the mean relative percentage of each morphotype associated to each sample. Morphotype richness was calculated as the total number of different ECM morphotypes encountered in each sample.

2.5. Analysis of soil properties

A portion of the soil samples from each site was sent to the Laboratory of Edaphologic analysis of the Facultad de Ciencias Agropecuarias (Universidad Nacional de Cordoba) to determine: % organic matter, % organic carbon, % total nitrogen, C:N, N-NO^{3-} (ppm), NH^{4+} (ppm) and phosphorus (ppm), pH 1:2,5 (Sparks, 1996). Three soil samples for each study area (1 sample per transect; 3 transect per site) were analyzed. Each sample was obtained from the mixture of 5 subsamples.

2.6. Data analysis

All mycorrhizal and soil variables were analyzed by three-way ANOVA with "fire", "area" and "season" and their interactions as main effects. In addition, we performed Spearman's correlation analysis between mycorrhizal and soil variables to examine for possible relationships. When data did not meet the assumptions

Table 1
Location, climatic characteristics and year of fire occurrence at the study sites.

Area	Fire	Latitude (°S)	Longitude (°W)	Elevation (m a.s.l)	Mean annual	
					Precipitation (mm)	Temperature (°C)
Challhuaco	1996	41° 15′ 19,0″	71° 16′ 53,0″	1140	1500	6,3
Otto	1998	41° 08′ 45,7″	71° 22′ 18,5″	1320	1500	5,1
Tronador	1999	41° 11′ 58,0″	71° 49′ 42,9″	1233	1750	4

Table 2
ANOVA values of colonization, diversity, dominance and richness of ECM morphotypes. Sources of variation in the analysis were "fire", "area", and "season".

Factors	ECM morphotypes							
	Colonization (%)		Diversity		Dominance		Richness	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Fire (F)	7,89	***	3,80	*	4,78	**	1,89	Ns
Area (A)	12,28	***	2,87	*	5,40	**	6,58	***
Season (S)	0,38	Ns	12,69	***	10,14	***	55,02	***
F×A	3,93	**	3,93	**	7,40	***	2,06	Ns
F×S	3,72	*	0,22	Ns	0,34	Ns	1,21	Ns
A×S	0,17	Ns	0,72	Ns	0,54	Ns	0,06	Ns
F×A×S	0,53	Ns	0,75	Ns	0,97	Ns	0,36	Ns

Ns $p \geqslant 0.1$;
* $p < 0.1$;
** $p < 0.05$;
*** $p < 0.01$.

of normal distribution and homogeneity of variance they were rank-transformed. All analyses were carried out with the *Infostat* Statistical Package (Di Rienzo et al., 2001).

3. Results

3.1. Ectomycorrhizal colonization

In total, 25,198 root tips were quantified, of which 22,449 were mycorrhizal tips (89%), corresponding to 23 different ECM morphotypes.

The data show that the percentage of mycorrhizal colonization was significantly higher in sites not affected by fire while no differences between seasons were observed (Table 2, Fig. 1a). However, there was a significant interaction factor between fire and forest area because the effects of fire were evident in Tronador in both seasons and in Otto in autumn while no effects were evident in Challhuaco in either season or in Otto in spring (Fig. 1a).

3.2. Composition of ECM morphotypes

The diversity index of morphotypes showed marginally significant differences between burned and unburned sites and forest areas but a significant interaction factor between them (Table 2). This is because diversity tended to be higher in burned sites in Tronador but not in the other areas (Fig. 1b). In addition, there was a significant effect of season because diversity was higher in spring. There was a significant effect of fire, areas, and season but also a significant interaction factor between fire and area on morphotype dominance (Table 2). In the unburned site at Tronador, dominance was higher than in the burned site, while in Challhuaco the opposite was observed, mainly in autumn. In the other combinations of area and season there were no evident effects of fire, while dominance was generally higher in autumn (Fig. 1c). There was a significant effect of area on morphotype richness (Table 2). Tronador tended to have higher values than Otto and Challhuaco. In spring, richness was significantly higher than in autumn (Fig. 1d).

