

# ***Nothofagus pumilio* forest affected by recent tephra deposition in northern Patagonia. I- Environmental traits influencing seedling growth**

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## **Abstract**

The 2011 Puyehue-Cordón Caulle volcanic eruption left vast areas of *Nothofagus pumilio* forests covered by high volumes of tephra, which buried the understory. This event offered a unique opportunity to analyse the impact of recent tephra deposition and the main environmental factors affecting the growth of *N. pumilio* seedlings. To this end, three study sites were selected and sampled three years after the eruption, two with a thick tephra layer (50 cm) but with different tree conditions: i) most trees alive or ii) most trees dead, and a third site, iii) with minimal tephra deposition. From each site, five *N. pumilio* 18-month-old seedlings were collected, morphometrically measured (shoot, epicotyl and main root length; shoot, epicotyl and root collar diameter), and environmental factors were also registered (light intensity, soil pH and conductivity, available P, bulk and particle soil density, and porosity). The main results indicated that three years after eruption the site with tephra deposition and dead trees (the most near to the crater) had the biggest seedlings, the lowest pH and the highest values for available P and light intensity. This temporally unique geological event showed that the regeneration potentiality of *N. pumilio* is high when environmental factors allow direct incident light on a substrate with high mineral content, even when the environment has previously been subjected to a significant degree of disturbance. Given the recurrence of volcanic events in northern Patagonia, this subject merits further long-term study.

**Keywords:** *Nothofagus pumilio*, forest ecology, high-magnitude disturbance, tephra, volcanic eruption, seedling development.

## 1. Introduction

Volcanic eruptions give rise to significant geological, ecological and social changes (Dale *et al.*, 2005; González *et al.*, 2014). Tephra fall is one of the major and most extensive disturbances and can be deposited several kilometres from the volcano, depending on the speed and orientation of the prevailing winds (Swanson and Major, 2005; González *et al.*, 2014). The deposit of fine ash to gravel-sized rock debris on the soil represents a high impact modification in the ecosystem dynamics, and generates the need to understand interactions between volcanic events and biological systems (Swanson and Major, 2005; Swanson *et al.*, 2016).

In the South and Central Andean area of Argentina and Chile volcanic eruptions are recurrent; over the last century there were 28 volcanic eruptions (González *et al.*, 2014). In the recent vulcanological history of this area the last eruption of the Puyehue-Cordón Caulle volcanic complex (PCCVC) stands out as having a marked impact on the environment. It began in June 2011 and remained active for about a year, generating significant tephra deposits over a large area of northern Patagonia in Argentina and Chile (Villarrosa and Outes, 2013). This not only affected plant cover noticeably (Grosfeld and Puntieri, 2013; González *et al.*, 2014; Ghermandi *et al.*, 2015; Swanson *et al.*, 2016), but also soil insects and microorganisms (Ferreiro *et al.*, 2015). One of the ecosystems most severely affected by the eruption were *Nothofagus* forests, with large areas covered by a tephra layer of more than 40 cm (Villarrosa and Outes, 2013; Ghermandi *et al.*, 2015; Swanson *et al.*, 2016).

*Nothofagus pumilio* (Lenga) is a deciduous endemic tree from temperate South American forests, and is one of the most important and widely distributed forestry species in Argentina and Chile (between 35°S and 55°S). Natural regeneration of *N. pumilio* occurs from seeds and mostly takes place in open areas, since it is a semi-heliophilic species (Rebertus and Veblen,

1993; Heinemann, 2007; Martínez Pastur *et al.*, 2007). The regeneration dynamics of *N. pumilio* forests is influenced by large-scale (avalanches, fires, winds and volcanisms) and small-scale disturbances (such as tree fall), which result in a regeneration strategy of gap dynamics (González *et al.*, 2006; Heinemann, 2007). Therefore, its regeneration is primarily associated with disturbances of varying intensity, including volcanic events (González *et al.*, 2006).

