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Evaluation of soil enzymes activities in an *Araucaria–Nothofagus* forest after a wildfire

Evaluación de las actividades de enzimas del suelo en un bosque de *Araucaria–Nothofagus* después de un incendio forestal

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ABSTRACT

Catastrophic events in temperate forest ecosystems, such as wildfires, alter the dynamics of biogeochemical processes. Soil enzymes are critical to soil nutrient cycling function and their potential activities can be sensitive bioindicators of the temperate forest ecosystems resilience after wildfire events. In this context, this is a preliminary study, which has as main objective to evaluate the soil enzymes activities and their relationships with soil chemical parameters in *Araucaria–Nothofagus* forest after three years of the wildfire. Soil samples were collected from 0-20 and 20-40 cm depths, from two burnt plots (P1 and P2) and one non-burnt control plot (PC), three years after wildfire. We analyzed a composite soil sample from each plots (PC, P1 and P2) and each depth. The soil enzyme activities measured were catalase (CA), cellulase (CE) and urease (UR). Moreover, total nitrogen, total carbon, Olsen phosphorous, total phosphorous, sum of exchangeable bases and pH was measured. A multiple linear regression analysis was carried out in order to relate the soil enzymes activities and soil chemical properties. The results showed that the enzymes activities did not show any evident seasonality. On the other hand, the multiple lineal regression analysis demonstrated a weak association between the soil chemical parameters and the CA activity (R^2 = 0.47) and CE activity (R^2 = 0.20), and a strong association with the UR activity (R^2 = 0.83). As a preliminary conclusion, soil UR activity could be a potential bioindicator of the alterations provoked by wildfire in *Araucaria–Nothofagus* forests, as three years post-wildfire there are still differences in its activity between burnt and non-burnt plots.

RESUMEN

Eventos catastróficos en los ecosistemas de bosques templados, como los incendios forestales, alteran la dinámica de los procesos biogeoquímicos. Las enzimas del suelo son fundamentales para el ciclaje de nutrientes y sus actividades potenciales pueden ser bioindicadores sensibles de la resiliencia de los ecosistemas de bosques templados después de eventos de incendios forestales. En este contexto, en este estudio preliminar, que tuvo como objetivo principal evaluar las actividades de las enzimas del suelo y sus relaciones con los parámetros químicos del suelo en un bosque de *Araucaria–Nothofagus* después de tres años de incendio forestal. Las muestras de suelo fueron recolectadas a una profundidad de 0-20 y 20-40 cm, desde dos parcelas quemadas (P1 y P2) y una parcela de control no quemada (PC), tres años después de un incendio forestal. Se analizaron muestras compuestas de cada parcela (PC, P1 y P2) y cada profundidad. Las actividades enzimáticas del suelo medidas fueron catalasa (CA), celulasa (CE) y ureasa (UR). Además, se midió el nitrógeno total, el carbono total, el fósforo Olsen, el fósforo total, la suma de bases intercambiables y el pH. Se realizó un análisis de regresión lineal múltiple para relacionar las actividades de las enzimas del suelo y las propiedades químicas del suelo. Los resultados mostraron que las actividades de las enzimas no mostraron ninguna estacionalidad evidente. Por otro lado, el análisis de regresión lineal múltiple demostró una asociación débil entre los parámetros químicos del suelo y la actividad CA (R^2 = 0,47) y la actividad CE (R^2 = 0,20), y una asociación fuerte con la actividad UR (R^2 = 0,83). Como conclusión preliminar, la actividad UR del suelo podría ser un bioindicador potencial de las alteraciones provocadas por los incendios forestales en los bosques de *Araucaria–Nothofagus*, ya que tres años después de los incendios forestales existían diferencias en su actividad entre parcelas quemadas y no quemadas.

Palabras clave: actividad enzimática; incendios forestales; *Araucaria–Nothofagus*, Chile.

INTRODUCTION

Temperate forest ecosystems normally have a limited access to macronutrients, as is the case for the humid forests in central and southern Chile, which to a high degree depend upon internal biological processes in their nutrient cycle (Vitousek *et al.*, 1998; Pérez *et al.,* 1998). Moreover, these mountain chain ecosystems, such as the *Araucaria–Nothofagus* forests, are adapted to exogenous catastrophic events, such as fires, volcanism and storms, which contribute to a regular dynamic of these forest communities (Veblen *et al.,* 1995). Despite these adaptations, the responses of the biological processes to catastrophic events like this are still not known. These reactions could serve as indicators of the ecosystem's resilience against alterations. The *Araucaria–Nothofagus* forest is affected by natural alterations, burning being a very important adjustment in the dynamics of these forests (Veblen *et al.,* 1995; González *et al.,* 2005). The forest wildfires alter the soil's biogeochemical processes through the loss of organic matter and the oxidation and volatilisation of nutrients (Caon *et al*., 2014). For this reason, the microbial processes and the enzyme activity of the soil are highly sensitive the event of a wildfire due to loss of organic matter (Jimenez *et al.,* 2002).