3.3. Soil properties

With the exception of C:N, all soil properties measured showed significant differences between burned and unburned sites (Table 3, Fig. 2d). Unburned sites showed higher values for organic matter (%) and organic C (%) in Challhuaco and Otto but not in Tronador indicated by a significant interaction factor between fire and area (Fig. 2a and b). These two parameters were higher in spring (Fig. 2a and b). Total N (%) followed a similar pattern (Fig. 2c). N-NO^{3-} and NH^{4+} were significantly affected by fire and area while only NH^{4+} was affected by season (Table 3). There was a significant interaction term among the three factors for these variables with the exception of fire by area on NH^{4+}. In autumn, N-NO^{3-} was higher in unburned site only in Challhuaco while in spring only in Otto. In the remaining combinations no evident differences were observed (Fig. 2e). In autumn, NH^{4+} was higher in unburned sites, mainly in Challhuaco and Tronador. In spring, the patterns were similar but only in Tronador were the differences clearly evident (Fig. 2f). Phosphorus was also higher in unburned sites in both seasons, mainly in Tronador (Fig. 2g). The pH was generally higher in burned sites in both seasons (Fig. 2h).

4. Discussion

Despite the importance of soil fungal communities in ecosystems (Allen, 1991; Smith and Read, 2008), it is not clear how disturbances such as fire affect the dynamics of these communities. Most of the available information seems to be contradictory due to the existence of differences in experimental methodologies, intensity and duration of fires, and the studied ecosystems.

The results of this study, carried out in three areas differing in precipitation regime and fire age, show that fire affects ectomycorrhizal communities and chemical soil parameters, but these effects were context dependent, that is, they varied according to the different areas and seasons.

4.1. Effects of fire on ECM colonization

The effects of fire on ECM colonization were mainly evident in Tronador, the area with the shortest time since fire occurrence (i.e. 6–7 years). Here, colonization was lower in the burned site. In the other two areas, differences in mycorrhizal colonization were negligible suggesting that the time elapsed since fire occurrence (i.e. 7–8 in Otto and 9–10 in Challhuaco) was sufficient to reach pre-disturbance levels. Similar patterns were observed in the other ECM parameters. We question that fire intensity was responsible for the observed results because Tronador seems to have suffered the least intense fire event while Challhuaco the most intense (see below) and thus, the opposite results would have been expected.

Similar results to those obtained here were reported in other studies for the northern hemisphere, where fire induced a decrease in the number of mycorrhizal tips of conifer species (Torres and Honrubia, 1997; Stendell et al., 1999; Dahlberg et al., 2001) as well as *Quercus ilex* (De Román and De Miguel, 2005).

4.2. Effects of fire on ECM composition

Richness and diversity were not significantly affected by fire in this study. The evidence in the literature is variable and it is sometimes difficult to compare and to draw conclusions. For example, published studies generally involve sites that range from immediate (i.e. short-term) to long-term impacts of fire and from low to high fire intensities. Some of them measured morphotype composition in roots while others performed molecular analyses in soil samples. They also ranged from seedlings to mature trees, growth in the greenhouse or in the forest, respectively.

However, in mature forests, fire can negatively affect richness and/or diversity of morpohtypes (Danielson, 1984) or have no effects at all (De Román and De Miguel, 2005). While Danielson (1984) measured the immediate effects of high intensity fire in *Pinus sylvestris*, De Román and De Miguel (2005) considered longer terms (i.e. 4–6 years) and low intensity fire on *Q. ilex*. According