Volcanic plumes from the PCCVC eruption generated tephra deposits of different thicknesses, and in the region close to the Cardenal Samoré International border the tephra layer lying on the forest soil exceeded 40 cm in depth, significantly affecting the mortality of understory plants and adult *Nothofagus* trees (Montiel *et al.*, 2016). During the first years following the PCCVC eruption, seed germination occurred directly on the thick tephra deposits, and seedling roots were not able to exploit the underlying soil (Grosfeld and Puntieri, 2013). Considering that the tephra nutrient content was low (particularly with respect to total N and available P), and much lower than in the forest soil, there may not be enough nutrients to satisfy the requirements of the vegetation (Cremona *et al.*, 2011). It is unknown how these factors could influence natural regeneration of dominant plant species, such as *N. pumilio*; therefore, the PCCVC volcanic event represents a unique opportunity to study the natural regeneration of native *Nothofagus* forests following a high magnitude disturbance, and could contribute to understanding the regeneration dynamics and vegetation succession of natural environments. This information is relevant in the current climate change scenario, and can be useful in the development of restoration strategies for different potentially severely affected environments. In this context, extensive research was carried out, oriented towards understanding the principal factors, both biotic and abiotic, that determine the restoration of

temperate ecosystems such as *Nothofagus* forest after a catastrophic event like a volcanic eruption. As part of this research, the aim of the present study was to analyse the impact of tephra deposits and different ecological factors on the growth of *N. pumilio* seedlings. We performed the study in native *N. pumilio* forests severely affected by tephra deposition from the PCCVC eruption, and compared with a forest with a minimal tephra layer on the soil. We examined environmental parameters associated with seedling growth, such as light intensity and physicochemical characteristics of the substrates (tephra and soil).

**2. Material and Methods**

*2.1. Study area and sampling*

This study was carried out in April 2014 (three years after the last PCCVC eruption) in native *N. pumilio* forests located in northern Patagonia, with sampling sites located in Argentina and Chile (Table 1). Soils of this area are predominantly Andisols, characterized by low bulk density, a high capacity to stabilize organic

low bulk density, a high capacity to stabilize organic matter, store water and an elevated total P content (Shoji *et al.*, 1993; Mazzarino and Gobbi, 2005; Satti *et al.*, 2007). Their main limitation is high P retention (Mazzarino and Gobbi, 2005; Satti *et al.*, 2007; Cornejo *et al.*, 2017). The climate of this region is characterized by an average annual temperature of 9.5 °C and mean annual precipitation ranging from 3000 in the west to 800 mm in the east (Conti, 1998). Some of these forests were severely affected by the last eruption of the PCCVC. This volcanic complex is located in the Southern zone of the Chilean Andes (40.5° S, 72.2° W) and is one of the most active volcanic complexes in South America, eight eruptions having occurred in the twentieth century alone (González *et al.*, 2014). Its most recent eruption occurred in 2011 and the complex remained active, with decreasing intensity, for almost a year. Tephra fall was the most widely-spread impact of the eruption. Pyroclastic material was distributed by the prevailing western winds over a vast area, especially in northern Argentinean Patagonia, its texture and thickness varying greatly within the fallout zone (Villarrosa and Outes, 2013; González *et al.*, 2014; Swanson *et al.*, 2016).

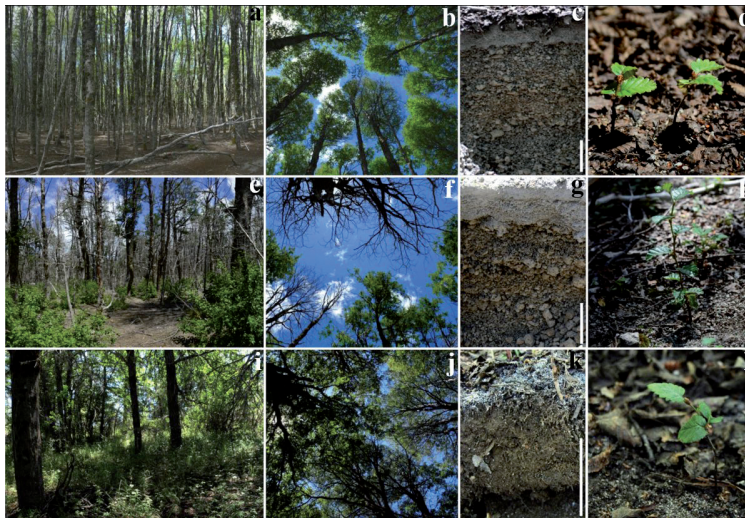
**Table 1.** Location and environmental characteristics of the two sites affected by tephra deposition after the eruption of the Puyehue-Cordón Caulle Volcanic Complex (PCCVC - Cardenal Samoré 1 and 2) and the unaffected site (Cerro Otto).