The soil enzymes activities are an integrating indicator of the biological activity and the physical and chemical conditions, which permits the evaluation of the microbial capacity in the catalytic processes, as well as the availability of nutrients by means of enzymatic processes (Reyes *et al*., 2011; Cardoso *et al*., 2013). The importance of certain soil enzymes has been described, such as catalase, cellulase and urease, serving as indicators of the biological activity of the soil in the event of alterations (García and Hernández, 1997; Smethurst *et al.,* 1998; Saviozzi *et al.,* 2001; Levi-Minzi *et al.,* 2002). Urease comes mainly from plants and microbes, and plays an indispensable role in the soil nitrogen cycling process (Lillo *et al*., 2011). The cellulase activity is related to the carbon cycling of the soil, specifically in the plant residues incorporation into the soil (Deng and Tabatabai, 1995). Catalase is an intracellular enzyme found in all aerobic bacteria and most facultative anaerobes, but absent in obligate anaerobes, and has been used as an indicator of soil fertility (Zhang *et al.*, 2005).

The level of activity of these enzymes was significantly higher in the soil of tropical forests as compared with deforested areas and crop farms in Asia (Dinesh *et al.,* 2004a). In European Mediterranean coniferous forests, a decrease in the urease activity in the soil has been verified after natural fire (Hernández *et al.,* 1997). In oak-hickory forests the activity of β-glucosidase, a cellulase acting in the final stage of the cellulose breakdown process in the soil, underwent a reduction after a prescribed fire (Boerner and Brinkman, 2003).

In Chile these biological processes of the soil, as potential indicators of alteration, still have not been duly investigated. In 2002 a great extension of natural forest was severely affected by burnings. Part of this extension was an important area of *Araucaria–Nothofagus* forest (CONAF, 2002). Given the vulnerability of these fragile ecosystems and the dependence upon internal processes in the nutrient cycle, knowledge about the soil enzymes activities is a potential tool for monitoring the capacity of these forests to recover and adapt to catastrophic events of great magnitude. The aim of the present study is to preliminary evaluation the soil enzymes activities of catalase (CA), cellulase (CE) and urease (UR) as potential bioindicators of ecosystems resilience after wildfire, and their relation to the soil's nutritional status in *Araucaria–Nothofagus* forests affected by highly severe wildfire.

MATERIALS AND METHODS

Study site description

The study area is located in the Tolhuaca National Park (38° 10' to 38° 15' and 71° 40' to 71° 50') in the Andes mountain chain of central-southern Chile, which was affected by a forest wildfire in February 2002 (CONAF, 2002). Three plots of land were defined in *Araucaria–Nothofagus* stands, each of 1000 m^2, one control plot (PC) not affected by fire, located at 1440 m a.s.l., and two plots affected by fire: P1, located at 1160 m above sea level y P2, located at 1240 m above sea level. The soil of the area is an Andisol, derived from ashes, scoria and lava from the Tolhuaca and Lonquimay volcanoes (Pollmann, 2001). The climate is cold temperate. The mean annual temperature is 8.6 °C, the maximum and minimum mean of the coldest month is 6.7 and -2.6 °C, respectively (Pollmann, 2002). The summer period (January) is dry, with a mean temperature of 15.1 °C. The annual precipitations are in the range of 2500-3500 mm, concentrated to the winter months.

Soil sampling procedure

A seasonal soil sampling was performed during 2004 (summer, autumn, winter and spring) in order to carry out a chemical characterization and measurement of the enzyme activity of the soil. For each experimental plot (PC, P1 and P2), two composite soil samples were taken at 0-20 cm and 20-40 cm depth, respectively. The samples were transported in polyethylene bags in insulating boxes. The collected soil was passed through a 2-mm sieve, homogenized and stored at 4 °C. The soil enzymes analyses were performed during the first week following the sampling. One part of the sieved soil was air-dried for its subsequent chemical analysis.

Analytical determinations of the chemical properties of the soil

The chemical properties of soil samples, such as, total nitrogen (total N), total carbon (total C), Olsen phosphorus (Olsen-P), total phosphorus (total P), sum of exchangeable bases (SB) and pH (1:2.5) in water, were analyzed using the methods described by Sadzawka *et al*. (2006) and officially recommended for Chilean soils.

Soil enzymes assay activities

The catalase (CA; EC 1.11.1.6) activity was determined by the manometric technique, in accordance with the method described by Steubing *et al.* (2002). The CA activity (O_2 mL g^{-1} min^{-1}) was expressed by the mL of liberated O_2 per gram of dry soil per minute. The cellulase (CE; EC 3.2.1.4) activity was determined in accordance with the method described by von Mersi and Schinner (1993), utilizing carboxymethyl cellulose (Merck) as a substrate. The CE activity (mg GLC g^{-1} 24 h^{-1}) is expressed in μg of glucose equivalents per gram of dry soil in 24 hours of incubation. The urease (UR; EC 3.5.1.5) activity was determined in accordance with the method described by Steubing *et al*. (2002), measuring the quantity of ammonium formed after the addition of urea (Merck) as a substrate, incubating for 2 h at 37 °C. The UR activity (mg N-NH_4 g^{-1} h^{-1}) is expressed in mg of N-NH_4 per gram of dry soil after 1 hour of incubation.