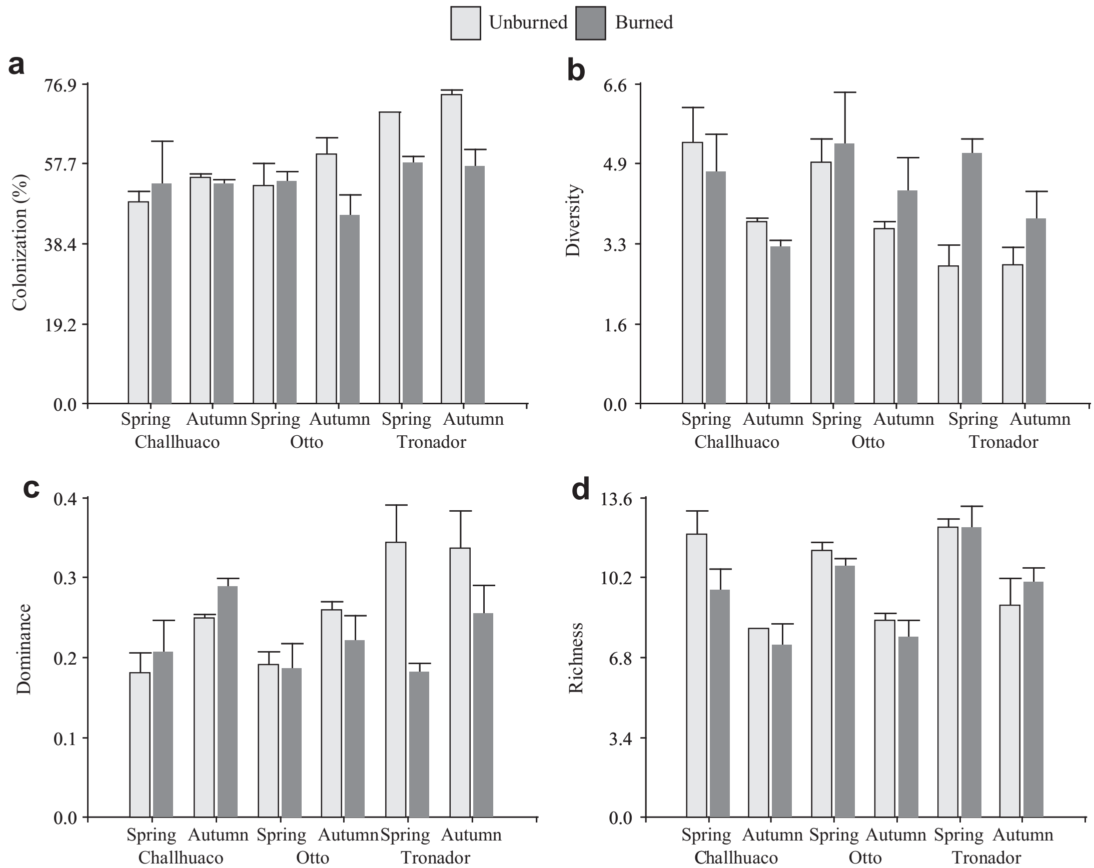

Fig. 1. ECM colonization and morphotype composition in unburned and burned areas in mature monospecific forest of *Nothofagus pumilio*. (a) Colonization (%), (b) diversity, (c) dominance, and (d) richness.

Table 3
ANOVA results on soil variables. Sources of variation in the analysis were "fire", "area", and "season".

Soil variables	Factors													
	Fire (F)		Area (A)		Season (S)		F×A		F×S		A×S		F×A×S	
	F	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*	*F*	*p*
Organic matter (%)	32,66	***	5,41	**	8,92	***	32,04	***	0,55	Ns	0,33	Ns	1,21	Ns
Organic carbon (%)	32,66	***	5,41	**	8,82	***	32,04	***	0,55	Ns	0,33	Ns	2,21	Ns
Total nitrogen (%)	23,85	***	7,55	***	0,01	Ns	28,88	***	0,18	Ns	2,92	*	1,77	Ns
C:N	0,28	Ns	1,76	Ns	17,85	***	1,85	Ns	0,31	Ns	8,59	***	0,79	Ns
N-NO^{3-} (ppm)	7,54	**	16,92	***	0,12	Ns	11,06	***	3,43	*	18,11	***	18,7	***
NH^{4+} (ppm)	69,59	***	48,46	***	66,6	***	1,61	Ns	3,29	*	3,92	**	7,93	***
Phosphorus (ppm)	19,39	***	19,3	***	1,3	Ns	5,97	***	0,76	Ns	2,45	Ns	1,18	Ns
pH (1:2,5)	56,72	***	16,41	***	7,26	**	5,35	**	3,67	*	5,97	***	0,11	Ns