Site	Latitude	Longitude	Altitude (m a.s.l.)	Annual precipitation (mm)*	Distance to PCCVC (km)	Tephra layer depth (cm)	Light intensity (lux)**
<b>Cardenal</b>	-40°	-71°	1156	3000	21.6	~50	12449 ±
<b>Samoré</b>	43.556´	55.504´					4126 <sup>b</sup>
<b>1</b>							
<b>Cardenal</b>	-40°	-71°	1102	3000	16.5	~50	50957 ±
<b>Samoré</b>	41.571´	58.118´					10350 <sup>a</sup>
<b>2</b>							
<b>Cerro</b>	-41°	-71°	1144	800	90.5	~1	2684 ±
<b>Otto</b>	8.673´	20.413´					1134 <sup>c</sup>

\* =According to Conti (1998), \*\* = Values are expressed as mean ± S.E. and different superscript letters denote significant statistical differences.

Two study sites were located close to the international road “Cardenal Samoré” (Table 1, Figure 1), which connects Argentina and Chile. In this region a tephra layer of approximately 50 cm lay on the forest soil and *N. pumilio* seedlings were growing in the tephra. At one of the sites, located 21.6 km from the PCCVC, most of the adult trees remained alive after the tephra fall (Cardenal Samoré 1 = CS1), while at the other site, 16.5 km from the PCCVC, a high proportion of

trees (over 70%) had died as a consequence of the volcanic eruption (Cardenal Samoré 2 = CS2). A third sampling site was situated on Cerro Otto, 94.6 km from the volcano, where the effect of the eruption was minimal and there was no tephra layer on the soil (Table 1, Figure 1). This site (Cerro Otto = CO), in terms of tephra, was considered an unaffected site, with *N. pumilio* seedlings growing directly in the soil.



**Figure 1.** Environmental characteristics of the three sampling sites, two of which are affected by elevated tephra deposition after the PCCVC eruption (Cardenal Samoré 1 = a-d, Cardenal Samoré 2 = e-h) and the unaffected site (Cerro Otto = i-l). General structure of the forest (a, e, i), canopy (b, f, j), accumulation of tephra on the soil (c, g, k; scale bars = 10 cm) and size of the seedlings present at each site (d, h, l; scale bars = 4 cm).

At each of these three sites five 18-month-old seedlings were collected. These belonged to the first germination batch following the eruption. Seedlings were carefully removed from the substrate in order to preserve root systems and the surrounding substrate: tephra at both sites located in Cardenal Samoré (CS1 and CS2) and soil in the unaffected site (CO). The samples were wrapped in plastic bags and stored at 4 °C for no longer than a week, when further procedures were carried out.

## 2.2. Evaluation of environmental factors and plant traits

Luminous intensity was measured using a light meter (Extech 407026, FLIR Systems Inc.) held over each of the sampled seedlings, at the same time of day on three consecutive sunny days.

In order to evaluate physicochemical properties of the substrates (tephra or soil), samples were air dried up to constant weight. They were then sieved through a

2 mm mesh and mixed with deionized water for determination of pH (2:5 w:v) and conductivity (1:5 w:v) by means of a pH-meter and electric conductivity meter, respectively. Available P was determined in an extract of NaHCO<sub>3</sub> 0.5 M at pH 8.5 using the procedure described by Olsen and Sommers (1982). To determine bulk density a steel cylinder of 100 mL was filled with the substrate and dried in an air-forced oven at 65 °C for 72 h, then the substrate was weighed and the relation between weight and total soil volume was calculated. A portion of 30 g of dry substrate was added to 50 mL water, and after 24 h the final volume was calculated to obtain particle density. Total porosity was calculated as the relative difference between particle density and bulk density, expressed as a percentage (Van Reeuwijk, 1993).