Each one of the enzymes was determined independently and by triplicate.

Statistical analysis

The values of the soil enzymes activities were analyzed using an ANOVA test and the differences between the means were analyzed by the Tukey test. Moreover, relationships between soil enzymes activities and soil chemical properties were explored using a multiple linear regression analysis. The analyses were carried out using the Statistica program v.6.0. All analyses consider a $p \leq 0.05$.

RESULTS AND DISCUSSION

Chemical characterization of the soil

Table 1 presents the maximum, minimum and mean values of the chemical variables measured during the study period for the two depths and the different plots: pH, total C, total N, Olsen-P, total P and sum of exchangeable bases. The values of the measured chemical parameters correspond to values observed in previous studies of Chilean volcanic ash-derived soil (Pollmann, 2001; Valenzuela *et al*., 2002; Alvear *et al*., 2007).

Table 1. Soil chemical properties measured at 0-20 and 20-40 cm depths from control plot (PC) and two burning (P1 and P2) *Araucaria–Nothofagus* forest soils from Tolhuaca National Park.

Cuadro 1. Propiedades químicas del suelo medidas a profundidades de 0-20 y 20-40 cm desde la parcela de control (PC) y dos parcelas suelos afectadas por el fuego (P1 y P2) en suelos de bosque de *Araucaria–Nothofagus* en el Parque Nacional Tolhuaca.

	PC			P1			P2		
0-20 cm depth	**max**	**Min**	**mean**	**max**	**min**	**mean**	**max**	**min**	**mean**
Water pH (1:2.5)	5.60	5.30	5.47	5.70	5.20	5.47	5.70	5.30	5.50
Total carbon (%)	14.70	13.60	14.23	14.30	12.90	13.37	11.40	10.40	10.87
Total nitrogen (%)	0.44	0.15	0.28	0.45	0.23	0.31	0.39	0.17	0.31
Olsen phosphorous (mg kg^{-1})	3.30	2.90	3.03	5.50	3.30	4.20	2.00	2.00	2.00
Total phosphorous (mg kg^{-1})	1466	1396	1440	1576	1064	1357	1845	1279	1485
Sum exchageable of bases ($cmol_+$ kg^{-1})	1.3	0.8	1.0	1.9	0.9	1.3	0.9	0.7	0.8
20-40 cm depth									
Water pH (1:2.5)	5.70	5.50	5.60	6.00	5.60	5.87	6.00	5.80	5.90
Total carbon (%)	11.50	9.00	10.03	10.20	5.50	7.93	10.20	6.70	8.20
Total nitrogen (%)	0.40	0.19	0.32	0.42	0.20	0.27	0.37	0.27	0.30
Olsen phosphorous (mg kg^{-1})	2.00	2.00	2.00	2.00	2.00	2.00	2.10	2.00	2.03
Total phosphorous (mg kg^{-1})	1530	1193	1329	1824	1352	1643	1377	1247	1313
Sum exchageable of bases ($cmol_+$ kg^{-1})	0.7	0.4	0.5	1.3	0.9	1.0	0.8	0.5	0.7

Soil enzymes activities

The CA activity varied between 0.50 and 0.99 O_2 mL g^{-1} min^{-1} in the superficial 20 cm (Figure 1). In general, significantly higher ($p \leq 0.05$) values were obtained for the CP and P1 0-20 cm, which do not differ statistically during the sampling period. Nevertheless, with increasing sampling depth, the CA activity diminished to values of 0.32-0.79 O_2 mL g^{-1} min^{-1}, which has been related to a decrease in the the soil's content of organic matter (SOM) (Johnson and Temple, 1964). The season of the year had no obvious observable effect on the CA activity, though showing a weak tendency towards a minor activity in autumn and winter. There was no significant difference in CA activity between the burnt plots and the control plot, indicating that the effect of the fire would not have any influence after two years. The restoration of the CA activity from the effects of the fire under the study conditions, contradicts the reports by Zhang *et al.* (2005), who found that the CA activity in *Picea balfouriana* forests eight years post-fire is still sensitive to the alterations provoked by the fire. The increase in CA activity in the burnt plots is probably related to a stabilization of the soil's aerobic microbiological population post-fire (Vázquez *et al*., 1993).