Ns $p \geqslant 0.1$.
* $p < 0.1$.
** $p < 0.05$.
*** $p < 0.01$.

to our results regarding soil properties, it could be presumed that the intensity of fires in this study was high albeit differing between areas (Table 3). Indeed, Alauzis et al. (2004) reported that fire intensity in Challhuaco was high. Therefore, it is possible that the lack of differences in richness and diversity found here may be related to the time elapsed since fire occurrence. For instance, in Tronador, the area with the shorter time length since fire occurrence, dominance was clearly higher in unburned sites. Recently, Rincón and Pueyo (2010) concluded that fire severity, site slope, and elapsed time after fire caused shifts in the presence or relative frequencies of a number of EM types in regenerated *Pinus pinaster* seedlings. The evidence so far suggests that ECM might be affected by fire in complex ways that include fire history, host plants, and site characteristics (see below).

4.3. Effects of fire on soil properties

While the volcanic soils in the Patagonia region have a high capacity to stabilize the organic matter and organic C, retain phosphorus and water, and buffer pH (Mazzarino et al., 1998), our results show that fire effects on soil properties persist for years. In Challhuaco, 4 years after the fire occurrence, Alauzis et al. (2004) showed a significant decrease in total organic C and N and a significant increase in pH. Our results suggest that even 8–10 years after