To evaluate seedling development, the following morphometric measures were taken using a digital calliper (resolution = 0.1 mm): shoot, epicotyl and main-root length; shoot, epicotyl and root collar diameter.

**2.3. Statistics**

One-way ANOVAs followed by Holm-Sidak post-hoc tests were used to compare the three sampling sites (CS1, CS2 and CO) for the following data: light inten-

sity, physicochemical substrate characteristics (pH, conductivity, available P, bulk density, particle density and porosity) and morphometric measures. Data not meeting ANOVA assumptions (epicotyl length and root diameter) were normalized using ln transformations before analyses, but the data are presented in their original scales of measurement. Finally, a Pearson Correlation Matrix and a Principal Component Analysis (PCA) for the different variables were performed. All statistical analyses were carried out using the IBM SPSS Statistics software v. 23 (IBM Corp.).

**3. Results**

Light intensity was higher in the forest with tephra deposition and the highest proportion of dead trees (CS2) than both the other sites. The other forest located in Cardenal Samoré (CS1) presented intermediate values and the unaffected site (CO) the lowest luminous intensity (Table 1) (CS2 vs. CS1, p = 0.007; CS2 vs. CO, p < 0.001; CS1 vs. CO, p = 0.075). Differences in light intensity were directly related to tree cover (Figure 1). Significant differences were observed for most of the physicochemical substrate characteristics analysed (Table 2).

**Table 2.** Physicochemical characteristics of the substrates corresponding to the sites severely affected by the eruption (Cardenal Samoré 1 and 2) and the unaffected site (Cerro Otto).

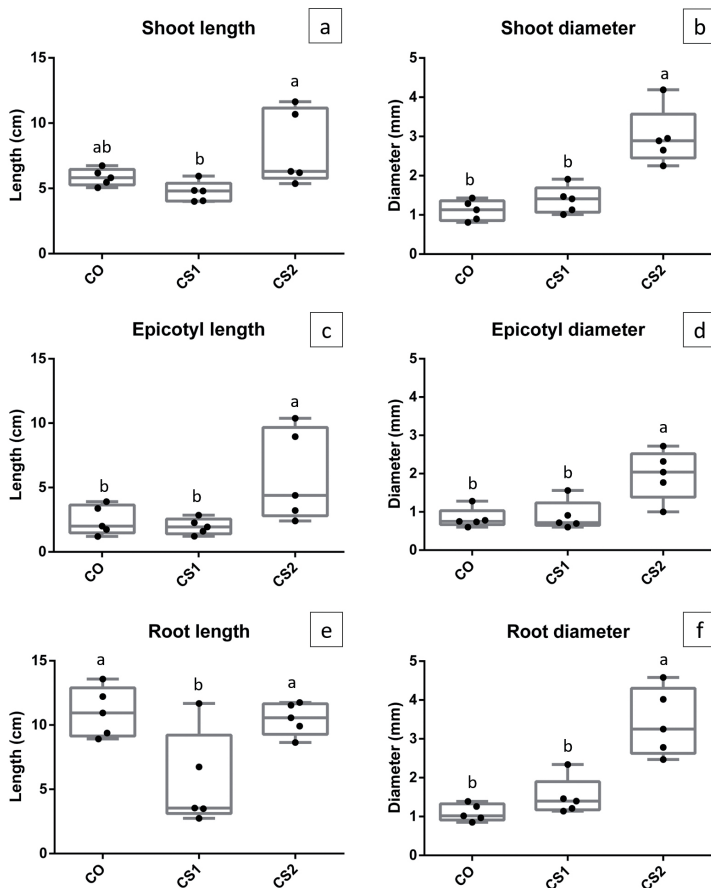
Site (type of substrate)	pH (in water)	Conductivity (µS/cm)	Available P (mg/kg)	Particle density (g/mL)	Bulk density (g/mL)	Porosity (%)
<b>Cardenal Samoré 1 (tephra)</b>	4.67 ± 0.04 <sup>b</sup>	96.41 ± 0.21 <sup>c</sup>	18.34 ± 2.32 <sup>b</sup>	1.83 ± 0.13 <sup>a</sup>	1.02 ± 0.02 <sup>b</sup>	44.0 ± 4.11 <sup>a</sup>
<b>Cardenal Samoré 2 (tephra)</b>	3.91 ± 0.01 <sup>c</sup>	341.4 ± 0.42 <sup>b</sup>	48.35 ± 6.38 <sup>a</sup>	1.93 ± 0.08 <sup>a</sup>	1.07 ± 0.01 <sup>a</sup>	44.2 ± 1.58 <sup>a</sup>
<b>Cerro Otto (soil)</b>	5.23 ± 0.02 <sup>a</sup>	853 ± 0.79 <sup>a</sup>	16.73 ± 0.41 <sup>b</sup>	1.34 ± 0.07 <sup>b</sup>	0.68 ± 0.01 <sup>c</sup>	48.7 ± 2.71 <sup>a</sup>