The CE activity varied between 101.2 and 788.9 mg GLC g^{-1} 24 h^{-1} at 0-20 cm depth (Figure 2). However, with increasing depth, CE activity diminished to a range of 62.7-537.6 mg GLC g^{-1} 24 h^{-1}, probably due to the lower SOM content, as discussed for CA activity. These results, coincide with reports by other authors, who indicate that a minor cellulose content, a low oxygen diffusion and low availability of nitrogen, influence CE activity (Wagner and Wolf, 1998). In summer, the highest CE activity was reported in PC at 0-20 cm, and the lowest was reported in spring. P1 0-20 cm presented the highest activity in autumn, while the P2 0-20 cm, PC 20-40 cm, P1 20-40 cm and P2 20-40 cm did not present differences between the different seasons of the year (Figure 2). In accordance with these results, no effect of the climatic season on the CE activity was observed. Nevertheless, Fioretto *et al.* (2005), reported seasonal variations of the CE activity in Mediterranean soils with predominating *Cistus incanus* L. vegetation,

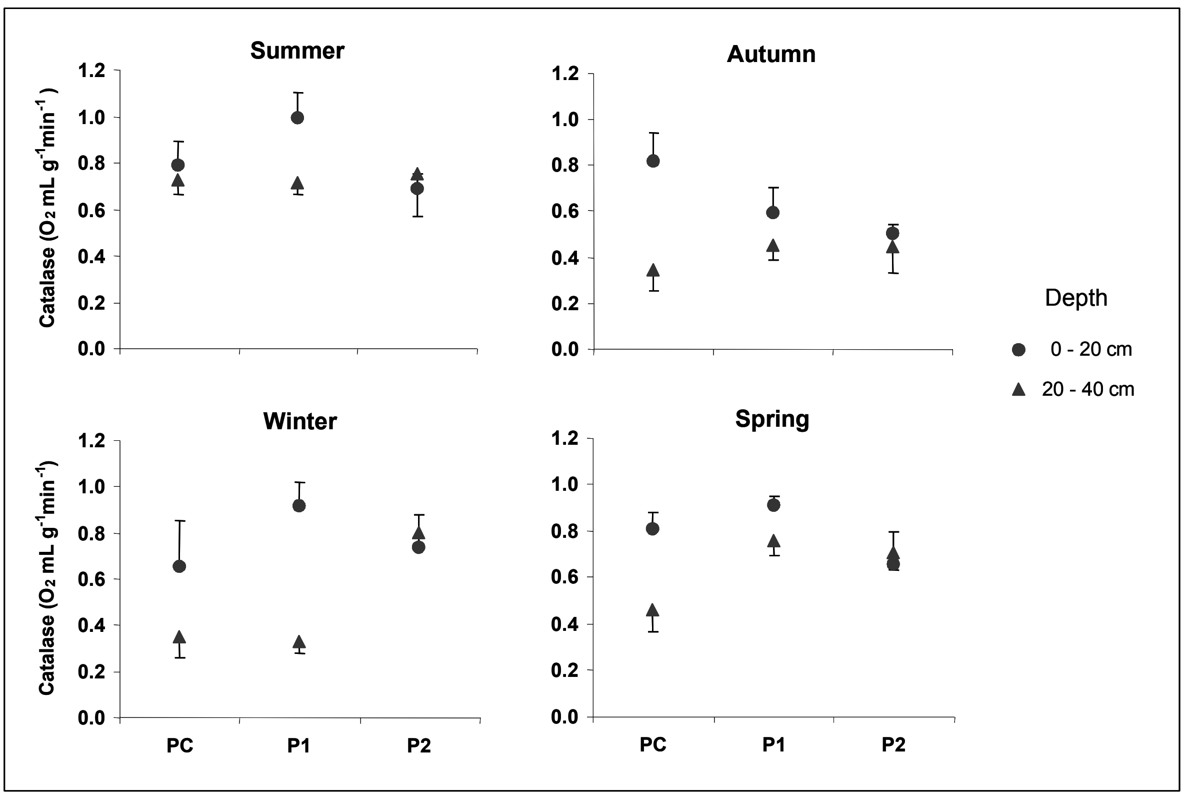

Figure 1. Catalase (CA) activity in different seasons of forest *Araucaria–Nothofagus* at 0-20 and 20-40 cm soil layers. Enzyme activity values are expressed as mean ± SD. (PC, control plot; P1 and P2, burnt plots). (n = 72).

Figura 1. Actividad de la catalasa (CA) en diferentes estaciones del bosque *Araucaria–Nothofagus* en profundidades de suelo de 0-20 y 20-40 cm. Los valores de la actividad enzimática se expresan como media ± DS. (PC, parcela control; P1 y P2, parcelas quemadas). (n = 72).

the highest values being observed in autumn and spring and the lowest in summer, independently of fire intensity. Moreover, Palese *et al*. (2004), reported that in soils with typical Mediterranean vegetation the seasonal variation in β-glucosidase activity, tending to diminish in autumn and increase in spring, can be modified by the effect of the temperature in the soil reached during the fire. No statistical differences of CE activity were observed between the control plot (PC) and the burnt plots (P1 and/or P2). This could be attributed to the recolonization of the soil of the burnt plot by fungi populations, being the main producers of cellulase (Martínez *et al*., 2006).