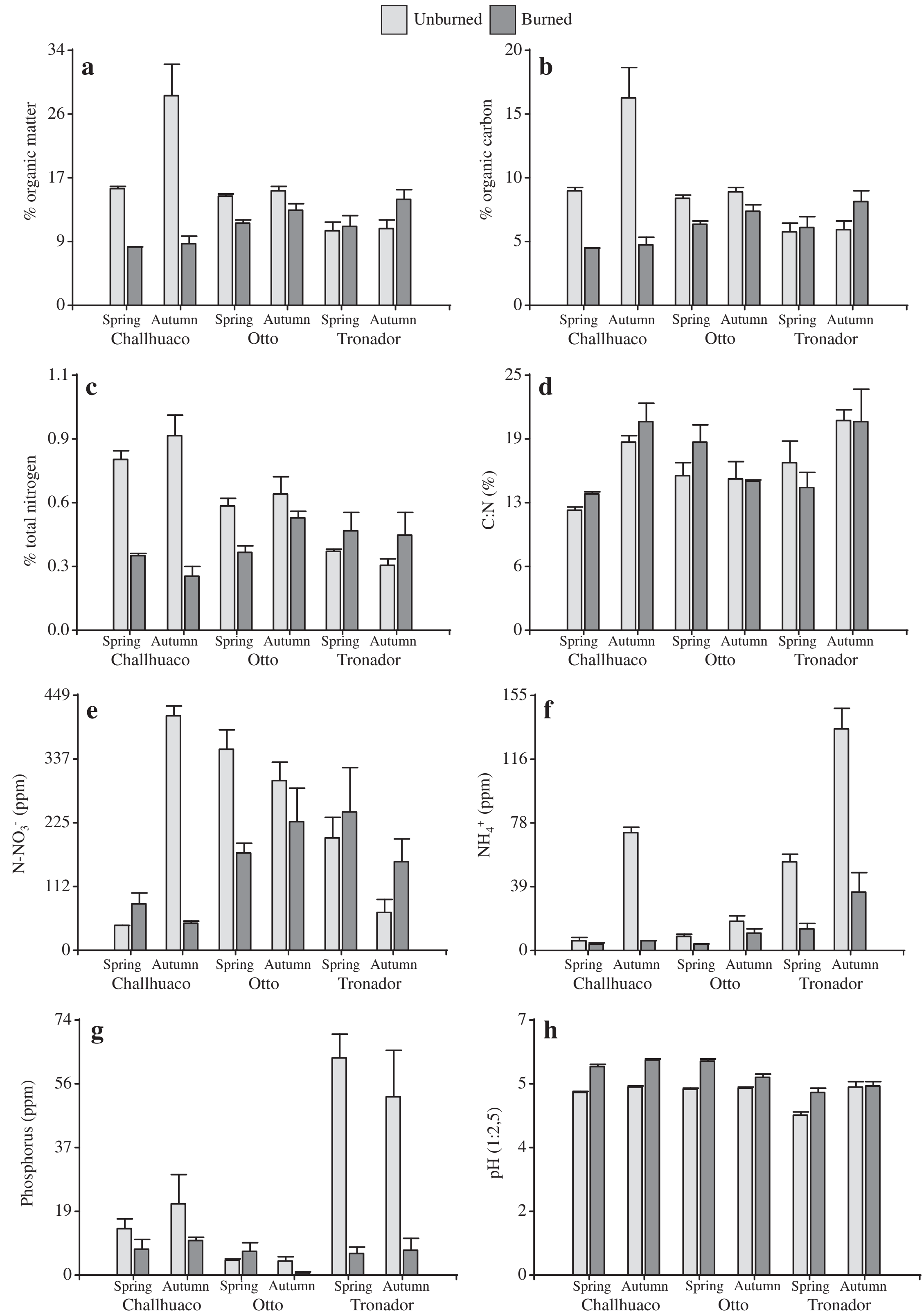

Fig. 2. Chemical parameters in burned and unburned soils in mature monospecific forest of *N. pumilio*. (a) Organic matter, (b) organic carbon, (c) total nitrogen, (d) C:N, (e) N-NO^{3-}, (f) NH^{4+}, (g) phosphorus, and (h) pH.

the fire occurrence the effects still remain evident in that area and to a lesser degree in Otto. In contrast, these effects were not evident in Tronador. Differences in phosphorous and NH^{4+} were mainly evident in Tronador with higher values in the unburned site. It has been shown that immediately after fire occurrence; there is an increase in phosphorous levels that tend to decrease returning to previous levels with time (Serrasolsas and Khanna, 1995; Certini, 2005). The substantial differences in phosphorus be-

Table 4
Spearman's correlation coefficient between % of colonization and the composition of ECM morphotypes with soil variables.

Soil variable	ECM morphotypes							
	Colonization (%)		Diversity		Dominance		Richness	
	R	*p*	*R*	*p*	*R*	*p*	*R*	*p*
Organic matter (%)	−0,06	Ns	0,1	Ns	0,28	Ns	−0,11	Ns
Organic carbon (%)	−0,06	Ns	0,1	Ns	0,28	Ns	−0,11	Ns
Total nitrogen (%)	−0,23	Ns	0,3	Ns	0,13	Ns	0,02	Ns
C:N	0,32	Ns	−0,48	***	0,22	Ns	−0,33	Ns
$N\text{-}NO^{3-}$ (ppm)	0,1	Ns	0,17	Ns	0,12	Ns	0,03	Ns
NH^{4+} (ppm)	0,58	***	−0,48	***	0,33	Ns	−0,08	Ns
Phosphorus (ppm)	0,54	***	−0,37	**	0,02	Ns	0,16	Ns
pH (1:2,5)	−0,4	**	−0,05	Ns	−0,16	Ns	−0,46	***

Ns $p \geqslant 0.05$.
** $p < 0.05$.
*** $p < 0.01$.

tween the burned and unburned sites from Tronador but not Chalhuaco and Otto, suggest that the effect of fire on some soil properties are also dependent on the time elapsed since fire occurrence. Altogether the results suggest that carbon, nitrogen, and phosphorous decreased in burned sites while pH increased.