Values are expressed as mean ± S.E., different superscript letters denote significant statistical differences for each of the variables analysed.

Conductivity and pH values were higher in the soil of the unaffected site (CO) than in the tephra of the two affected sites (CS1 and CS2), while available P was much higher in CS2 (with tephra and dead trees) than in the other two sites (CO and CS1), reaching 48 ppm of available P. Differences were also registered for both bulk and particle densities, which were higher in both sites with tephra (CS1 and CS2) than in the unaffected site (CO). However, porosity was

similar for all the substrates analysed (Table 2).

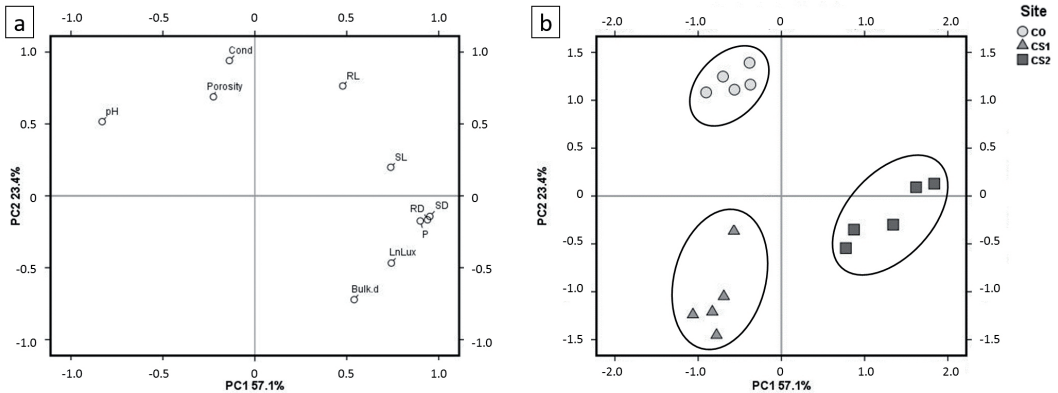
Seedlings from CS2 had the highest values for all the measured diameters (shoot, epicotyl and root diameter), while those growing in CS1 and CO had similar values (Figure 2). Shoot and root lengths were similar for seedlings from CS2 and CO, and higher than the seedlings located in CS1, while epicotyl length was higher in CS2 than in the other two sites (Figure 2).



**Figure 2.** Morphometric measures registered in *Nothofagus pumilio* seedlings in the sites with tephra, Cardenal Samoré 1 (CS1) and Cardenal Samoré 2 (CS2); and in the unaffected site, Cerro Otto (CO). Shoot length (a) and diameter (b); epicotyl length (c) and diameter (d); root length (e) and diameter (f). In the boxplots: boxes represent the interquartile range and the line inside the boxes represents the median. Whiskers indicate the range of data. Different letters above the boxplots indicate differences between the study sites.