Regarding the UR activity, values of 58.5-277.7 mg $N\text{-}NH_4$ g^{-1} h^{-1} were registered in the samples from the 0-20 cm depth (Figure 3). This activity diminished with depth (20-40 cm) to values of 86.3-198.1 mg $N\text{-}NH_4$ g^{-1} h^{-1}. The observed decrease of UR activity with increasing soil depth may be related to a minor temperature (Reyes *et al*., 2011). The UR activity values for PC 0-20 cm depth, were higher during the whole sampling period, as compared with P1 and P2 (Figure 3). The results showed a slight seasonal tendency, where for all the plots a major activity was registered in summer and a minor activity in spring, a period when snow accumulated in the study zone. The UR activity in the superficial 0-20 cm, was significantly higher ($p \leq 0.05$) in the PC plot, as compared with the burnt plots P1 and P2 (Figure 3). Previous studies confirm the tendency of the UR activity to diminish in zones affected by burning, because as a consequence of the fire, the organic forms of N oxidize (Hernández *et al*., 1997). On the other hand, Lillo *et al*. (2011) reported that the levels of urease activity showed a similarity in the middle zone of the altitudinal transect, Conguillío National Park, favored by the accumulation of organic matter.

Relationships between soil enzymes activities and soil chemical parameters

The results of the multiple linear regression analysis show that the CA activity presents a low correlation coefficient with regard to the chemical properties of the soil considered in this study (Table 2). The multiple

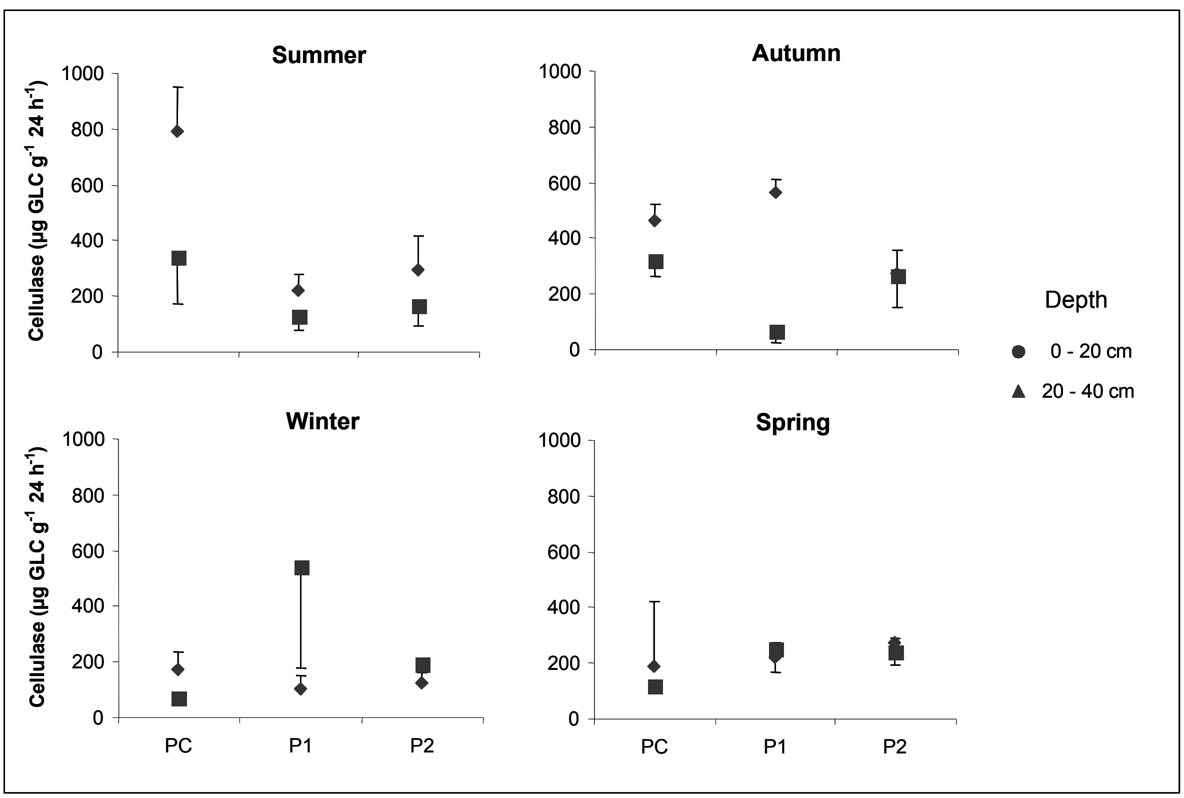

Figure 2. Cellulase (CE) activity in different seasons of forest *Araucaria–Nothofagus* at 0-20 and 20-40 cm soil layers. Enzyme activity values are expressed as mean ± SD. (PC, control plot; P1 and P2, burnt plots). (n = 68).

Figura 2. Actividad de celulasa (CE) en diferentes estaciones del bosque *Araucaria–Nothofagus* en profundidades de suelo de 0-20 y 20-40 cm. Los valores de la actividad enzimática se expresan como media ± DS. (PC, parcela control; P1 y P2, parcelas quemadas). (n = 68).