4.4. Relationship between ectomycorrhizas and soil properties

Fire affects mainly the upper soil layers (Neary et al., 1999; Pattinson et al., 1999; Certini, 2005) causing changes in the composition of biotic communities (Neary et al., 1999; Mao et al., 2002). It is known that changes in soil nutrient availability affects the dynamics of mycorrhizal fungal communities after fire (Dahlberg et al., 2001). Treseder et al. (2004) concluded that colonization of ECM fungi in boreal forests of Alaska requires up to 15 years to return to pre-disturbance levels and that this recovery is closely related to the recovery of soil organic matter. In our study, ECM colonization positively correlated with NH^{4+} and phosphorus and negatively with pH but no significant correlation with organic matter or any other soil variable was observed (Table 4). Altogether these results suggest that the effect of fire on ECM colonization in Tronador might be mediated by the changes in NH^{4+} and phosphorus observed in that area (Table 4).

In addition, diversity negatively correlated with NH^{4+}, phosphorus and C/N while richness negatively correlated with pH. These results suggest that phosphorous and nitrogen availability rather than organic matter relates to some ectomycorrhizal variables and that fire may also affect ectomycorrhizal composition indirectly by the effects on those chemical properties.

5. Conclusions

Overall, our results indicate that long term effects of fire on ectomycorrhizas and soil properties in *N. pumilio* forests are context dependent. The belowground biotic and abiotic components in these forests are probably related to the time elapsed since fire occurrence combined with site characteristics. The results also suggest that the direct and indirect effects of fire in these forest systems persist for more than 10 years. These findings together with those reported in the literature suggest that further studies are needed to understand patterns and mechanisms regarding the effects of fire on belowground components in temperate ecosystems.

Acknowledgements

This study was supported by CONICET (*Consejo Nacional de Investigaciones Científicas y Tecnológicas*), PIP N° 6193, Argentina. The Nahuel Huapi National Park personnel facilitated sampling activities within the park. Sonia Fontenla for her valuable participation on the location of the burned areas. Dr. Larry Peterson and two anonymous reviewers made useful comments on the manuscript. M. Silvana Longo is fellow and C. Urcelay and E. Nouhra are researchers of CONICET.