According to the factorial analysis performed by means of principal component (PCA) extraction, the first two principal components explained 80.5 % of total variance (Figure 3a). Shoot and root diameter and shoot length were highly correlated to available P and light intensity data (Table 3). Moreover, a strong positive relation was found between porosity and electric conductivity and these factors were negatively correlated to bulk density, while pH had a strong negative correlation with available P and bulk density. The individual seedlings were clearly separated into

three distinct groups, which corresponded to their sampling sites of origin (Figure 3b). The different positions of the three sampling sites in the multivariate space were mainly explained by plant performance, available P and light intensity for CS2 (forest with tephra deposition and a high proportion of dead trees); and by pH, porosity and conductivity for CO (unaffected site), while CS1 (forest with tephra where most adult trees remained alive after the eruption) was mostly characterized by low values of root and shoot length.



**Figure 3.** Principal component analysis (PCA) of the different morphological traits evaluated in *Nothofagus pumilio* seedlings (SL, RL: shoot and root length, respectively; SD, RD: shoot and root diameter, respectively) and the physicochemical characteristics determined for the substrates (Bulk.d: bulk density; Cond: conductivity).

**Table 3.** Correlation matrix obtained for all the variables analysed at the three different sites studied after the eruption of the PCCVC (morphometric measures, light intensity and physicochemical properties of the substrate).

Variables	pH	Cond.	Bulk.d	Porosity	P	SL	SD	RL	RD
<b>Lux</b>	-0.831 ***	-0.448 *	0.577 *	-0.690 **	0.793 ***	0.405 ns	0.733 **	0.031 ns	0.698 **
<b>Ph</b>		0.592 **	-0.858 ***	0.483 ***	-0.897 ***	-0.469 *	-0.835 ***	0.000 ns	-0.852 ***
<b>Cond.</b>			-0.842 ***	0.598 ***	-0.240 ns	0.091 ns	-0.292 ns	0.587 *	-0.319 ns
<b>Bulk.d</b>				-0.346 ns	0.628 **	0.142 ns	0.640 **	-0.272 ns	0.707 **
<b>Porosity</b>					-0.258 ns	-0.237 ns	-0.286 ns	0.372 ns	-0.178 ns
<b>P</b>						0.481 *	0.799 ***	0.312 ns	0.840 ***
<b>SL</b>							0.688 **	0.370 ns	0.627 **
<b>SD</b>								0.331 ns	0.967 ***
<b>RL</b>									0.275 ns

Lux: Light intensity, SL: Shoot length, SD: Shoot diameter, RL: Root length, RD: Root diameter, Cond.: Conductivity, Bulk.d: Bulk density.

Significance: ns = non-significant, \*  $p < 0.05$ , \*\*  $p < 0.01$ , \*\*\*  $p < 0.001$ .

#### 4. Discussion

In spite of the stressful environmental conditions that follow volcanic eruptions, such as thick tephra deposits, low soil nutrient content, instability of substrate surface, drought and changes in light dynamics, pioneer woody plants are able to become established relatively soon (Antos and Zobel, 2005; Obase *et al.*, 2007). In this study our results showed that *N. pumilio* seedlings were able to grow on the thick tephra layer and survived for at least three years after the eruption, even though their root systems were not in contact with the buried forest soil (Figure 1, c and g). These results are in agreement with previous studies carried out in Patagonia, which reported that some native forest species, such as *Araucaria araucana*,

*Austrocedrus chilensis* and different *Nothofagus* species, are capable of colonizing and growing rapidly on tephra deposits (González *et al.*, 2014), which in several cases can be helped by microbial interactions at soil-root level (Marín *et al.*, 2016; 2017; Mestre *et al.*, 2017). For example, 17 months after the eruption of Hudson volcano, Vogel (1996) described the massive establishment of *N. pumilio* seedlings growing directly on the tephra. However, their survival capacity was uncertain, most probably as a consequence of nutritional deficiencies, mainly N and P (González *et al.*, 2014). Similar recolonization strategies were registered in some *N. pumilio* forests affected by the last eruption of the PCCVC (Grosfeld and Puntieri, 2013; Magnin *et al.*, 2016; Montiel *et al.*, 2016), but this should be observed in the long term to analyse



effectively whether nutrient depletion could be a determinant factor limiting seedling establishment in this context.