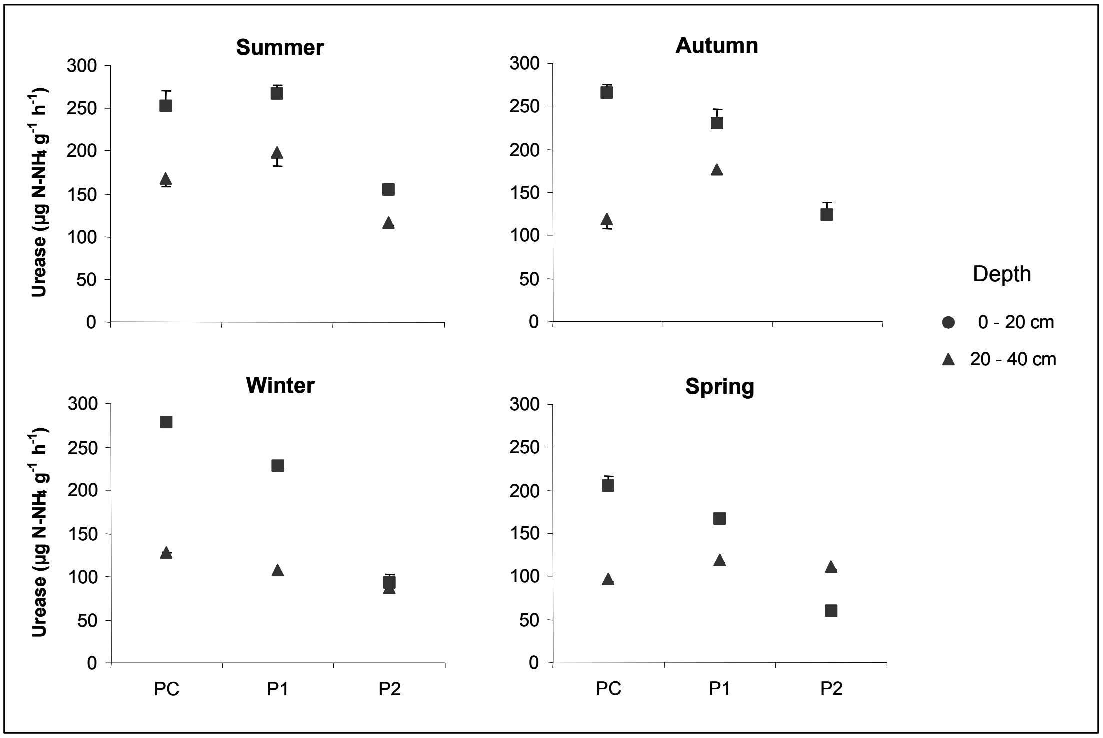

Figure 3. Urease (UR) activity in different seasons of forest *Araucaria–Nothofagus* at 0-20 and 20-40 cm soil layers. Enzyme activity values are expressed as mean ± SD. (PC, control plot; P1 and P2, burnt plots). (n = 72)

Figura 3. Actividad de ureasa (UR) en diferentes estaciones del bosque *Araucaria–Nothofagus* en profundidades de suelo de 0-20 y 20-40 cm. Los valores de la actividad enzimática se expresan como media ± DS. (PC, parcela control; P1 y P2, parcelas quemadas). (n = 72).

Table 2. Correlation coefficient for the models adjusted between the soil enzymes activities and chemical properties.

Cuadro 2. Coeficiente de correlación para los modelos ajustados entre las actividades de las enzimas del suelo y las propiedades químicas.

	Adjusted R^2	Level of significance	
Catalase	0.47	0.000	***
Cellulase	0.20	0.018	*
Urease	0.83	0.000	***

*, **, *** significant at the 0.05, 0.01 and <0.01 level of probability, respectively.

linear regression coefficients (Table 3), showed that the CA activity model is explained mainly by the regression coefficient corresponding to the parameters sum of bases and total N.

Leirós *et al*. (2000), studying *Quercus* forests located in Galicia, found significant correlations between CA activity and total N and C content, C/N relation and available Ca^{2+} and K^+. Whereas Dinesh *et al.* (2004b) found a significant correlation between CA and organic C, total N, P and K in mangrove forests. On the other hand, Frankenberger and Dick (1983), did not find any significant correlations between CA and a number of chemical soil parameters (pH, organic C, total N and capacity of cationic exchange) analyzing ten series of non-cultivated soil in California. The CA activity is a defense mechanism of the aerobic microorganisms facing oxidative stress, probably independent of the C and P content of the soil. However, literature is scarce with regard to this point.

In order to fulfill the assumption of normality for the multiple regression analysis it was necessary to transform the CE activity data (Log_{10} data). The correlation between CE activity and the chemical properties of the soil is very low (Table 2), the pH, Olsen-P and SB, being the coefficients of importance in the regression model (Table 3). Andersson *et al.* (2004), found a significant relation between CE and the C:N relation, while Trasar-Cepeda *et al.* (1998), obtained significant correlations between CE and total C and N. On the other hand, García and Hernández (1997), obtained a significant correlation between the β-glucosidase activity (a cellulase) and the organic matter of the soil, as did Jimenez *et al.*

Table 3. Multiple regression coefficients between soil enzymes activities and soil chemical parameters.

Cuadro 3. Coeficientes de regresión múltiple entre las actividades de las enzimas del suelo y los parámetros químicos del suelo.