References

Agerer, R., 1991. Characterization of ectomycorrhiza. In: Norris, J.R., Read, D.J., Varma, A.K. (Eds.), Techniques for the Study of Mycorrhizae. Methods in Microbiology, vol. 23. Academic Press, London, pp. 25–73.
Agerer, R., 1999. Anatomical characteristics of identified ectomycorrhizas: an attempt towards a natural classification. In: Varma, A.K., Hock, B. (Eds.), Mycorrhiza, Structure, Function, Molecular Biology and Biotechnology, second ed. Springer, Berlin, pp. 633–682.
Alauzis, M.V., Mazzarino, M.J., Raffaele, E., Roselli, L., 2004. Wildfires in NW Patagonia: long-term effects on a *Nothofagus* forest soil. For. Ecol. Manag. 192, 131–142.
Allen, M.F., 1988. Re-establishment of VA mycorrhizae following severe disturbance. comparative patch dynamics of a shrub desert and a subalpine volcano. Proc. Roy. Soc. Edinburgh 94B, 63–71.
Allen, M.F., 1991. The Ecology of Mycorrhizae. Cambridge University Press, Nueva York.
Attiwill, P.M., 1994. Ecological disturbance and the conservative management of eucalypt forest in Australia. For. Ecol. Manag. 63, 301–346.
Avis, P.G., McLaughlin, D.J., Dentinger, B.C., Reich, P.B., 2003. Long-term increase in nitrogen supply alters above- and below-ground ectomycorrhizal communities and increases the dominance of *Russula* spp. in a temperate oak savanna. New Phytol. 160, 239–253.
Baar, J., Kuyper, T.W., 1998. Restoration of aboveground ectomycorrhizal flora in stands of *Pinus sylvestris* (Scots Pine) in the Netherlands by removal of litter and humus. Restor. Ecol. 6, 227–237.
Baar, J., Horton, T.R., Kretzer, A.M., Bruns, T.D., 1999. Mycorrhizal colonization of *Pinus muricata* from resistant propagules after a stand-replacing wildfire. New Phytol. 143, 409–418.
Bond, W.J., Keeley, J.E., 2005. Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. Trends. Ecol. Evol. 20, 387–394.
Certini, G., 2005. Effects of fire on properties of forest soils: a review. Oecologia 143, 1–10.
Cornelissen, J.H.C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G., Poorter, H., 2003. A handbook of protocols for standardized and easy measrement of plant functional traits worldwide. Aust. J. Bot. 51, 335–380.
Dahlberg, A., Schimmel, J., Taylor, A.F.S., Johannesson, H., 2001. Post-fire legacy of ectomycorrhizal fungal communities in the Swedish boreal forest in relation to fire severity and logging intensity. Biol. Conserv. 100, 151–161.
Danielson, R.M., 1984. Ectomycorrhizal associations in jack pine stands in northeastern Alberta. Can. J. Bot. 62, 932–939.
De Román, M., De Miguel, A.M., 2005. Post-fire, seasonal and annual dynamics of the ectomycorrhizal community in a *Quercus ilex* L. forest over a 3-year period. Mycorrhiza 15, 471–482.
Di Rienzo, J., Robledo, W., Casanoves, F., Balzarini, M., González, L., Guzmán, A., Tablada, E., 2001. *Infostat*. Versión Beta. Estadística y Biometría, Facultad de Ciencias Agropecuarias. Universidad Nacional de Córdoba, Córdoba.
Gehring, C.A., Whithan, T.G., 1994. Comparisons of ectomycorrhizae in Pinyon Pines (*Pinus edulis*; Pinaceae) across extremes of soil type and herbivory. Am. J. Bot. 81, 1509–1516.
Grogan, P., Baar, J., Bruns, T.D., 2000. Below-ground ectomycorrhizal community structure in a recently burned bishop pine forest. J. Ecol. 88, 1051–1062.
Helm, D.J., Allen, E.B., Trappe, J.M., 1999. Plant growth and ectomycorrhiza formation by transplants on deglaciated land near Exit Glacier, Alaska. Mycorrhiza 8, 297–304.

Horton, T.R., Cázares, E., Bruns, T.D., 1998. Ectomycorrhizal, vesicular–arbuscular and dark septate fungal colonization of bishop pine (*Pinus muricata*) seedlings in the first months of growth after wildfire. Mycorrhiza 8, 11–18.

Jonsson, L., Dahlberg, A., Nilsson, M.C., Zackrisson, O., Karen, O., 1999. Ectomycorrhizal fungal communities in late-successional Swedish boreal forests, and their composition following wildfire. Mol. Ecol. 8, 205–215.

Klopatek, C.C., Freise, C.F., Allen, M.F., Klopatek, J.M., 1994. Comparisons of laboratory and field burning experiments on mycorrhizae distribution, density and diversity. J. Soc. Am. For. 94, 762–776 (Twelfth Conference on Fire and Forest Mineralogy, Special Issue).

Klopatek, J.M., Klopatek, C.C., DeBano, L.F., 1991. Fire effects on nutrient pools of woodland floor materials and soils in a pinyon-juniper ecosystem. Fire Environ. SE69, 154–160.

Magurran, A.E., 1988. Ecological Diversity and its Measurement. Princeton University Press, Princeton, New Jersey.

Mah, K., Tackaberry, L.E., Egger, K.N., Massicotte, H.B., 2001. The impacts of broadcast burning after clear-cutting on the diversity of ectomycorrhizal fungi associated with hybrid spruce seedlings in central British Columbia. Can. J. Forest Res. 31, 224–235.