Our results reveal that specimens located in the forest with thick tephra deposits and a high proportion of dead trees, which corresponded to the most severely affected study site (CS2), showed the highest values for all the morphometric variables analysed (Figure 2), in concordance with higher growing rates when compared with the other two sites. This behaviour is mainly related to the high light intensity received at soil surface level (Figure 1, Table 1) and the high available P of the tephra in this site. *Nothofagus pumilio* is characterized as a species with a regeneration strategy of “gap dynamics”; therefore, it usually germinates and grows slowly in the shaded understory for long periods, until the formation of a canopy gap allows greater light availability (Heinemann, 2007; Martínez Pastur *et al.*, 2007).

In the most affected site of this study (CS2), because of low canopy coverage, light was not a limiting factor for seedling growth; this, together with the high level of available P determined the fast seedling development observed here. In mature *Nothofagus* forest, low P availability is a restrictive factor due to the high P-fixing capacity of volcanic soils (La Manna *et al.*, 2011; Seguel *et al.*, 2013; Cornejo *et al.*, 2017), but most of the dominant plant species behaved as non-P-limited, probably due to a high percentage of mycorrhizal colonization (Diehl *et al.*, 2008). High P availability in CS2 site could be due to the low pH of the tephra (Table 2), since P dissolution rate increases as pH decreases (Dahlgren *et al.*, 2004). This behaviour can be due to a pH decrease by acid rain or S oxidation in the tephra as previously reported in other latitudes (Cronin *et al.*, 1997). This acidification could be responsible for an increase of phytotoxic aluminum ( $Al^{3+}$ ) which can explain the notorious increase of root diameter (Figure 2e) since the most important

effect of the  $Al^{3+}$  phytotoxicity is the root thickening. Another important factor is that recently-deposited tephra contains a certain amount of P which is readily soluble in acid solutions (Shoji *et al.*, 1993), and it has a low quantity of organic matter that can immobilize organic P (Borie and Rubio, 2003; Borie *et al.*, 2010). This nutrient is particularly important for plant development and performance (Dahlgren *et al.*, 2004), and its importance for *N. pumilio* growth was reflected through the Principal Component Analyses (PCA, Figure 3), which revealed it as the experimental variable most directly associated with shoot and root diameters. These results are in agreement with Magnin *et al.* (2016), who found that the length growth of the juvenile *N. pumilio* trees located close to the volcano (and affected by tephra deposition) increased significantly after the eruption, suggesting that the P released by leaching from the ash deposition could have induced an increase in the growth of terrestrial plants. In contrast, seedlings from site CS1 presented the lowest values in almost all the morphometric measures, possibly due the combination of the same two factors in an unfavourable way: low luminous intensity and lower P availability (Figure 3), reinforcing the high importance of both environmental factors in the *N. pumilio* seedling growth (Heinemann, 2007; Martínez Pastur *et al.*, 2007). Considering a preliminary methodological analysis, and based on our results, shoot and root diameter seem to be better indicators of seedling response to the different environmental factors analyzed than shoot and root length, also evidenced by means of PCA (Figure 3a).

In this work we focused on *N. pumilio* seedlings after the PCCVC eruption, and environmental factors that could influence their growth. *Nothofagus pumilio* is an interesting species and a good study model, not only because of its economic and ecological importance, but also because it occupies vast areas of the Andean-Patagonian native forests in the southern

region of Argentina and Chile, one of the most active volcanic areas worldwide.

## 5. Conclusions

Our results highlight the regeneration capacity of native *N. pumilio* forests after a volcanic eruption, which represents a major geological disturbance. In this context, the ability of *N. pumilio* seedlings to become successfully established and develop directly in the tephra deposits in forests severely affected by the eruption is noteworthy, their development being related principally to light intensity and available P. It is noticeable that seedling growth is influenced by several factors that should also be considered during the regeneration process and subsequent succession, such as fungal communities associated with their root systems. In this sense, volcanic eruptions provide an exceptional opportunity to study different processes in dynamic landscapes, such as the principal factors determining recruitment of pioneer plant species. This is a temporally unique and essential study; therefore, long-term research is necessary in order to understand interactions between factors following large-scale disturbances. These results will contribute to improving cultivation strategies for native forestry species, and to the design of restoration activities in different affected environments.

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