	Catalase	Cellulase	Urease
Intercept	-0.689 NS	-2.463 NS	-690.798 **
pH w	0.164 NS	0.799 *	115.210 **
Total N	0.561 *	-0.620 NS	-290.597 ***
Total C	0.007 NS	0.067 NS	23.933 ***
Olsen-P	0.055 NS	-0.191 **	5.174 NS
Total P	-0.000 NS	-0.000 NS	-0.013 NS
Sum of exchangeable bases	0.301 ***	0.441 **	37.950 *

*, **, *** significant at the 0.05, 0.01 and <0.001 level of probability, respectively. NS, not significant.

(2002), who reported a significant correlation between β-glucosidase and total N, pH and organic C. Nevertheless, Lillo *et al*. (2011) did not find any significant correlation between CE and the content of organic matter of the soil, neither with the pH. The weak association between the CE activity and the chemical parameters of the soil measured in this study, are in agreement with similar results obtained by Balota *et al.* (2004), who did not find any significant correlation between CE and a number of chemical parameters in agricultural soils (pH, P, Ca, Mg, CEC and saturation of bases). It seems that the low correlation between the chemical parameters of the soil and the CE activity would be related to the type of temperate forest vegetation, and therefore with the type of organic matter (Lillo *et al*., 2011). Moreover, the degradation of cellulose is highly dependent on the synergism occurring between the different enzymes of the cellulolytic complex (Bhat and Bhat, 1997). On the other hand, a factor that could be influencing the CE activity in the soils of these temperate forests is the presence of trace elements, such as e.g. Al (III) and Fe (II), probably forming complexes with SOM, in this way inhibiting the enzyme activity (Deng and Tabatabai, 1995).

In relation to the UR activity, this has a high and significant association with the chemical parameters of the soil ($p \leq 0.05$). This model explains 83% of the UR activity (Table 2). In this adjusted model, the significant multiple regression coefficients correspond to total N, total C, SB and pH, whereas total P and Olsen-P are not significant. With regard to this, Baligar *et al*. (2005), studied the UR activity in response to the application of P, their results showed a non-significant correlation coefficient. The studies of Trasar-Cepeda *et al*. (1998), Jimenez *et al*. (2002) and Baligar *et al*. (2005), have demonstrated the correlation between the UR activity and the total N and C content, while Zantua *et al*. (1977), and Frankenberger and Dick (1983) have reported significant correlations between UR and organic C. The strong correlation between the chemical parameters and the UR activity is coherent with the sensitivity of this enzyme activity to the effect of the fire in the 0-20 cm depth, being greatest in the unaltered ecosystem (PC). The *Araucaria–Nothofagus* ecosystem has a limited access to N (Lusk, 2001), the UR activity being involved in the use of organic nitrogen (urea resulting from animal metabolism, and urea analogous compounds). This is probably the reason for the strong correlation between UR activity and total N and C content (Trasar-Cepeda *et al*., 1998).

In the case of CA and CE there is a weak correlation between the estimated and the observed activity of the enzymes CA, CE and UR (Figure 4). For CA and CE it would be necessary to study the relation between the fractions of the measured chemical parameters, such as soluble C, soluble P and mineralizable N. Though, there is a better adjustment of the UR activity behaviour model. Here it is possible to observe differences between the plots; the data is arranged according to the magnitude of the chemical soil parameters considered in the study.

This is a first exploratory study, which has the purpose of evaluating the association of the enzyme activity of the soil post-wildfire, with a few chemical soil variables (total N, total C, total P, Olsen-P, sum of exchangeable bases and pH) in *Araucaria–Nothofagus* forests in the Andes mountain. The objective of correlating variables does not have a predictive purpose. Its only purpose is to observe the relation between the parameters that could affect the enzyme activity. Finally, the purpose of this investigation has been to report the events in the *Araucaria–Nothofagus* forest post-fire and does not claim to predict the behaviour of the enzymes facing changes in the levels of chemical substances in the soil.

CONCLUSIONS

The main preliminary conclusions of this study were: (i) no seasonality could be determined regarding soil enzymes activities; (ii) the soil enzymes activities of CA, CE and UR decreased with increasing depth; (iii) there were no differences between the control plot (PC) and the burnt plots (P1 and/or P2) regarding CA and CE activities, therefore, three years post-fire the detection of changes in the activity of these enzymes does not possess sensibility; (iv) the soil chemical parameters measured in this study are not associated in the same way with the enzyme activity of CA, CE and UR respectively; (v) the UR activity is regulated by the chemical parameters of the soil; (vi) UR activity could