Mao, X.A., Xu, Z.H., Luo, R.S., Mathers, N.J., Zhang, Y.H., Saffigna, P.G., 2002. Nitrate in soil humic acids revealed by nitrogen-14 nuclear magnetic resonance spectroscopy. Aust. J. Soil Res. 40, 717–726.

Mazzarino, M.J., Bertiller, M.B., Schlichter, T.M., Gobbi, M., 1998. Nutrient cycling in Patagonian ecosystems. Ecol. Austral. 8, 167–181.

Neary, D.G., Klopatek, C.C., DeBano, L.F., Ffolliott, P.F., 1999. Fire effects on belowground sustainability: a review and synthesis. For. Ecol. Manag. 122, 51–71.

Pattinson, G.S., Hammill, K.A., Sutton, B.G., McGee, P.A., 1999. Simulated fire reduces the density of arbuscular mycorrhizal fungi at the soil surface. Mycol. Res. 103, 491–496.

Purdy, B.G., Macdonald, S.E., Dale, M.R.T., 2002. The regeneration niche of white spruce following fire in the mixedwood boreal forest. Silva. Fenn. 36, 289–306.

Rincón, A., Pueyo, J.J., 2010. Effect of fire severity and site slope on diversity and structure of the ectomycorrhizal fungal community associated with post-fire regenerated *Pinus pinaster* Ait. seedlings. For. Ecol. Manag. 260, 361–369.

Serrasolsas, I., Khanna, P.K., 1995. Changes in heated and autoclaved forest soils of S.E. Australia. II. Phosphorus and phosphatase activity. Biogeochemistry 29, 25–41.

Smith, S.E., Read, D.J., 2008. Mycorrhizal Symbiosis,, Academic Press, Amsterdam, Boston.

Sousa, W.P., 1984. The role of disturbance in natural communities. Annu. Rev. Ecol. Evol. Syst. 15, 53–391.

Sparks, D.L., 1996. Methods of Soil Analysis. Part 3. Chemical Methods. SSSA, Madison, WI, USA.

Stendell, E.R., Horton, T.R., Bruns, T.D., 1999. Early effects of prescribed fire on the structure of the ectomycorrhizal fungus community in a Sierra Nevada ponderosa pine forest. Mycol. Res. 103, 1353–1359.

Torres, P., Honrubia, M., 1997. Changes and effects of a natural fire on ectomycorrhizal inoculums potential of soil in a *Pinus halepensis* forest. For. Ecol. Manag. 6, 189–196.

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.

Veblen, T.T., Donoso, C., Kitzberger, T., Rebertus, A.J., 1996. Ecology of southern Chilean and Argentinean *Nothofagus* forests. In: Veblen, T.T., Hill, R.S., Read, J. (Eds.), The Ecology and Biogeography of *Nothofagus* Forests. Yale University Press, New Haven, CT, pp. 293–353.

Veblen, T.T., Kitzberger, T., Raffaele, E., Lorenz, D.C., 2003. Fire History and Vegetation Changes in Northern Patagonia, Argentina. Fire and climatic changes in temperate ecosystems of the western Americas. In: Veblen, T.T., Baker, W., Montenegro, G., Swetnam, T. (Eds.), Ecological Studies 160. Springer–Verlag, New York, USA, pp. 265–295.

Veblen, T.T., Lorenz, D.C., 1987. Post-fire stand development of *Austrocedrus–Nothofagus* forests in Patagonia. Vegetatio 73, 113–126.

Veblen, T.T., Lorenz, D.C., 1988. Recent vegetation changes along the forest/steppe ecotone in northern Patagonia. A. Assoc. Am. Geog. 78, 93–111.

Veblen, T.T., Mermoz, M., Martin, C., Kitzberger, T., 1992. Ecological impacts of introduced animals in Nahuel Huapi National Park. Argentina. Conserv. Biol. 6, 71–83.

Visser, S., 1995. Ectomycorrhizal fungal succession in jack pine following wildfire. New Phytol. 129, 389–401.