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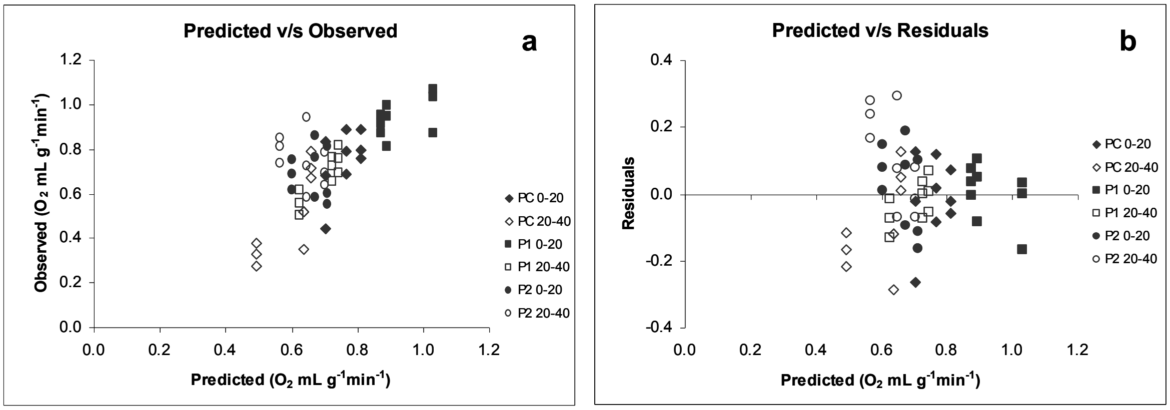

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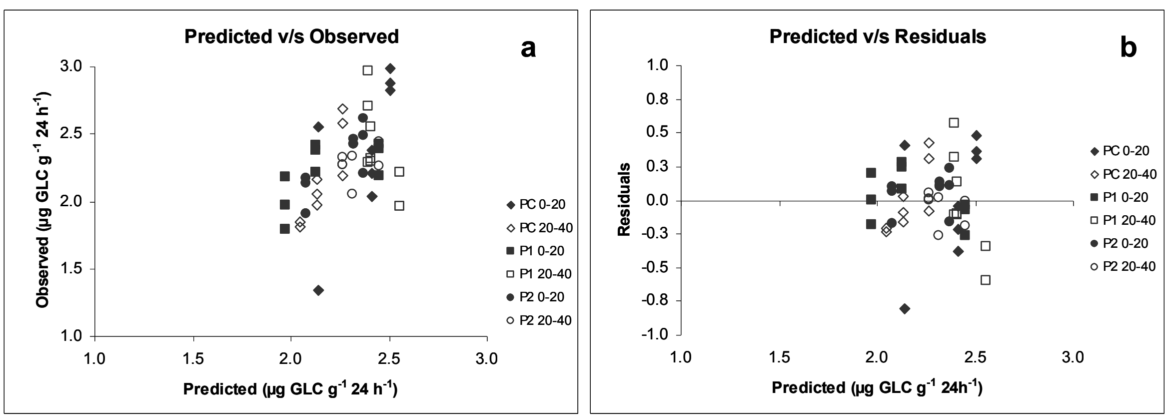

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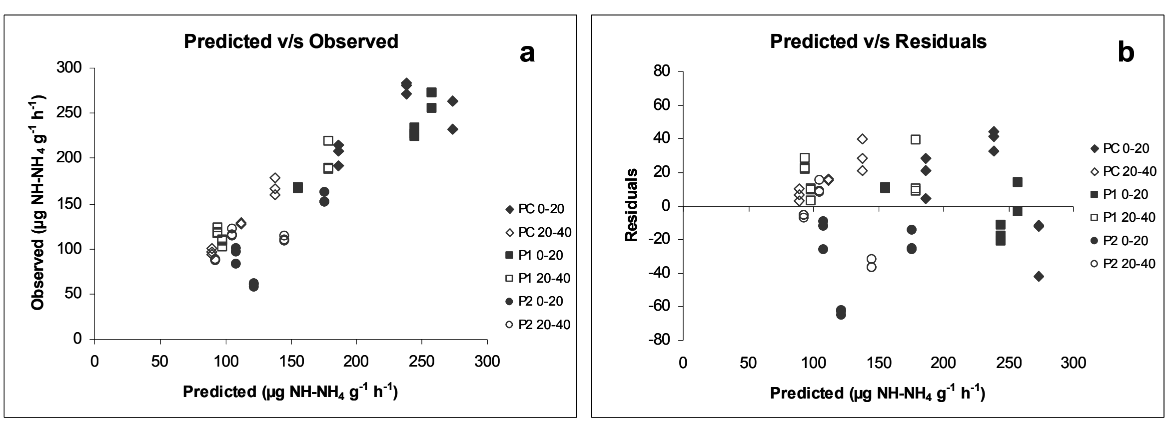

Figure 4. Relationship between A) catalase (n = 54), B) cellulose (n = 54) and C) urease (n = 54) with chemical parameters of the soil; model adjusted for observed versus predicted data (a); model adjusted for residuals versus predicted data (b).

Figura 4. Relación entre A) catalasa (n = 54), B) celulosa (n = 54) y C) ureasa (n = 54) con parámetros químicos del suelo; modelo ajustado para los datos observados frente a los previstos (a); Modelo ajustado por residuos frente a datos previstos (b).

be a potential indicator of the alterations provoked by fire in soils of *Araucaria–Nothofagus* forests, as three years post-fire there are still differences in its activity between burnt and non-burnt plots.

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